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INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

Stochastic Processes and Hitting Times in Mathematical Neurosciences

Jonathan Touboul

N° 1

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Stochastic Processes and Hitting Times in Mathematical Neurosciences

Jonathan Touboul *

Thème BIO — Systèmes biologiques
Projet Odyssée †

Rapport de recherche n° 1 — August 22, 2008 — 118 pages

Abstract: Dans ce rapport de recherche nous definissons un cadre mathématique pour étudier la dynamique de réseaux de neurones intègre-et-tire en présence de bruit extérieur. De tels réseaux sont habituellement étudiés en utilisant l'équation de Fokker-Planck (Brunel, Hakim par exemple). Dans cette étude on utilise les puissants outils développés pour les réseaux de communication et définissons un formalisme pour l'étude de neurones à spikes gouvernés par un bruit extérieur. Grâce à ce formalisme nous posons des questions d'intérêt biologique afin de caractériser les différents régimes du réseau. Notons que dans ce modèle, la distribution de l'intervale inter-spikes est un paramètre fondamental. Dans ce rapport nous developpons et appliquons de nombreux outils de calcul stochastique afin de caractériser ces distributions de probabilité. Ce poinnt de vue nous donne une stratégie pour simuler ce type de réseaux aléatoires. Nous avons implémenté cette méthode de simulation en extension du simulateur événementiel Mvaspike.

Key-words: neuron models, stochastic network, event-driven modelization, event-driven simulation, communication network, stochastic integrate-and-fire neurons.

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Processus stochastiques et temps d'atteinte en neurosciences mathematiques.

Résumé : In this research report we define a new event-based mathematical framework for studying the dynamics of networks of integrate-and-fire neuron driven by external noise. Such networks are classically studied using the Fokker-Planck equation (Brunel, Hakim). In this study, we use the powerful tools developed for communication networks theory and define a formalism for the study of spiking neuron networks driven by an external noise. With this formalism, we address biological questions to characterize the different network regimes. In this framework, the probability distribution of the interspike interval is a fundamental parameter. We developed and apply several tools for defining and computing the probability density function (pdf) of the time of the first spike, using stochastic analysis. This point of view gives us an event-driven strategy for simulating this type of random networks. This strategy has been implemented in an extension of the event-driven simulator Mvaspike.

Mots-clés : modèles de neurones, réseau stochastique, modélisation événementielle, simulation événementielle, réseau de communication, neurones intègre-et-tire stochastiques.

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Résumé

Ce document constitue mon mémoire de Master 2 Recherche "Probabilités et Applications", filière Processus Stochastiques. J'ai en effet effectué mon mémoire de Master au sein de l'équipe Odyssée de l'INRIA Sophia-Antipolis, et j'ai travaillé sur la modélisation stochastique des neurones et des réseaux de neurones biologiques. De ce travail a résulté deux publications dans des conférences: un poster en collaboration avec Romain Brette présenté à la conférence NeuroMath 2006 qui s'est tenue à Andorre, et une communication orale en collaboration avec Olivier Faugeras et Theodore Papadopoulo de l'équipe Odyssee et Denis Talay, Etienne Tanré et Mireille Bossy de l'équipe Omega, qui sera présenté à la conférence NeuroComp les 23 et 24 octobre.

Ce document se compose de 3 parties principales.

La première partie est une introduction à la modélisation en neurosciences. Dans cette partie, je définis les notions principales qui interviennent dans les modèles de neurosciences, et j'expose les principaux modèles mathématiques, d'abord dans un cadre déterministe, puis dans un cadre stochastique.

La seconde partie traite des temps d'atteinte de processus stochastiques et de leurs approximations. Le problème que nous cherchons à résoudre consiste à expliciter ou caractériser les densités de probabilité des temps d'atteinte de certains processus stochastiques à une frontière qui peut être constante ou variable. Pour ce faire, nous étudions deux articles de J. Durbin [16, 17] qui donnent une représentation des temps d'atteinte d'un processus gaussien (ou du mouvement brownien) d'une courbe. Ces articles donnent aussi une série qui converge dans sous certaines hypothèses sur la frontière. Nous prouvons dans le cas du processus d'Ornstein-Uhlenbeck qu'une approximation proposée par Durbin dans son article de 1985 est exacte lorsque la frontière considérée est constante égale à la dérive du processus.

Nous explicitons ensuite des formules caractérisant les transformées de Laplace des temps d'atteinte via des solutions d'EDP elliptiques ou paraboliques, et appliquons ces formulations pour trouver des temps d'atteinte de processus simples (mouvement brownien, Ornstein-Uhlenbeck). Nous nous servons de ces caractérisations pour prouver des convergences en loi et presque sures de temps d'atteinte en fonction de la condition initiale du processus.

Enfin, nous appliquons les méthodes décrites ci-dessus pour simuler des densités de probabilités de temps d'atteinte utiles en neurosciences, donnant la distribution du premier temps de spike pour certains modèles de neurones. Ce travail sera l'objet de la présentation à la conférence NeuroComp.

La troisième partie développe un pont entre une classe de réseaux de neurones biologiques et un cadre mathématique unique, déjà quelque peu étudié par des mathématiciens. Ce travail est l'objet du poster présenté à la conférence NeuroMath.

Abstract

This document is my master's 2 research thesis, in the section Stochastic Processes, of University Paris VI (Pierre et Marie Curie). I did this thesis in the Odyssée team of INRIA Sophia-Antipolis, and my work deals with stochastic modelisation of biological neuron and neural networks. This work has lead to two publications in conferences: a poster together with Romain Brette, at the NeuroMath conference in Andorra, and an oral communication together with Olivier Faugeras and Theodore Papadopoulo of the Odyssee team and Denis Talay, Etienne Tanré and Mireille Bossy of the Omega team, which will be presented at the conference NeuroComp on October 23rd and 24th.

This document is composed of three main parts.

The first part is an introduction the neuroscience modelisation. In this part, I would define the main notions used in mathematical models for neuroscience, and I review the main mathematical models of neurons, deterministic and probabilistic.

The second part deals with hitting times of stochastic processes and with their approximations. The issue we deal with in this part is the problem of characterizing the probability densities of hitting times of some stochastic processes with a constant or moving frontier. To do so, we first study Durbin's method, which he presents in two articles [16, 17], giving a representation of the hitting times of a Gaussian process (or of the Brownian motion) with a curve. These articles gives a series representation, which converges under some conditions on the boundary function, to the real probability density. We also prove in the case of the Ornstein-Uhlenbeck process for a very special boundary that a first order approximation gives the real pdf, giving another example (Durbin shows the same property for the Brownian motion crossing a linear boundary in his article of 1985.

Then we make explicit some formulas characterizing the Laplace transforms of hitting times using elliptic or parabolic Partial Differential Equations (PDE), and apply those formulas to find the laws of hitting times of the Brownian motion and the Ornstein-Uhlenbeck process. We use those characterizations to prove also some convergences in law and almost sure of those hitting times when the starting point of the process under consideration tends to the barrier.

Finally, we apply those methods to simulate the probability density functions usefull in neuroscience, giving or approximating the probability distribution of the first spike for some neural models. This work will be presented in the NeuroComp conference.

The third part of this document builds a bridge between a class of biological neural networks and a single general mathematical framework, which has been studied since the last ten years by the community of stochastic networks. This study has been presented (with the poster joint) in the NeuroMath conference in Andorra.

Part I

Some Neuroscience Basics

Chapter 1

Biological Spiking Neuron Models

This chapter deals with the biological neuron models we will use in this document. Its aim is clearly not to give a comprehensive introduction to such a complex field as neurobiology, but to provide the reader with the basic concepts we will deal with in the rest of this document. The presentation of the biological background is highly simplistic and selective. It is basically a review of the introductory chapters of the excellent book of Gerstner and Kirsler [22]. All the figures and some parts of the text of this chapter is directly taken from this book. Further details can be found therein or in the book of Dayan and Abbott [14].

First we will introduce several elementary notions of neuroscience, in particular the concepts of action potentials, postsynaptic potentials, firing thresholds and refractoryness

Then we will introduce the main mathematical equations used to model spiking neurons. The approach chosen is to start from the more precises models and to reduce thoses models to simpler models, which would be more reasonnables for a mathematical study. These models are essentially deterministic models, and we will show how the stochastic nature of some phenomena has been introduced so far.

1.1 Introduction

The structure and function of the brain has been widely studied over the last century. The brain is composed of elementary processing units connected to each other in an intricate pattern, the neurons. But the cortex does not consist exclusively of neurons. Beside the various types of neurons, there is a large number of "supporter" cells, called glia cells, required for energy supply and structural stabilization of the brain tissue, but do not seem to be involved in information processing, so we will not discuss them any further.

We will also only deal in document with spiking neuron models and will neglect all the existing analog neuron.

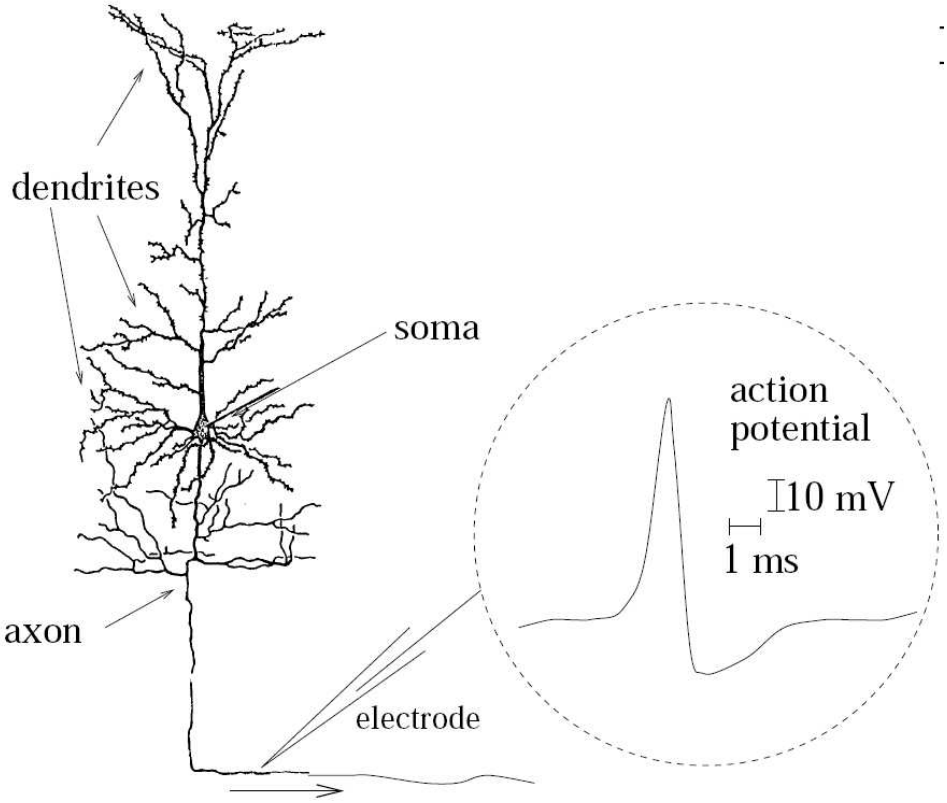


Figure 1.1: Single Neuron structure (drawing by Ramón and Cajal), reproduced in [22]

1.1.1 Structure of the Neuron

A typical neuron can be divided in three functionally distinct parts: the dendrites, the soma and the axon (see Fig. 1.1).

- The dendrite plays the role of input device: it collects the signals from other neurons and transmits them to the soma.
- The soma is the "central processing unit". It performs a non linear processing of the informations coming from other neurons together with the noise, and generates an output signal.
- This output signal is transported via the axon to be delivered to other neurons.

The junction between two neurons is called a synapse. It is common to refer to the sending neuron as the presynaptic cell and to the receiving neuron as the postsynaptic cell.

1.1.2 The Neuronal Signal

The neuronal signal consists in short electrical impulses. These pulses are called *action potentials* or *spikes*. They have an amplitude of about 100 mV and a typical duration of 1 or 2 ms. Since every spikes of a given neuron look alike, it is supposed that the form of the action potential does not carry any information. So it is rather the number and the relative timing of spikes which matter. In all the models we study, spikes will be considered as the elementary unit of signal transmission.

Action potential in a sequence of spikes emitted by the same neuron (spike train) are usually well separated. Even with a very strong input it is impossible to generate a second spike immediately after a first one. The minimal duration of time between two spikes is called the absolute *refractory period*. This phase is followed by a second one, the relative refractory period, during which it is difficult but not impossible to excite the cell.

1.1.3 The Neural Transmission

The site where the axon of a presynaptic neuron is in contact with a postsynaptic neuron is called *synapse*. The synapse can be one of two types of transmission: chemical or electrical.

The most customary is the chemical one. When a spike arrives at the synapse, neurotransmitter is released inside the tiny gap between the pre- and the postsynaptic membrane (the synaptic cleft) and this neurotransmitter is detected by the postsynaptic membrane which will open ion channels and let ions from the extracellular fluid flow into the cell. This ion flux is then translated into an electrical signal, the postsynaptic potential.

The electrical synapse (or gap junction) uses specific membrane proteins able to make direct electrical connections between two neurons.

1.1.4 Neuronal Coupling

One of the most important biological variable is the membrane potential, which is the difference of electrical potential between the cell and its neighborhood. Experimentally one can access to this variable. When no spike is received by the neuron, its membrane potential remains constant. When a spike is received, the potential changes and returns regularly to its resting potential. If the change of potential is postive, the synapse is said to be excitatory and if the change is negative the synapse is said to be inhibitory.

1.1.5 The problem of neural coding

The mammalian brain contains more than 10^{10} densely packed neurons connected in an intricate network. In every small volume of cortex, thousands of spikes are emitted each milisecond. The problem is to undestand how the information is coded in the spacio-temporal

pattern of pulses emitted. How the signal is decoded? This is a fundamental issue in neuroscience. No definitive answear is known so far, but many conjectures have been launched. This section is important for our mathematical study because it gives us the pertinent variables to model and study.

Traditionnally it has been thought that most relevant information was contained in the mean firing rate, i.e. the mean number of spikes emitted by unit of time, neglecting the exact timing of spikes. This is criticized now with a lot of experimental evidences suggesting that this type of coding is far too simplistic. For instance reaction times of human visual system has proved that there is no time for the brain to compute the mean firing rate because only a few spikes can be emitted during the period of time the scene is seen and the reaction takes place (see for instance the experiments of Thorpe et al, 1996).

In the following section we review some potential coding scheme.

Spike count (Average over time)

As discussed in the preliminaries, the common definition of spike rates is the average over time, i.e. the number of spikes emited during a period of time T, divided by T. This definition has been successful is experiments on sensory motor systems (for example for the stretch receptor in a muscle spindle, Adrian, 1926). From a mathematical point of view it leads us to consider the output of a neuron as a scalar continuous variable (the firing rate).

Spike density (Averages over several runs)

The variable considered is a function, the so-called peri-stimulus-time histogram. The time t is measured w.r.t. the start of the simulation and the same simulation is repeated several times (see Fig 1.2). A time step Δt is chosen, typically a few milliseconds, and the spikes are considered as functions of the type $\mathbb{1}_{[t^*,t^*+\Delta t]}(t)$ where t^* is the firing time. All these functions are summed over all the repetitions of the experiments and divided by the number of experiments.

This is of particular interest for our probabilistic study because it can be interpreted as the probability density of spiking of the neuron.

From a biological point of view it makes sense if one assume that a population of independant neurons receive the same stimulus : the brain can then compute this time of peri-stimulus-time histogram form a single run.

Population activity (Averages over several neurons)

The assumption for using this representation of coding is the same that the assumption used in the study of spike density: many neurons have similar properties and respond to the same stimuli. The spikes of a population of neuron $\mathcal{M}$ are sent to a set of neurons $\mathcal{N}$. It is assumed that every neuron of $\mathcal{N}$ receives the outputs of all the neurons of $\mathcal{M}$. The relevant information in this model is the proportion of "active neurons" of the presynaptic

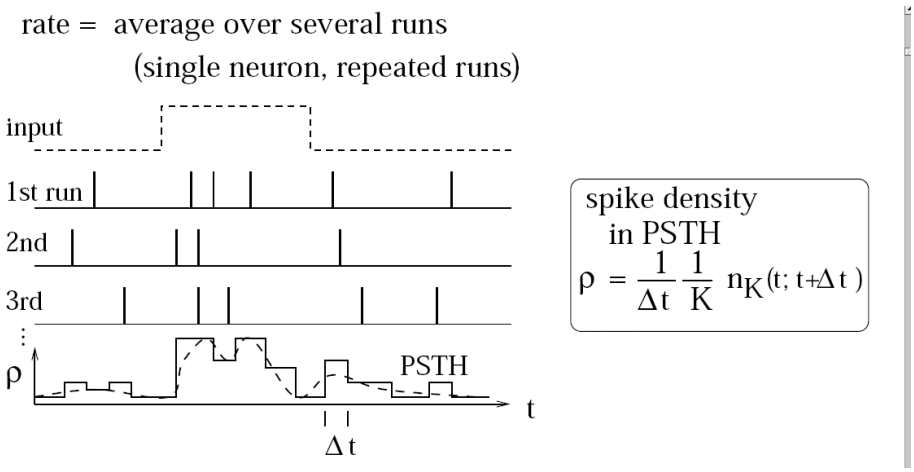


Figure 1.2: Definition of the spike density as an average over several runs of the experiment (taken for Gerstner-Kirstler [22])

population $\mathcal{M}$.

$$A(t, \Delta t) = \frac{1}{\Delta t} \frac{n_{\text{active}}(t; t + \Delta t)}{|\mathcal{M}|} \tag{1.1.1}$$

where $n_{\text{active}}(s; t)$ is the number of spikes occuring in any neuron of the population $\mathcal{M}$ during the period of time $[s, t]$.

The population activity may vary very rapidly and can reflect changes in the stimulus conditions. Nevertheless the population is not homogeneous in general in the brain and one has to find suitable pools of neuron to apply this representation.

In an heterogeneous population we can replace the definition (1.1.1) by a weighted average over the population.

In the above sections we only refered to statistics of spikes. We can also model the neural code using the spike timing information (which will be refered in the sequel as event-driven models).

Time to first spike

It is not unrealistic to imagine a code where for each neuron the timing of the *first* spike after a reference contains all the information about the stimulus. In a pure version of this coding scheme only the first spike emitted transports information. All following spikes are irrelevant.

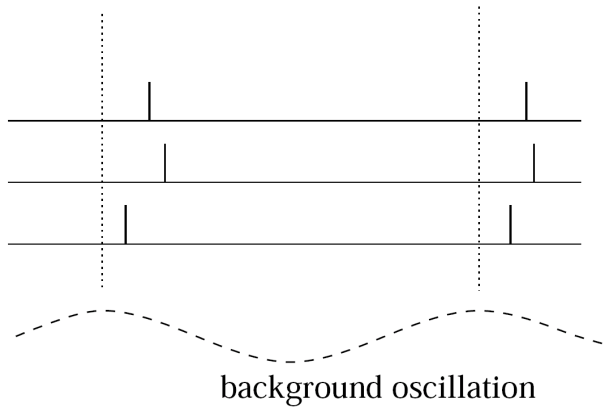


Figure 1.3: Phase coding: the neurons fire at different phases with respect to the background oscillation (dashed line). Taken from [22]

This model clearly seems simplistic but biological experiments (see for instance Thorpe et al, 1996) has proved that the brain does not have time to evaluate more than one spike from each neuron per processing step. This simple model allows us to try mathematical studies and it would be also of special interest for us in the rest of this work.

Phase coding

When the stimulus applied is not a single event but a periodic signal, the "time to first spike" code is no more relevant. Oscillations in the brain are in fact quite common phenomena. In these oscillations the information could be carried by the phase of a pulse with respect to the global oscillation observed, called background oscillation (see Fig.1.3). There are biological evidences that the phase of a spike during global oscillations conveys informations (see for instance O'Keefe and Recce, 1993).

Correlations and Synchronies

One can also use spikes form other neurons as the reference signal for a spike code. For instance, synchronies between neurons could convey information which is not contained in the firing rate of neurons (see Fig.1.4).

More generally, any precise spacio-temporal pulse pattern could be a meaningful event (neurons spiking with a determined delay between each other). This type of coding has been widely studied by Abeles.

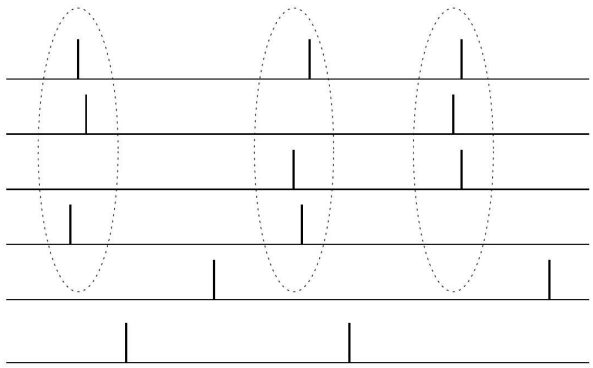


Figure 1.4: Synchrony: the upper four neurons are nearly synchronous, two other neurons at the bottom are not synchronized. Taken from Gerstner-Kirstler [22]

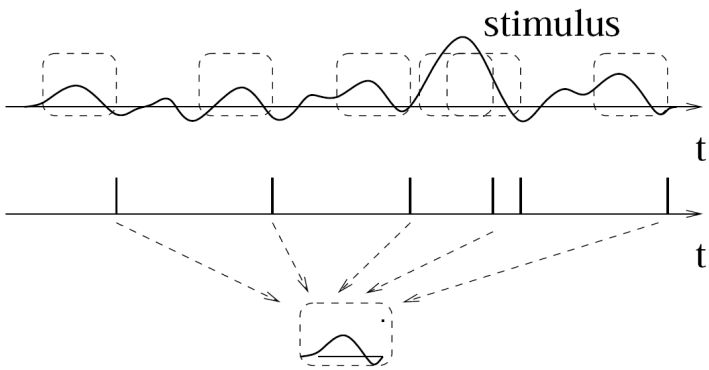


Figure 1.5: Reverse correlation technique: the stimulus in the top trace has caused the spike train shown below. the time course of the stimulus just before the spikes has been averaged to yield the typical course at the bottom

Stimulus reconstruction and reverse correlation

Let us consider a neuron driven by a time dependant stimulus $s(t)$. Every time a spike occurs, we note the time course of the stimulus in a time window of duration Δt (in general about 100 ms) immediately before the spike. Averaging the results over several spikes yields the typical time course of the stimulus just before the spike. This procedure is called reverse correlation (see Fig 1.5)

The typical time course of the stimulus can be interpreted as the "meaning" of a single spike. This approach has been successful in many experiments (Eckorn et al 1993, Bialek et al 1991, ...). This way it is possible to reconstruct the stimulus linearly. This simple reconstruction has given fair estimates of the time course of the stimulus in some experiments.

1.2 Single Neuron Models

This chapter deals with the mathematical models of neurons. We first take a biological point of view to explain the emission of action potentials, then present some detailed neuron model such as the Hodgkin-Huxley (HH) model which models at the level of the ion channels in the cell. This model is very difficult to handle mathematically so we present then some reductions of the HH model, to get more simple neuron models (such as formal spiking neuron models).s

1.2.1 Detailed neuron models

From a biophysical point of view action potential are the result of currents passing through ion channels in the cell membrane. Hodgkin and Huxley, studying the giant axon of the squid, succeeded in measuring these currents and described the dynamics in terms of non linear differential equations. The HH equations are the starting point of detailed models, and accounts for numerous ion channels, different types of synapses, spacial geometry of individual neurons.

Hodgkin-Huxley Model

Hodgkin and Huxley (1952) found three different types of ion current involved in the dynamics of the membrane potential of neurons: sodium, potassium and the leak current consisting mainly in Cl^- ions. Specific voltage-dependant ion channels (one for sodium and one for potassium) control the flow of those ions through the cell membrane.

The model has the electrical interpretation represented in Fig. 1.6. When an input current $I(t)$ is injected into the cell, the membrane is charged like a capacitor, and the current leaks through the channels in the cell membrane.

Mathematically we have:

$$C\frac{du}{dt} = I(t) - \sum_k I_k(t) \tag{1.2.1}$$

where k are the different ion channels.

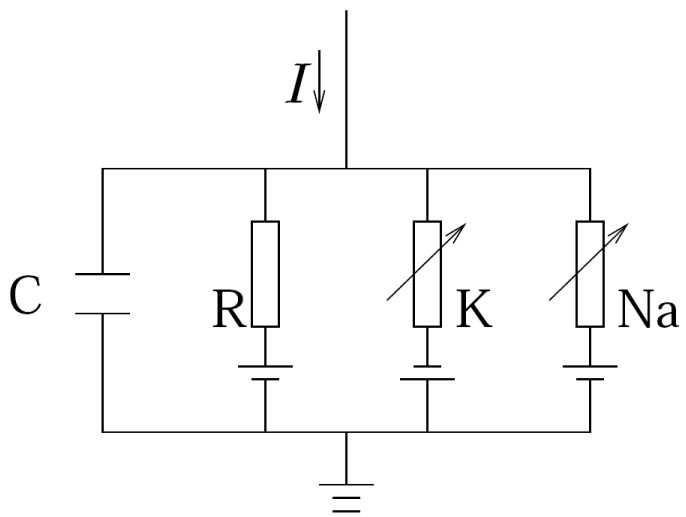


Figure 1.6: Equivalent electric circuit of the model of Hodgkin-Huxley. The passive electrical properties of the cell membrane are described by a capacitance C and a resistor R. The non-linear properties come from the voltage-dependant ion channel for sodium and potassium

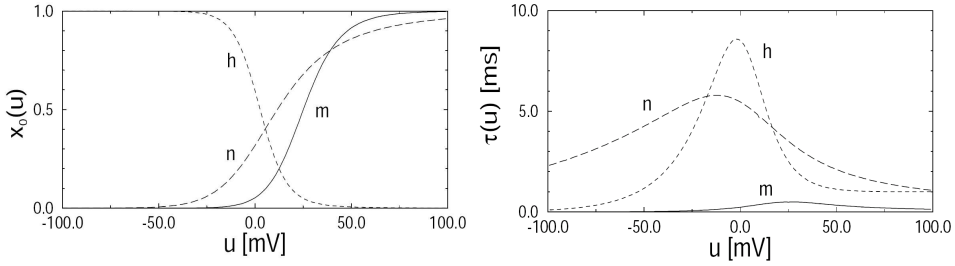


Figure 1.7: Equilibrium functions (left) and time constant (right) for the gating variables m, n, h in the Hodgkin-Huxley model.

All ion channels are described by their voltage-dependant conductance $g_k(u)$. To model these conductances we introduce three additionnal variables : m, n and h. The combined action of m and h controls Na^+ channels and the variable n controls the K^+ channels.

$$\begin{cases} I_{Na} & = g_{Na} m^3 h (u - E_{Na}) \\ I_K & = g_K n^4 (u - E_K) \\ I_l & = g_l (u - E_l) \end{cases} \tag{1.2.2}$$

The parameters E_{Na}, E_K and E_l are the *reversal potentials* and g_{Na}, g_K and g_l are the maximal conductances of the ion species. The three variables m, n and h, also called gating variables, evolve according to the differential equations:

$$\frac{dm}{dt} = \alpha_m(u)(1-m) - \beta_m(u)m \tag{1.2.3a}$$

$$\frac{dn}{dt} = \alpha_n(u)(1-n) - \beta_n(u)n$$

$$\frac{dh}{dt} = \alpha_h(u)(1-h) - \beta_h(u)h \tag{1.2.3b}$$

The various functions α and β are empirical functions, initially taken as exponential (cf [22], see Fig. 1.7). These equations generate spikes automatically because of the non-linearity of the equations.

These equations are a good model for the electrophysiological properties of the giant axon of the squid. However, cortical neurons of vertebrates exhibit other physiological properties because other ions are involved, or ion channels exhibit other behavior (e.g. noninactivating sodium current, calcium current).

Synapses Models

So far, we mentionned two types of ion channels: the voltage-activated and the *calcium*-activated ion channels. The third type of ion channel we have to deal with is the *transmitter*-activated ion channel involved in the synaptic transmission. The model proposed here does not take into account the precise biophysical properties of this phenomenon (ion concentrations in the cleft, metabolic receptors, ...) but describe transmitter-activated ion channels as an explicit time-dependant conductivity $g_{\text{syn}}(t)$. The current passing through these channels depends, as usual, on the difference between its reversal potential E_{syn} and the actual value of the membrane potential u :

$$I_{\text{syn}}(t) = g_{\text{syn}}(t)(u - E_{\text{syn}}) \tag{1.2.4}$$

Typically, the $g_{\text{syn}}(t)$ function is chosen as a superposition of exponential functions. The form of this function changes wether if the synapse is excitatory or inhibitory, and we refer to [22] for the precise expression of $g_{\text{syn}}(t)$ in those two cases.

Spike Transport in Passive Dendrite

The action potential propagates inside the dendrites before arriving to the soma, and when a spike is fired, it propagates along the axon. So far we modeled the neuron as having the same electrical potential all along. But there are also longitudinal currents along the dendrite. The cable equation drives the membrane potential along a passive dendrite as a function of time and space. After electro-physiological considerations, one find the passive cable equation which is :

$$\frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2}(t,x) - u(t,x) + i_{\text{ext}}(t,x) \tag{1.2.5}$$

$$\frac{\partial i}{\partial t}(t,x) = \frac{\partial^2 i}{\partial x^2}(t,x) - i(t,x) + \frac{\partial i_{\text{ext}}}{\partial x}(t,x) \tag{1.2.6}$$

$$\tag{1.2.7}$$

Where u describes the membrane potential at time t and in the position x and i the current passing through the dendrite at the position x and time t. Note that it suffices to solve one of these equations because u and i are simply related ($\frac{\partial u}{\partial x} = r_L i$ where r_L is the longitudinal resitence per unit of lenght).

Those two equations are linear so can be solved by the usual methods (Green function for instance can be computed easily for an infinite cable, Fourier method, ...).

Spike Transport in Active Dendrites

In the context of a realistic modeling of biological neurons, one has to take into account the non-linear phenomena occuring in the spike transportation in the dendrite. Those non-linearities can be linked with the ion channels like in the HH equation. We have seen that

ion channels can exhibit complex dynamics governed by a system of differential equations. The current through one of these channels is thus non simply a nonlinear function of the actual value of the membrane potential but can also depend on the past time course of the membrane potential, which we denote $i_{\text{ion}}[u](t,x)$. The extended cable equation takes the form:

$$\frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2}(t,x) - u(t,x) - i_{\text{ion}}[u](t,x) + i_{\text{ext}}(t,x) \tag{1.2.8}$$

A more realistic description is obtained if we take into account the fact that the input from the synapse cannot be treated as an ideal current source, but because of the dynamics of ion channels, the current resulting from an incoming spike is proportionnal to the difference between the membrane potential and the corresponding ionic reversal portential.

So in the equation (1.2.8) the external input current $i_{\text{ext}}(t,x)$ has to be replaced by an appropriate synaptic input current :

$$-i_{\text{syn}}(t,x) = -g_{\text{syn}}(t,x)\,(u(t,x) - E_{\text{syn}})$$

, with g_{syn} being the synaptic conductivity and E_{syn} the corresponding reveral potential. So we obtain:

$$\frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2}(t,x) - u(t,x) - i_{\text{ion}}[u](t,x) - g_{\text{syn}}(t,x)\,(u(t,x) - E_{\text{syn}}) \tag{1.2.9}$$

This is still a linear differential equation but with time-dependant coefficients.

The form of the synaptic conductivity g_{syn} is often written as the solution of a differential equation, for instance exponentially decaying with time constant τ_{syn} (a model we will use in our studies):

$$\begin{cases} \frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2}(t,x) - u(t,x) - i_{\text{ion}}[u](t,x) - g_{\text{syn}}(t,x)\,(u(t,x) - E_{\text{syn}}) \\ \frac{\partial g_{\text{syn}}}{\partial t}(t,x) - \frac{1}{\tau_{\text{syn}}} g_{\text{syn}}(t,x) = S(t,x) \end{cases} \tag{1.2.10}$$

where $S(t,x)$ is the input current, generally a sum of Dirac functions describing the presynaptic spike train arriving in the synapse at the position x.

This new equation is no more linear because the two unknowns u and g_{syn} are multiplicated.

1.2.2 Two-dimensional neuron models

We have presented in the previous section detailed neuron models described by non-linear differential equations of dimension 4 or more. It's very difficult to analyse such types of

systems. So people had to make simplifications in the model to be able to study the mathematical properties of the neurons. In this section we present first the approximation method of the four-variable HH models into a two-variables model, using temporal properties of the constants of the above equation to gather variables.

General two-dimensionnal neuron models

In this section we perform a systematic reduction of the four-dimensional HH model to two dimensions. To achieve this plan, we have to eliminate two of the four initial variable (namely u, m, n and h). The essential ideas of the reduction can be applied to detailed neuron models containing more ions channels.

The general approach for reduction is to observe qualitatively that the time scale of the gating variable m is much faster than that of u, n and h. This suggests to treat m as an instantaneous variable, and replace it by its steady state value $m_0(u(t))$. This is called the *quasi steady-state approximation*.

Secondly, we observe experimentally that the time-constants $\tau_n(u)$ and $\tau_h(u)$ are roughly the same, whatever the voltage u, and the graphs of $n_0(u)$ and $1 - h_0(u)$ are similar. This suggests that we may approximate the two variables n and $1 - h$ by a same variable ω.

More generally, assume that we have a linear approximation of type $(b - h) \backsimeq a\,n$ where a and b are real valued constants. and we set $\omega = b - h = a\,n$. Then we get from equations (1.2.1), (1.2.2) and (1.2.3) the following equation :

$$C\,\frac{du}{dt} = -g_{\mathrm{Na}}\,[m_0(u)]^3\,(b-\omega)\,(u - E_{\mathrm{Na}}) - g_{\mathrm{K}}\left(\frac{\omega}{a}\right)^4\,(u - E_{\mathrm{K}}) \\ -g_L\,(u - E_L) + I \tag{1.2.11}$$

In the rest of the section we will write this equation for more generality and readability in the following way :

$$\frac{du}{dt} = \frac{1}{\tau}[F(u,\omega) + R\,I] \tag{1.2.12}$$

Here $R = \frac{1}{g_L}$ and $\tau = R\,C$.

The three equations (1.2.3) can be simplified also since m is considered as instantaneous. The equation (1.2.3a) is replaced by $m = m_0(u)$, and the two equations (1.2.3b) and (1.2.3b) are replace by one equation on ω:

$$\frac{d\omega}{dt} = \frac{1}{\tau_\omega}G(u,\omega), \tag{1.2.13}$$

where τ_ω is a parameter and G a function to specify.
The two equations (1.2.12) and (1.2.13) define a general two-dimensional neuron model In the two following sections we detail which are the parameters of this system of differential

equations in two usual cases, and that yield to two well-known neuron models: the *Morris-Lecar* model and the *FitzHugh-Nagumo* model.

Morris-Lecar Model

Morris and Lecar (1981) proposed a two-dimensional description of neuronal spike dynamics of this type. In dimensionless variables the Morris-Lecar equations read:

$$\frac{du}{dt} = -g_1 \hat{m}_0(u)\,(u-1) - g_2 \hat{\omega}\,(u - V_2) - g_L(u - V_L) + I \tag{1.2.14a}$$

$$\frac{d\hat{\omega}}{dt} = -\frac{1}{\tau(u)}\left[\hat{\omega} - \omega_0(u)\right] \tag{1.2.14b}$$

The additionnal variable $\hat{\omega}$ is called the *recovery variable*.

If we compare relations (1.2.14a) with (1.2.11), we note that the first current term is no more multiplicated by $(b - \omega)$. Moreover, $\hat{m}_0$ and $\hat{\omega}$ do not have any exponent. To understand better this model we could set $\hat{m}_0 = [m_0(u)]^3$ and $\hat{\omega} = \left(\frac{\omega}{a}\right)^4$. The functions have typically sigmoidal shapes, so are usually approximated by:

$$m_0(u) = \frac{1}{2}\left[1 + \tanh\left(\frac{u - u_1}{u_2}\right)\right] \tag{1.2.15}$$

$$\omega_0(u) = \frac{1}{2}\left[1 + \tanh\left(\frac{u - u_3}{u_4}\right)\right] \tag{1.2.16}$$

$$\tau(u) = \frac{\tau_\omega}{\cosh\left(\frac{u-u_3}{u_4}\right)} \tag{1.2.17}$$

where u_i and τ_ω are constant parameters.

FitzHugh-Nagumo model

FitzHugh and Nagumo were probably the first to propose two-dimensional reductions of the HH model, of type (1.2.12) and (1.2.13). They obtain sharp pulse-like ocillations reminiscent of spike trains proposing for the function F and G the following form:

$$\begin{aligned} F(u,\omega) &= u - \tfrac{1}{3}u^3 - \omega \\ G(u,\omega) &= b_0 + b_1\, u - \omega \end{aligned} \tag{1.2.18}$$

Note that the dependance in the recovery variable ω is linear, and the non-linearity is contained in the cubic term of F.

1.2.3 Formal Spiking Neuron Models

Detailed conductance-based neuron models reproduce electrophysiological with accuracy but they are very difficult to analyse because of their intrinsic complexity. For this reason, simple phenomenological spiking neuron models are very popular. In this section we discuss formal threshold models of neuronal firing.

The general principle is to assume that the membrane potential has a given dynamics while it is underneath the threshold, and when the membrane potential hits a given threshold θ, then a spike is emitted. So globally one has to study the only variable u and the models differ essentially in the dynamics of u.

First we will deal with the popular and simple integrate-and-fire (IF) model. Then we will explain another classical simple model, the Spike Response Model (SRM), and we will conclude on the relation between those models and the ion channel models.

Integrate-and-fire models

In this section we give a brief overview of IF models. Those models are of special interest for us: all the neuron models studied in this document are IF-models, more or less complex.

1. The **Perfect Integrate-and-Fire** model is the most simple neuron model, and maybe the less realistic of the widely used formal neuron models. The membrane potential is an integrator: it integrates all the entries. When this potential reaches a threshold value θ, the neuron fires and the membrane potential is reset a fixed value u_r.

$$\begin{array}{ll} C\frac{du}{dt} & = I(t) \\ u(t_0^-) & = \theta \quad \Rightarrow u(t_0) = u_r \quad \bigoplus \quad \text{spike emitted} \end{array} \tag{1.2.19}$$

2. The **Leaky Integrate-and-Fire** (LIF model) is similar to the Perfect IF model but we take into account the leak of the membrane potential. It can be interpreted as the electrical circuit of Fig. 1.8

   The standard equation governing the membrane potential of a LIF neuron is:

$$\begin{array}{ll} \tau_m\frac{du}{dt} & = -u(t) + R\,I(t) \\ u(t_0^-) & = \theta \quad \Rightarrow u(t_0) = u_r \quad \bigoplus \quad \text{spike emitted} \end{array} \tag{1.2.20}$$

   In its general version, the leaky integrate-and-fire model may incorporate an absolute refractory period. In this case, if u reaches θ at time $t^{(f)}$, we interrupt the dynamics of u during a period of time Δ^{abs} and restart the integration at time $t^{(f)} + Delta^{\text{abs}}$ with the new initial condition u_r.

   Note that this model is easily fully solved for constant current input $I(t) = I_0$, and that we have a close form for the membrane potential for an arbitrary input.

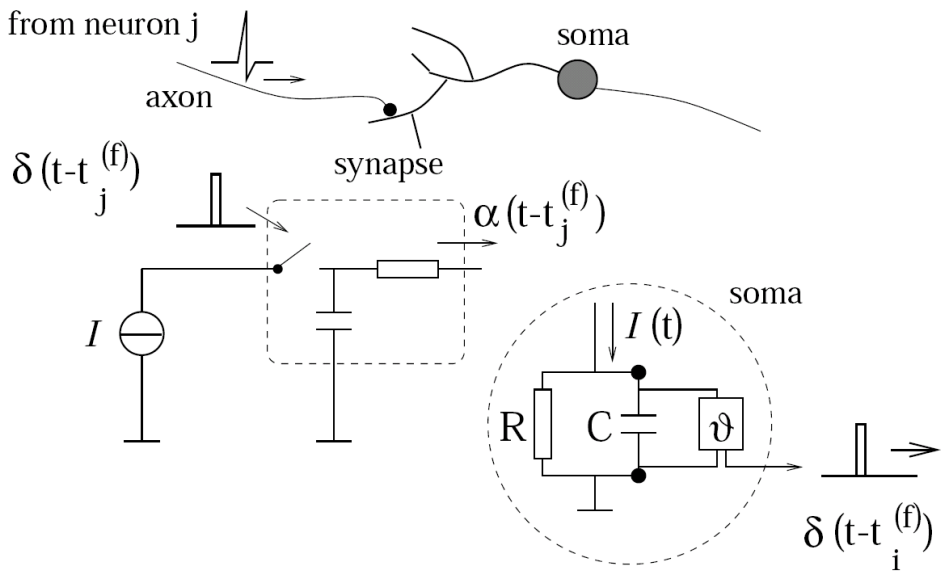


Figure 1.8: Schematic diagram of the leaky integrate-and-fire model. The basic circuit is the module inside the dashed circle on the right hand side. A current $I(t)$ charges the RC circuit. The voltage accross the capacitance, $u(t)$, is compared to the threshold θ. When it reaches θ, say at time $t_i^{(f)}$, then an output pulse $\delta(t - t_j^{(f)})$ is generated. In the left part we see that a presynaptic spike is low-pass filtered at the synapse and generate an impulse current $\alpha(t - t_j^{(f)}$

3. The **Nonlinear Integrate-and-Fire model**: In the general *nonlinear* integrate-and-fire model the equation of the dynamics of the membrane potential between two spikes is given by :

$$\tau \frac{du}{dt} = F(u) + G(u)\, I \tag{1.2.21}$$

As before, the dynamics is stopped if u reaches the threshold θ, u is reset to u_r and a spike is emitted. $G(u)$ can be interpreted as a voltage dependant input resistance and $-F(u)/(u - u_{\text{rest}})$ correspond to a voltage-dependant decay constant. For instance we can have a quadratic model (Latham, Izhikevitch) given by the equation (1.2.22):

$$\frac{du}{dt} = u^2 + I \tag{1.2.22}$$

In 2005, Brette and Gerstner defined the model of the exponential integrate-and fire neuron on the same idea, taking the interspike dynamics of the membrane potential following the differential equation:

$$C\frac{du}{dt} = -g_l(u - E_l) + g_l \Delta_t e^{(\frac{u - V_t}{\Delta_t})} + I \tag{1.2.23}$$

or added an adaptation variable w and get the two-dimensionnal formal spiking equation:

$$\begin{cases} C\frac{du}{dt} & = -g_l(u - E_l) + g_l \Delta_t e^{(\frac{u - V_t}{\Delta_t})} + I \\ \tau_w \frac{dw}{dt} & = a(u - E_l) - w \end{cases} \tag{1.2.24}$$

4. **Stimulation with synaptic currents** So far we considered an isolated neuron stimulated by an external current $I(t)$. In a more realistic situation, the IF neuron is part of a network an the input current is generated by the activity of presynaptic neurons.

   In the framework of the IF model, each presynaptic spike generates a postsynaptic current pulse. A spike received at time $t^{(f)}$ creates in the postsynaptic neuron a current $\alpha(t - t^{(f)})$ and the total input of neuron i is the sum over all current pulses of the neighbors of i. Denoting $\mathcal{V}(i)$ the set of neighbors of i we can write the current input:

$$I(t) = \sum_{j \in \mathcal{V}(i)} \sum_{\{t_j^{(f)} \text{ firing instants of } j\}} \alpha(t - t_j^{(f)}). \tag{1.2.25}$$

Though equation (1.2.25) is realistic, in fact the amplitude of the postsynaptic current is modulated by the membrane potential of i, u_i, because of the change of conductance mentionned in the section 1.2.1 and more precisely in the equation (1.2.4):

$$\alpha(t - t_j^{(f)}) = -g(t - t_j^{(f)})\,(u_i(t) - E_{\mathrm{syn}})\,. \tag{1.2.26}$$

Spike Response Model

The Spike Response Model (SRM) is a generalization of the LIF model. In the non-linear generalization of the LIF model we took parameters of the LIF model voltage dependant but here in the SRM we take time-dependant parameters. Another difference is the formulation of the model, which is no more in terms of differential equation but in terms of integral over the past. This model is rather general and allows us to model the refractorness in very general terms (reduced responsiveness after an output spike, increase of threshold after firing and hyperpolarizing spike afterpotential).

1. **Definition of the SRM**: here again the state of a neuron i is defined by its membrane potential u_i. In the absence of spike, it is at its resting value $u_{\mathrm{rest}} = 0$. Each incoming spike will perturb u_i and it takes some time before u_i returns 0. We denote ϵ the function describing the time-course of the response to an incoming spike. If after summing the effects of all the incoming spikes u_i reaches the threshold, then a spike is triggered and u_i is reset to the function describing the time course of the membrane potential after a spike, denoted η. Assume that the neuron i has fired its last spike at time t_i. The evolution of u_i is given by:

$$\begin{aligned} u_i(t) = \eta(t - t_i) + \sum_{j \in \mathcal{V}(i)} w_{i,j} \sum_{\{t_j^{(f)} \text{ firing instants of } j\}} \epsilon_{i,j}(t - t_i, t - t_j^{(f)}) \\ + \int_0^\infty \kappa(t - t_i, s) I^{\mathrm{ext}}(t - s) ds \end{aligned} \tag{1.2.27}$$

   Moreover, in contrast to the IF models, the threshold θ is not fixed but may also depend on the time elapsed till the last spike $\theta(t - t_i)$.

   During the absolute refractory period Δ^{abs}, we may for instance set θ to a large value to avoid firing and let it relax back to its equilibrium value for $t > t_i + \Delta^{\mathrm{abs}}$.

   The functions η, κ and $\epsilon_{i,j}$ are response kernels that describe the effect of spike emission and spike reception on the membrane potential:

   - The kernel η describes the standard form of an action potential of neuron i including the negative overshoot which follows a spike (afterpotential).

- The kernel $\kappa(t-t_i, s)$ is the linear response of the membrane potential to an input current. It describes the time course of the deviation of the membrane potential caused by a short current pulse (*impulse response*). The time dependance of this kernel allows us to model the effect of the spike: just after t_i many ion channels are open so the membrane resistance is reduced.
- The kernel $\epsilon_{i,j}(t-t_i, s)$ is a function of $s = t - t_j^{(f)}$ and can be interpreted as the time course of the *postsynaptic potential* evoqued by the firing of a presynaptic neuron j at time $t_j^{(f)}$. The dependance in $t - t_i$ models the refractoriness of a neuron after having fired.

Note that the dynamic threshold $\theta(t - t_i)$ can in general be formally replaced by a constant threshold changing some terms of the SRM.

2. **Mapping the LIF model to the SRM :** It is of special interest to note that the LIF model for instance is a particular case of the SRM model. Let us consider a LIF neuron driven by an external current $I^{\text{ext}}(t)$ and postsynaptic current pulses $\alpha(t - t_j^{(f)})$. The potential u_i is thus given by:

$$\tau_m \frac{du_i}{dt} = -u_i(t) + R \sum_j w_{i,j} \sum_{t_j^{(f)})} \alpha(t - t_j^{(f)}) + R\, I^{\text{ext}}(t) \tag{1.2.28}$$

Let us now integrate (1.2.28) starting from time t_i with initial condition $u_i(t_i) = u_r$, and let us identifiate the parameters of the corresponding SRM model:

$$\begin{aligned} u(t) =& u_r e^{-(t-t_i)/\tau_m} \\ &+ \sum_j w_{i,j} \sum_{t_j^{(f)})} \frac{1}{C} \int_0^{t-t_i} e^{-s/\tau_m} \alpha(t - t_j^{(f)} - s)\, ds \\ &+ \frac{1}{C} \int_0^{t-t_i} e^{-s/\tau_m} I_i^{\text{ext}}(t-s)\, ds \end{aligned} \tag{1.2.29}$$

So we can easily identify the expression (1.2.29) with the expression of the general SRM (1.2.27) with:

$$\eta(s) = u_r e^{-s/\tau_m} \tag{1.2.30a}$$

$$\epsilon(s,t) = \frac{1}{C} \int_0^s e^{-t'/\tau_m} \alpha(t - t') dt' \tag{1.2.30b}$$

$$\kappa(s,t) = \frac{1}{C} e^{-t/\tau_m} \mathbb{1}_{s \geq t} \mathbb{1}_{t \geq 0} \tag{1.2.30c}$$

Lastly, in order to have an explicit expression for the ϵ kernel, let us specify the time course of the postsynaptic current $\alpha(t)$. We can for instance take $\alpha(t)$ exponentially decaying:

$$\alpha(s) = \frac{q}{\tau_s} exp(-s/\tau_s) \mathbb{1}_{s \geq 0} \tag{1.2.31}$$

From detailed neuron models to formal spiking neurons

In this section we study the relation between detailed conductance-based neuron models and formal spiking neurons as introduced above. Therefore we aim for a reduction towards a spiking neuron model where spikes are triggered when the membrane potential reaches a voltage thereshold. Specifically, we establish an approximation of the HH model in a special SRM model. To do so, we neglect the time-course of the action potential which is more or less stereotyped.

Let us consider that a spike has been triggered at time t^*, and that no further stimulation is applied to the neuron afterwards. The voltage trajectory will have a pulse-like excursion before it eventually returns to its resting potential. For $t > t^*$, we set $u(t) = \eta(t - t^*) + u_{\text{rest}}$, where η is the standard shape of the pulse and u_{rest} the resting potential. If a current pulse is applied at t>t*, the membrane potential will be slightly perturbed form its trajectory and. If the input current is sufficiently small, the perturbation can be described by a linear impulse response kernel κ. So we have to characterize the kernels η and κ, and the value of the threshold θ. The two kernels are experimentally computed simulating an HH neuron with specified inputs. It is rather difficult to define a hard threshold for a HH neuron. On one hand, we can say that the HH neuron show a sort of threshold behavior (over a certain value of the membrane potential it is very difficult to avoid a spike for the neuron), it is very difficult to estimate the voltage threshold from simulations. In [22] the authors discuss of the types of excitations and the way to estimate the threshold.

Chapter 2

Randomness in spiking neuron models

In vivo recordings of neuronal activity are characterized by a high degree of irregularity. A single neuron react in general in a very reliable and reproductible manner to fluctuating currents that are injected via intracellular electrodes (when the same signal is injected, the action potentials occur with precisely the same timing relative to the simulation). On the other hand, neurons produce irregular spike trains in the absence of any temporally structured stimuli. Irregular spontaneous activity and trial-to-trial variations are often considered as noise. The origin of irregularities is poorly known, and often added externally to the neuronal dynamics in the IF or SRM equations in order to mimic the unpredictability of neuronal recordings.

2.1 Noise sources

We can distinguish between intrinsic noise sources that generates stochastic behavior on the level of the *neuronal dynamics* and extrinsic sources arising from network effects and synaptic transmission.

- An omnipresent noise source is the thermal noise. Due to the discrete nature of electric charge carriers, the voltage u across any electrical resistor R fluctuates at finite temperature (Johnson noise). Since neuronal dynamics is described by an equivalent electrical circuit containing resistors, the neuronal membrane potential fluctuates as well. Fluctuations due to Johnson noise are, however, of minor importance compared to other noise sources in neurons.
- Another noise source arises from the finite number of ion channels. Most ion channel have only two states: they are open or they are closed. The electrical conductivity

of a patch of membrane is proportionnal to the number of open ion channels. For a given constant membrane potential u, a fraction $P_i(u)$ of ion channels of type i is open *on average*. So the conductivity fluctuates and so does the potential. Note that there exists models taking into account the finite number of ion channel, and that they can reproduce the observed variability (Chow and White, 1996).

- Noise due to signal transmission and network effects (extrinsic noise): Synaptic transmission failures, randomness of excitatory and inhibitory connections, for instance.

2.2 Statistics of spike trains

One of my works during this study has been to establish a method to approximate spike trains statistics for simple neuron models. In this section we will explain basic concepts for the statistical description of neuronal spike trains. A central notion is the interspike interval (ISI) distribution. This study is based on some basic properties of the renewal processes.

2.2.1 Input-dependant renewal systems

We consider a single neuron such as an IF or SRM unit. Conditionnally to the last firing time $\hat{t} < t$, the membrane potential u is completely determined, for instance for the SRM we have:

$$u(t|\hat{t}) = \eta(t-\hat{t}) + \int_0^\infty \kappa(t-\hat{t}, s) I(t-s) ds, \tag{2.2.1}$$

and for the LIF model:

$$u(t|\hat{t}) = u_r exp\left(-\frac{t-\hat{t}}{\tau}\right) + \frac{1}{C}\int_0^{t-\hat{t}} exp\left(-\frac{s}{\tau}\right) I(t-s) ds, \tag{2.2.2}$$

Here we assumte that I is a given function of time. The problem can be described as :

Knowing the input and the last firing time $\hat{t}$ we would like to predict the next spike emitted.

In the absence of noise, the next firing time is determined by the threshold condition $u = \theta$. In the presence of noise, the next time spike is the random time defined by the hitting of u of the constant barrier θ. The problem is to compute the probability distribution of the next firing time.

The sequence of spike times can be considered as a generalized renewal process in the equations (2.2.1) and (2.2.2). It would be a simple renewal process if the process I was stationnary. If not, the process depends both on the time elapsed till the last spike emitted

and the time-shifted input $I(t'), \hat{t} < t' < t$ received till the last spike. These are called *modulated renewal process* and has been studied by Reich et al for instance in 1998, or non-stationnary renewal process, or inhomogeneous Markov interval process.

2.2.2 Interval distribution

The estimation of the ISI distributions has been widely studied from an experimental point of view, given a certain *stationnary* input (if the input is no more stationnary, then the interspike intervals have not the same probability law). This allows experimentalists to apply the classical statistical treatments to the iid sequence of interspike intervals (the durations between two consecutive spikes).

When the input is no more stationnary, experimentalists can also apply statistical methods on an isolated neuron stimulated by a known input current $I(t)$ and with some unknown noise source. In this case the law of the interspike interval is assumed to be absolutely continuous w.r.t Lebesgue's measure and we denote $P_I(t|\hat{t})$ the probability density function.

As usually, we can define the survivor function : $S_I(t|\hat{t}) = 1 - \int_{\hat{t}}^{t} P_I(t'|\hat{t})dt'$ which is the probability that the neuron stays quiescent between $\hat{t}$ and t. The rate of decay of the survivor function (called usuallu *hasard function*) is defined by

$$\rho_I(t|\hat{t}) = -\frac{\frac{dS_I(t|\hat{t})}{dt}}{S_I(t|\hat{t})} \tag{2.2.3}$$

or equivalently

$$S_I(t|\hat{t}) = exp\left[-\int_{\hat{t}}^{t} \rho_I(t'|\hat{t})dt'\right]$$

First of all we will define those variables in the very particular case of a stationnary renewal process.

2.2.3 Sationnary renewal processes

First of all, in the case of stationnary processes, the ISI have the same law and depends only on the time elapsed till the last spike. So we will simplify the notations the following way:

$$\begin{aligned} P_I(t|\hat{t}) &\longrightarrow P_0(t-\hat{t}), \\ S_I(t|\hat{t}) &\longrightarrow S_0(t-\hat{t}), \\ rho_I(t|\hat{t}) &\longrightarrow \rho_0(t-\hat{t}). \end{aligned}$$

1. **Mean Firing rate:** First of all, let us define the mean interval:

$$< s >= \int_0^{\infty} sP_0(s)ds \tag{2.2.4}$$

The mean firing rate is defined as $\nu = \frac{1}{<s>}$. Hence,

$$\nu = \left[\int_0^\infty sP_0(s)ds\right]^{-1} = \left[\int_0^\infty S_0(s)ds\right]^{-1} \tag{2.2.5}$$

(the equality comes by integration by parts).

2. **Autocorrelation function:** Consider a spike train $S_j(t) = \sum_f \delta(t - t_j^{(f)})$. of length T. The autocorrelation function $C_{ii}(s)$ of the spike train is defined as the density probability of finding two spikes separated by a time interval s:

$$C_{ii}(s) =< S_i(t)S_i(t+s) >_t \tag{2.2.6}$$

where $< \cdot >_t$ denotes the average over time:

$$< f(\cdot) >_t = \lim_{T\to\infty} \frac{1}{T}\int_{-T/2}^{T/2} f(t)\,dt$$

3. **Noise spectrum:** The power spectrum (or power spectral density) of a spike train is defined as $\mathcal{P}(\omega) = \lim_{T\to\infty} \mathcal{P}_T(\omega)$ where $\mathcal{P}_T(\omega)$ is the power of a segment of length T of the spike train,

$$\mathcal{P}_T(\omega) = \frac{1}{T}\left|\int_{-T/2}^{T/2} S_i(t)e^{-i\omega t}\,dt\right|^2 \tag{2.2.7}$$

The power spectrum $\mathcal{P}(\omega)$ is the Fourier transform $\hat{C}_{ii}(\omega)$ of the autocorrelation function (Wiener-Khinchin theorem).

Proof.

$$\begin{aligned}
\hat{C}_{ii}(\omega) &= \int_{-\infty}^{\infty} < S_i(t)S_i(t+s) > e^{-i\omega s}ds \\
&= \lim_{T\to\infty}\frac{1}{T}\int_{-T/2}^{T/2} S_i(t)\int_{-\infty}^{\infty} S_i(t+s)e^{-i\omega s}dsdt \\
&= \left(\lim_{T\to\infty}\frac{1}{T}\int_{-T/2}^{T/2} S_i(t)e^{-i\omega t}dt\right)\left(\int_{-\infty}^{\infty} S_i(s)e^{-i\omega s}ds\right) \\
&= \left|\int_{-\infty}^{\infty} S_i(t)e^{-i\omega t}\,dt\right|^2
\end{aligned}$$

□

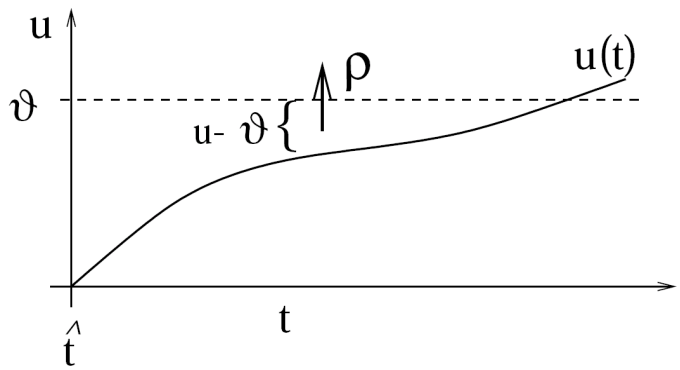


Figure 2.1: Noisy Threshold: a neuron can fire at time t with a probability $\rho(u(t)-\theta)$ even though the membrane potential u has not reached the threshold θ.

2.3 Escape noise

There are various way to introduce noise in formal spiking neuron models. In this section we focus on a "noisy threshold" (also called escape or hasard model). We are interested in the effect of the noise on the distribution of interspike intervals. In the escape model, we consider that the neuron can fire even though the formal threshold θ has not been reached or may stay quiescent event though the formal threshold has been passed.

Mathematically, we introduce an "escape rate" (or firing intensity) which depends on the momentary state of the neuron (see Fig.2.1).

2.3.1 Escape rate and hasard function

Given an input I and the firing time $\hat{t}$ of the last spike, we can compute the membrane potential of the SRM or an IF neuron from equations (2.2.1) and (2.2.2). In the deterministic model the next spike occurs when u reaches the threshold θ. In order to introduce some variability into the generation of spike, we replace the strict threshold by a stochastic firing criterion. In the noisy threshold model, spikes can occur *at any time* with a probability density depending on the position membrane potential (noisyless) w.r.t the threshold:

$$\rho = f(u-\theta). \tag{2.3.1}$$

In the point-process theory, f is known as the "stochastic intensity", and we will also refer to ρ as the firing intensity.

$$\rho_I(t|\hat{t}) = f(u(t|\hat{t})-\theta). \tag{2.3.2}$$

where ρ_I is nothing else than the hasard introduced in equation (2.2.3).

We can also in this type of considerations assume that the escape rate depends not only on u but also on its time derivative $\dot{u}$

$$\rho_I(t|\hat{t}) = f(u(t|\hat{t}), \dot{u}(t|\hat{t})). \tag{2.3.3}$$

The choice of the escape function f in (2.3.2) or (2.3.3)are arbitrary, but a reasonnable condition is to require $f \underset{u\to-\infty}{\longrightarrow} 0$. This function could also explicitly depend on the time $t - \hat{t}$ to model the refractory period.

2.3.2 Interval distribution and mean firing rate

In this section we combine the escape rate model with the concepts of renewal theory and calculate the input-dependant interval distribution $P_I(t|\hat{t})$ for escape rate models. We have:

$$P_I(t|\hat{t}) = \rho_I(t|\hat{t}) exp\left[\int_{\hat{t}}^{t} \rho_I(t'|\hat{t})\right] dt' \tag{2.3.4}$$

For the sake of readability we assume here that the function f only depends on u, so it yields:

$$P_I(t|\hat{t}) = f(u(t|\hat{t}) - \theta) exp\left(-\int_{\hat{t}}^{t} f(u(t'|\hat{t}) - \theta) dt'\right)$$

Let us now introduce refractoriness in the model. Consider u having the form:

$$u(t|\hat{t}) = \eta(t - \hat{t}) + h(t)$$

where $h(t) = \int_0^\infty \kappa(s) I(t-s) ds$. We have:

$$P_I(t|\hat{t}) = f(\eta(t - \hat{t}) + h(t) - \theta) exp\left[-\int_{\hat{t}}^{t} f(\eta(t' - \hat{t}) + h(t') - \theta) dt'\right]$$

Simulations have been made of this type of models by Gerstner and Kirstler and results are showed in [22]. we reproduce here in Fig 2.2. They show that with this model one can reproduce the ISI distribution qualitatively found in cortical neurons.

2.4 Slow noise in the parameters

In this model some parameters of the neuron model are randomly reset after each spike of the neuron. This can be an approxination for instance if the noise is slow w.r.t. the neuronal

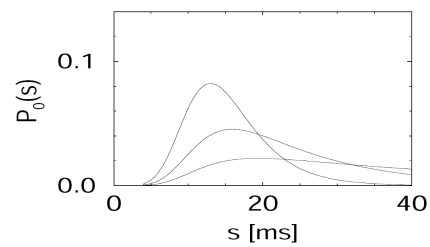


Figure 2.2: A: Iterval distribution $P_0(s)$ for a SRM_0 neuron with absolute refractory period $\Delta^{\mathrm{abs}} = 4ms$ followed by an exponentially decreasing afterpotential, stimulated by a constant current (the different curves correspond to $I_0 = 0.7$, 0.5, 0.3.

dynamics. In principle, any of the neuron parameters (threshold, membrane time constant, refractory period, ...) can be affected by this type of noise.

In this model one can compute again the ISI for instance in a SRM model subject to this type of noise.

2.5 Diffusive Noise

If we add a "noise term" in the LIF neuron equation (1.2.20), say a process $(\xi(t))_{t\geq 0}$ on the right hand side of the equation, for instance a Brownian motion (in general multiplicated by $\sigma\sqrt{\tau_m}$ where σ models the amplitude of the noise and τ_m is the time constant of the neuron, it results a *stochastic differential equation*:

$$\tau_m du_t = -u(t)\,dt + R\,I(t)\,dt + d\xi_t \tag{2.5.1}$$

which is an Ornstein-Uhlenbeck process. The neuron fires every time the membrane potential hits the barrier θ. The analysis of eq. (2.5.1) with the threshold condition is the topic of this section. But let us first introduce why one can think at this model:

2.5.1 Stochastic spike arrival

A typical neuron receives input spikes from thousands of other neurons which in turn receive inputs form their presynaptic neurons and so forth. It is obviously impossible to incorporate all neurons in the brain into a huge network model. Instead it is reasonnable ot focus on a specific

2.6 Stochastic resonance

2.7 Stochastic firing rates models

Part II

Hitting Times Approximations

Chapter 3

First passage density of a continuous gaussian process to a general boundary

As we will show in the section 6.2,hitting times in mathematical neuroscience are of particular interest, for instance to compute the sequences of spike times, which can be considered as a very interesting event of the neuronal dynamics. Those hitting times are useful for instance to study the integrate-and-fire models (see 1.2.3).

Most of the noisy models studied are defined by differential equations. If we assume that we are in a random environment, or if we model the different entries of each neuron as a noise (by a diffusion limit for instance), the dynamic of a single neuron under the firing threshold will be driven by a stochastic differential equation, and the spike time given by the hitting time of this process to the firing threshold, denoted θ in the sequel. Some models assume this threshold can be a function.

On an other hand (see chapter 5), by means of the Dubins-Schwarz theorem, the firing time of a neuron described by a diffusion SDE hitting a fixed boundary can be seen as a Gaussian process crossing a general boundary.

So the article of J. Durbin [16], *the first-passage density of a continuous Gaussian process to a general boundary* will be of particular interest for us to study.

We give in this section the main results of this articles and the proofs.

This article gives an explicit expression of the first-passage density, which is rather hard to compute usually. Then a series approximation is given, which is computationally simple and which converges under some assumptions on the barrier to the exact probability density function (pdf) of the hitting time.

3.1 Introduction

Let Y_t be a continuous Gaussian process with mean 0 [1] and covariance function $\rho(s,t)$ for $0 \leq s \leq t$:

$$\rho(s,t) := \mathbb{E}\left[Y_s\, Y_t\right] \tag{3.1.1}$$

Let $a(\cdot)$ be a deterministic function which is the boundary considered. We are interested in the hitting time

$$\tau_a := \inf\left\{t > 0;\;\; Y_t = a(t)\right\} \tag{3.1.2}$$

We assume that this hitting time τ_a is absolutely continuous with respect to Lebesgue's measure and denote $p(t)$ its density. The aim of this section is to compute a compact formula for $p(t)$ under mild restrictions on $a(t)$ and $\rho(s,t)$.

Remark 1. Strassen in its paper [35] shown that actually when $a(t)$ is of class C^1 then the first hitting time of the Brownian motion to the curve $a(t)$ has a continuous pdf w.r.t. Lebesgue's measure.

Since the process is continuous, we can assume without loss of generality that the boundary is crossed from below. This case is the case in neuroscience for instance, and the crossing from above can be obtain by replacing Y by $-Y$ and a by $-a$.

In the following section we define the main tools useful for the computation of the probability density function (pdf) and introduce the theorems of representation of these pdf.

3.2 Representation of the probability density function

Definition 3.2.1. Let $I(s,Y)$ be the indicator function:

$$\begin{aligned} I(s,Y) &:= \mathbb{1}_{\{Y \text{ did not crossed the boundary prior to time s}\}} \\ &= \mathbb{1}_{\{\tau_a(Y) \geq s\}} \end{aligned} \tag{3.2.1}$$

Let $b(t)$ be the limit, if it exists, defined by:

$$b(t) := \lim_{s \nearrow t} \frac{1}{t-s} \mathbb{E}\left[I(s,Y)\left(a(s) - Y_s\right) | Y_t = a(t)\right] \tag{3.2.2}$$

This limit can be seen as the inverse of the derivative of the conditional expectation of the function $I(s,Y)(a(s) - Y_s)$ conditionally to $Y_t = a(t)$.

[1] if not we only have to substract the mean function $m(t) := \mathbb{E}\left[Y_t\right]$ to the process Y_t and study instead of Y_t the process $Y_t - m(t)$ crossing the boundary $a(t) - m(t)$ instead of $a(t)$.

Definition 3.2.2. Let $f(t)$ be the density of Y_t on the boundary, that is:

$$f(t) := \frac{1}{\sqrt{2\pi\rho(t,t)}} e^{-\frac{a(t)^2}{2\rho(t,t)}} \tag{3.2.3}$$

Theorem 3.2.1. *Assume that:*

A.1 The boundary function $a(t)$ is continuous in $[0,t)$ and left differentiable at t.

A.2 The covariance function $\rho(s,u)$ is positive definite and has continuous first order partial derivatives on the set : $\{(s,t); 0 \leq s \leq u \leq t\}$[2]

A.3 The variance of the increment $y(t) - y(s)$ satisfies the condition:

$$\lim_{s \nearrow t} \frac{1}{t-s} \mathbb{E}\left[(y(t) - y(s))^2\right] = \lambda_t \tag{3.2.4}$$

where $0 < \lambda_t < \infty$.

Note that since $\mathbb{E}\left[(y(t) - y(s))^2\right] = \rho(t,t) - 2\rho(s,t) + \rho(s,s)$, (3.2.4) is equivalent to the requirement:

$$\lim_{s \nearrow t} \left[\frac{\partial \rho(s,t)}{\partial s} - \frac{\partial \rho(s,t)}{\partial t}\right] = \lambda_t \tag{3.2.5}$$

Then the first passage density of Y_t to the boundary $a(t)$ is given by:

$$p(t) = b(t)\, f(t) \tag{3.2.6}$$

Remark 2. The structure of the formula (3.2.6) is very simple. Nevertheless the indicator if very difficult to handle, since it is closely linked to the first hitting time of the boundary. The first function b tells us everything we need to know prior to time t and the second factor f is only an information about the local distribution of the process on the barrier. However, in the cases where the calculation of b is untractable, the formula (3.2.6) can be used to construct approximations of the hitting time.

This theorem is proved in the article [16] using the Gaussian properties of the process and referring to the behavior of the Brownian motion.

We will not show this theorem in such a general form but rather show it for the Brownian motion crossing a general boundary, just because in our further studies we will only use the "Brownian version" of this theorem.

[2] where appropriate left (resp. right) derivatives are taken at s=t (resp. $s = 0$) and $u = t$

Theorem 3.2.2. *Let a be a continuous function on $[0,\infty)$ with continuous first-order derivative on $(0,\infty)$, and such that $a(0)>0$.*

Let B be a Brownian motion with $B(0)=0$ and let $T:=\inf\{r>0;\ \ B_r=a(r)\}$.

Let p denote the probability density function of T, i.e. the Radon-Nikodym derivative of the probability distribution of T with respect to Lebesgue's measure.

Denote q the transition density function of the Brownian motion B, i.e. for all $t>0$ and $x,y\in\mathbb{R}$:

$$q(t,x,y)=\frac{1}{\sqrt{2\pi t}}\exp\left\{-\frac{(y-x)^2}{2t}\right\}. \tag{3.2.7}$$

Then the probability density function satisfies the following fixed-point equation:

$$\left(\frac{a(t)}{t}-a'(t)\right)q(t,0,a(t))=p(t)+\int_0^t p(r)\left\{\frac{a(t)-a(r)}{t-r}-a'(t)\right\}q(t-r,a(r),a(t))\,dr. \tag{3.2.8}$$

Proof. Let $t>0$ be a fixed real, and let $y>a(t)$. If $B(t)=y$, then obviously $T<t$. Thus by the strong Markov property of B, conditioning on the first hitting time of the frontier $a(t)$, say r, we have:

$$q(t,0,y)=\int_0^t p(r)q(t-r,a(r),y)\,dr \tag{3.2.9}$$

We know the function $q(t,x,y)$, and we can see easily that it is differentiable with respect to y and that this derivative is equal to $-\frac{(y-x)}{t}q(t,x,y)$. Let us now differentiate (3.2.9) with respect to y (say apply the differential operator $-\frac{\partial}{\partial y}$), we get:

$$\begin{aligned}\frac{y}{t}q(t,0,y)&=-\frac{\partial}{\partial y}\int_0^t p(r)q(t-r,a(r),y)\,dr\\&=\int_0^t p(r)\frac{y-a(r)}{t-r}q(t-r,a(r),y)\,dr\end{aligned} \tag{3.2.10}$$

Indeed, we can differentiate under the integral because the integrand, after differentiation, is integrable (because bounded on a finite interval, recall the form of the function q defined in (3.2.7)).

Let now $y\to a(t)$. Let $\delta>0$ a fixed number smaller than t. Let us denote:

$$I_1(t,\delta,y):=\int_0^{t-\delta} p(r)\frac{y-a(r)}{t-r}q(t-r,a(r),y)\,dr \tag{3.2.11}$$

$$I_2(t,\delta,y):=\int_{t-\delta}^{t} p(r)\frac{y-a(r)}{t-r}q(t-r,a(r),y)\,dr \tag{3.2.12}$$

First of all we consider the function $I_1(t,\delta,y)$. Let now $y \to a(t)$. For y close to $a(t)$ we have $|y-a(r)| \leq 1+|a(r)-a(t)|$, and we can bound the integrand with a L^1 function on $(0,t-\delta)$ so Lebesgue's theorem applies and we get the following limit:

$$I_1(t,\delta,y) \xrightarrow[y\searrow a(t)]{} \int_0^{t-\delta} p(r)\frac{a(t)-a(r)}{t-r} q(t-r,a(r),a(t))\,dr \tag{3.2.13}$$

Finally we can take the limit when $\delta \to 0$ and we get:

$$\lim_{y\searrow a(t)} \lim_{\delta\searrow 0} I_1(t,\delta,y) = \int_0^{t} p(r)\frac{a(t)-a(r)}{t-r} q(t-r,a(r),a(t))\,dr \tag{3.2.14}$$

Let us now consider I_2 defined by (3.2.12) and let us compute its limit when $y \to a(t)$ and $\delta \to 0$. To do this, let us write (3.2.12) as:

$$\begin{aligned} I_2(t,\delta,y) &:= \int_{t-\delta}^{t} p(r)\left(\frac{y-a(t)}{t-r}+\frac{a(t)-a(r)}{t-r}\right) q(t-r,a(r),y)\,dr \\ &= \int_{t-\delta}^{t} p(r)\frac{1}{\sqrt{2\pi(t-r)}}\left(\frac{y-a(t)}{t-r}+A_{r,t}\right) e^{-\frac{(y-a(t))^2}{2(t-r)}+B_{r,t,y}}\,dr \end{aligned} \tag{3.2.15}$$

where $A_{t,r} = \frac{a(t)-a(r)}{t-r}$ and $B_{r,t,y} = \frac{1}{2}A_{r,t}(a(r)+a(t)-2y)$.

Now we recall that the function

$$\frac{1}{2\pi(t-r)}\frac{y-a(t)}{t-r} exp\left\{-\frac{(y-a(t))^2}{2(t-r)}\right\}$$

tends in distribution to the Dirac function at time t (it can be seen as the density function at $t-r$ of the hitting time of $a(t)$ by a Brownian motion starting at y.

Note also that $B_{t,t,a(t)} = 0$

So we have :

$$\begin{aligned} I_2(t,\delta,y) \xrightarrow[y\searrow a(t)]{} & p(t) + \int_{t-\delta}^{t} A_{r,t}p(r)\frac{1}{\sqrt{2\pi(t-r)}} e^{\frac{1}{2}A_{r,t}(a(r)-a(t))}\,dr \\ &= p(t) + \int_{t-\delta}^{t} A_{r,t}p(r)\frac{1}{\sqrt{2\pi(t-r)}} e^{\frac{(a(r)-a(t))^2}{2(t-r)}}\,dr \end{aligned} \tag{3.2.16}$$

The integrand of the second term of formula (3.2.16) is bounded so the integral tends to 0 when $\delta \to 0$.

Eventually we get:

$$\lim_{y\searrow a(t)} \lim_{\delta\searrow 0} I_2(t,\delta,y) = p(t) \tag{3.2.17}$$

Finally we conclude using together (3.2.9), (3.2.14) and (3.2.17):
Introducing (3.2.14) and (3.2.17) in (3.2.10) we get :

$$\frac{a(t)}{t}q(t,0,a(t)) = p(t) + \int_0^t p(r)\frac{a(t)-a(r)}{t-r}q(t-r,a(r),a(t))\,dr$$

Then subtracting $a'(t)q(t,0,a(t))$ and using the integral representation of $q(t,0,a(t))$ given in (3.2.9), we have:

$$\left(\frac{a(t)}{t} - a'(t)\right)q(t,0,a(t)) = p(t) + \int_0^t p(r)q(t-r,a(r),a(t))\left(\frac{a(t)-a(r)}{t-r} - a'(t)\right)dr \tag{3.2.18}$$

□

Let us now prove the equivalence between Durbin's general representation (3.2.6) and the fixed point equation (3.2.8) in the case of the Brownian motion.

Note that the fixed point integral equation appearing makes sense intuitively because in the initial Durbin's theorem the indicator function used is the indicator of $T < s$ this will yield as we will see to the fixed point equation.

Theorem 3.2.3. *The fixed point equation* (3.2.8) *is equivalent to Durbin's equation* (3.2.6) *for the Brownian motion.*

Proof. In the case when the Gaussian process is a Brownian motion, taking the notations of theorem 3.2.1, we have:

$$f(t) = q(t,0,a(t)). \tag{3.2.19}$$

$$\begin{aligned} b(t) &= \lim_{s\nearrow t}\frac{1}{t-s}\mathbb{E}\left[\mathbb{1}_{T\geq s}\left(a(s)-Y_s\right)|Y_t = a(t)\right] \\ &= \lim_{s\nearrow t}\frac{1}{t-s}\mathbb{E}\left[(a(s)-Y_s)|Y_t = a(t)\right] - \lim_{s\nearrow t}\frac{1}{t-s}\mathbb{E}\left[\mathbb{1}_{T<s}\left(a(s)-Y_s\right)|Y_t = a(t)\right] \\ &=: E_1 + E_2 \end{aligned} \tag{3.2.20}$$

Then we know that the conditional expectation of Y_s knowing Y_t is $\frac{s}{t}Y_t$.
So the first term of (3.2.20) reads:

$$\begin{aligned} \mathbb{E}\left[Y_s|Y_t = a(t)\right] &= \frac{s}{t}a(t) \\ &= a(t) + \frac{s-t}{t}a(t) \end{aligned} \tag{3.2.21}$$

Hence we get:

$$\begin{aligned} b(t) &= \lim_{s \nearrow t} \left(\frac{a(s) - a(t)}{t - s} + \frac{a(t)}{t} \right) + E_2 \\ &= \frac{a(t)}{t} - a'(t) + E_2 \end{aligned} \tag{3.2.22}$$

Let us now compute the second expectation (E_2)

$$\begin{aligned} E_2 &= \lim_{s \nearrow t} \frac{1}{t - s} \mathbb{E}\left[\mathbb{1}_{T<s} \left(a(s) - Y_s \right) | Y_t = a(t) \right] \\ &= \lim_{s \nearrow t} \int_0^s \frac{1}{t - s} \mathbb{E}\left[(a(s) - Y_s) | Y_u = a(u), \;\; Y_t = a(t) \right] \frac{p(u)}{q(t, 0, a(t))} du \end{aligned}$$

conditioning on the first hitting time u of the process Y to the barrier $a(t)$.

Let us now compute the conditional expectation of Y_s on the set : $\{Y_u = a(u), \;\; Y_t = a(t)\}$. The strong Markov property of Y implies that the behavior of the path between u and t is unaffected by the fact that the path of Y must not cross $a(t)$ prior to u. This allows us to compute the conditional expectation, recalling that the regression coefficient of Y_s on Y_t given $Y_u = a(u)$ is $\frac{s-u}{t-u}$

$$\begin{aligned} \mathbb{E}\left[Y_s | Y_t = a(t), \;\; Y_u = a(u) \right] &= a(u) + \frac{s - u}{t - u} \left(a(t) - a(u) \right). \\ &= a(t) + \frac{s - t}{t - u} \left(a(t) - a(u) \right) \end{aligned}$$

So we get:

$$\begin{aligned} \lim_{s \nearrow t} \mathbb{E}\left[a(s) - Y_s | Y_t = a(t), \;\; Y_u = a(u) \right] &= \lim_{s \nearrow t} \frac{a(s) - a(t)}{t - s} + \frac{a(t) - a(u)}{t - u} \\ &= \frac{a(t) - a(u)}{t - u} - a'(t) \end{aligned}$$

So eventually the following formula for E_2 holds:

$$E_2 = \int_0^t \left(\frac{a(t) - a(u)}{t - u} - a'(t) \right) p(u) \frac{q(t - u, a(u), a(t))}{q(t, 0, a(t))} du \tag{3.2.23}$$

So finally, using the formula (3.2.6), we have the fixed point equation searched:

$$p(t) = \left(\frac{a(t)}{t} - a'(t)\right) q(t, 0, a(t)) + \int_0^t \left(\frac{a(t) - a(u)}{t - u} - a'(t)\right) p(u) q(t - u, a(u), a(t))\, du \quad (3.2.24)$$

□

3.3 Approximations of the probability density function

As stated in section 3.2, the indicator of (3.2.6) is difficult to handle and there is no way to compute $b(t)$ except in very particular cases.

The aim of this section is to provide approximations of the probability density functions of hitting times of the Brownian motion to a general boundary using the representations given in section 3.2.

3.3.1 A series expression

The aim of this subsection is to state and prove the series expression of the pdf searched, as Durbin did in its article [17]. In this paper the author provide a computable form of the pdf of the type:

$$p(t) = \sum_{j=1}^{k} (-1)^{j-1} q_j(t) + (-1)^k r_k(t), \quad k \in \mathbb{N} \quad (3.3.1)$$

where

$$q_j(t) = \int_0^t \int_0^{t_1} \cdots \int_0^{t_{j-2}} \left[\frac{a(t_{j-1})}{t_{j-1}} - a'(t_{j-1})\right] \times \prod_{i=1}^{j-1} \left[\frac{a(t_{i-1}) - a(t_i)}{t_{i-1} - t_i} - a'(t_{i-1})\right] f(t_{j-1}, \cdots, t_1, t)\, dt_{j-1} \cdots dt_1 \quad (t_0 = t) \quad (3.3.2)$$

and

$$r_k(t) = \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} b(t_k) \prod_{i=1}^{k} \left[\frac{a(t_{i-1}) - a(t_i)}{t_{i-1} - t_i} - a'(t_{i-1})\right] \times f(t_k, \cdots, t_1, t)\, dt_k \cdots dt_1 \quad (t_0 = t) \quad (3.3.3)$$

In (3.3.2) and (3.3.3), $a'(\cdot)$ denotes the derivative of a and $f(t_{j-1}, \cdots, t_1, t)$ denotes the joint density of $\left(Y_{t_{j-1}}, \ldots, Y_{t_1}, Y_t\right)$ on the boundary, i.e. at values $a(t_{j-1}), \ldots a(t_1), a(t)$.

Assumption 3.3.1. In all the sequel we assume that:

$$\frac{a(s)}{s} - a'(s) > 0 \quad \forall s > 0 \tag{3.3.4}$$

Remark 3. This assumption is equivalent to the requirement that the intercept at $s = 0$ of the tangent to $a(s)$ at s is strictly positive for all s.

Proof of the series expansion

Proof. [series expansion] The proof of the expansion (3.3.1) is done by induction.

First for $k = 1$, we use the fixed point equation (3.2.24) and its proof and we have:

$$\begin{aligned} b(t) &= \frac{a(t)}{t} - a'(t) - \int_0^t b(r) \left[\frac{a(t) - a(r)}{t - r} - a'(t) \right] f(r|t) dr \\ &= q_1(t) - r_1(t) \end{aligned}$$

Let us now assume that equation (3.3.1) is true for a determined k and let us prove that this equation holds for $k + 1$:

By definition (3.3.3), we have:

$$\begin{aligned} r_k(t) = \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} b(t_k) \prod_{i=1}^{k} \left[\frac{a(t_{i-1}) - a(t_i)}{t_{i-1} - t_i} - a'(t_{i-1}) \right] \\ \times f(t_k, \cdots, t_1, t)\, dt_k \cdots dt_1 \quad (t_0 = t) \end{aligned}$$

We extand this expression using the expression of b:

$$\begin{aligned} b(t_k) &= \lim_{s \nearrow t} \frac{1}{t_k - s} \mathbb{E}\left[\mathbb{1}_{T \geq s} (a(s) - Y_s) | Y_{t_k} = a(t_k) \right] \\ &= \frac{a(t_k)}{t_k} - a'(t_k) - \int_0^{t_k} b(t_{k+1}) \left[\frac{a(t_k) - a(t_{k+1})}{t_k - t_{k+1}} - a'(t_k) \right] f(t_{k+1} | t_k, \cdots, t_1) dt_{k+1} \end{aligned}$$

using the same arguments as the case $k = 1$.

So eventually we get

$$r_k(t) = q_{k+1}(t) - r_{k+1}(t)$$

So the expansion (3.3.1) is proved. □

Now the aim of the sequel is to prove that the rest (3.3.3) tends to zero so that the truncated Durbin expansion will be an approximation of the real pdf.

Error bounds and rate of convergence.

Assumption 3.3.2. We assume in this section that the boundary is wholly concave (i.e.the boundary is concave everywhere).

Then for all $s < r$, we have: $\frac{a(s)-a(r)}{r-s} - a'(r) \geq 0$, so we can see immediately from (3.3.2) and (3.3.3) that $0 \leq r_k(t) \leq q_{k+1}(t)$, provided that $0 \leq b(r) \leq \frac{a(r)}{r} - a'(r)$ which was the assumption 3.3.1.

We denote $\alpha(r, \tau)$ the tangent to $a(\tau)$ at $\tau = r$. We denote $I^*(s, Y)$ the indicator function of the event: "Y has crossed this tangent prior to time s", for $s < r$. It is well known that the first passage density of Y to a straight line boundary at time r is $\frac{d}{r}f(r)$, where $d = a(r) - a'(r)r$ and $f(r)$ is the density of Y_r on the line. (cf for instance the proof given for the Brownian with drift in section 4.2.1).

Let us now apply Durbin's general formula for the crossing of the tangent, we get:

$$\frac{a(r)}{r} - a'(r) = \lim_{s \nearrow r} \frac{1}{r-s} \mathbb{E}\left[I^*(s, Y)(\alpha(r, s) - Y_s) | Y_r = a(r)\right]$$

We compare this equation to the $b(t)$ of the "original problem":

$$b(r) = \lim_{s \nearrow r} \frac{1}{r-s} \mathbb{E}\left[I(s, Y)(a(s) - Y_s) | Y_r = a(r)\right]$$

Now, since the boundary is wholly concave, then tangent is always "above" the boundary. Every path which fails to cross $a(t)$ necessary fails to cross $\alpha(r, s)$ (or each path crossing the tangent has necessary already crossed the boundary). Mathematically, this remark means that

$$I(s, Y) \leq I^*(s, Y)$$

From the concavity assumption, we also have that $a(s) \leq \alpha(r, s)$ for all $s < r$. It follows that $b(r) \leq \frac{a(r)}{r} - a'(r)$ comparing the two expressions given above together with those simple inequalities.

So we can conclude using the definition of the general term and the rest of the Durbin's extension that $r_k(t) \leq q_{k+1}(t)$ for all k and t.

We note also that from the definition of Durbin's extension (3.3.1) that $r_k(t) = q_k(t) - r_{k-1}(t) \leq q_k(t)$

Proof.

$$\begin{aligned} p(t) &= \sum_{j=1}^{k}(-1)^{j-1}q_j(t) + (-1)^k r_k(t) \\ &= \sum_{j=1}^{k-1}(-1)^{j-1}q_j(t) + (-1)^{k-1}q_k(t) + (-1)^k r_k(t) \\ &= \sum_{j=1}^{k-1}(-1)^{j-1}q_j(t) + (-1)^{k-1}r_{k-1}(t) \end{aligned}$$

Hence we have $r_k(t) = q_k(t) - r_{k-1}(t) \leq q_k(t)$. □

This means that when computing the series, the error is always bounded by the last term computed.

Assumption 3.3.3. Assume now that the boundary is wholly convex.

We can make the same analysis between two integral variables t_i, t_{i+1}, we have the following similar properties:

- $\frac{a(t_{i-1})-a(t_i)}{t_{i-1}-t_i} - a'(t_{i-1}) \leq 0$
- using assumption 3.3.1 $q_1 \geq 0$, $q_2 \leq 0$, $q_3 \geq 0$, and so on, thus the series $\sum_{j=1}^{k}(-1)^{j-1}q_j(t)$ is a series of non-negative terms.
- $r_k(t) \geq q_{k+1}(t)$ so the bound obtain for the concave case does not apply.

In the convex case we do not consider the tangent to the function but the cord from the point $(0, a(0))$ to $(r, a(r))$. By the convexity of $a(t)$ we know that the function $a(u)$ is always underneath this cord for $0 \leq u \leq r$. Let $\beta(s,\tau)$ be the line joining those two points and I^{**} denote the indicator of the event :"Y has crossed $\beta(s,\tau)$ prior to time s". Here as before we only have to know the first-passage time of the Brownian to an affine curve, which is $\frac{a(0)}{r}f(r)$.

So we get:

$$\frac{a(0)}{r} = \lim_{s \nearrow r} \frac{1}{r-s}\mathbb{E}\left[I^{**}(s,Y)(\beta(r,s) - Y_s)|Y_r = a(r)\right]$$

Here every path crossing a prior to time r must have crossed $\beta(r,\tau)$. so $I(s,Y) \leq I^{**}(s,Y)$ for all $s < r$, and we have $a(s) \leq \beta(r,s)$. Hence for the concave case, $b(r) \leq \frac{a(0)}{r}$.

Finally, let u_k denote the integral:

$$u_k(t) := \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} \frac{a(0)}{t_k} \prod_{i=1}^{k} \left[\frac{a(t_{i-1}) - a(t_i)}{t_{i-1} - t_i} - a'(t_{i-1}) \right] \times f(t_k, \cdots, t_1, t)\, dt_k \cdots dt_1 \quad (t_0 = t)$$

we have $|r_k(t)| \leq |u_k(t)|$

Theorem 3.3.1. *Under the assumption 3.3.2 or 3.3.3, we have*

$$r_k(t) \xrightarrow[k\to\infty]{} 0 \tag{3.3.5}$$

In the proof of the theorem we will use the following lemma, we state and prove before the proof of the main theorem.

Lemma 3.3.2. Let $W := (W_t)_{t\geq 0}$ be a standard Brownian motion. Then $(\xi_t)_{t\leq 0} := (W_{-t})_{t\leq 0}$ is a Markov process with the inhomogeneous transition density function :

$$p(s,x,t,y) = \frac{1}{\sqrt{2\pi t(t-s)/s}} e^{-(y-\frac{t}{s}x)^2/2[\frac{t}{s}(t-s)]} \tag{3.3.6}$$

Proof. The Brownian motion is clearly a Markov process, with transition density function:

$$p(s,x,t,y) = \frac{1}{\sqrt{2\pi(t-s)}} e^{-\frac{(y-x)^2}{2(t-s)}}$$

It is clear that $\xi_t := W_{-t}$ is also a Markov process. Indeed, let $t \leq 0$, $A \in \mathcal{F}^{\xi}_{\geq t}$ where $\mathcal{F}^{\xi}$ is the filtration associated to the process ξ. Then $A \in \mathcal{F}^{W}_{\leq -t}$.

$$\begin{aligned}
\mathbb{P}\left[A|\mathcal{F}^{\xi}_{\geq t}\right] &= \mathbb{P}\left[A|\mathcal{F}^{W}_{\leq -t}\right] \\
&= \mathbb{P}\left[A|\mathcal{F}^{W}_{=-t}\right] \quad \text{by the Markov property of } W \\
&= \mathbb{P}\left[A|\mathcal{F}^{\xi}_{=t}\right]
\end{aligned}$$

which ends the proof of the Markovian property of ξ.

Let us now compute the transition function.

Let $s < t \leq 0$. The joint density p_{ξ_s,ξ_t} is given by:

$$\begin{aligned}
p_{\xi_s,\xi_t}(x,y) &= p_{W_{-s},W_{-t}}(x,y) \\
&= \frac{1}{\sqrt{-2\pi t}\sqrt{2\pi(-s+t)}} e^{-y^2/(-2t)} e^{-(x-y)^2/(-s+t}
\end{aligned}$$

So now let us compute the conditional probability density function:

$$\begin{aligned} p_{\xi_t}(y|\xi_s = x) &= \frac{p_{\xi_s,\xi_t}(x,y)}{p_{\xi_s}(x)} \\ &= \frac{1}{\sqrt{2\pi t(t-s)/s}} e^{-\frac{(y-(t/s)x)^2}{2(t/s)(t-s)}} \end{aligned}$$

□

Proof. [Theorem 3.3.1] Recall that

$$r_k(t) = \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} b(t_k) \prod_{i=1}^{k} \left[\frac{a(t_{i-1}) - a(t_i)}{t_{i-1} - t_i} - a'(t_{i-1}) \right] \times f(t_k, \cdots, t_1, t)\, dt_k \cdots dt_1 \quad (t_0 = t)$$

Let us denote $\gamma(t)$ the maximum of $|\frac{a(r)-a(s)}{r-s} - a'(r)|$ for $0 < s < r \leq t$. We have:

$$\begin{aligned} |r_k(t)| &\leq \gamma(t)^k \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} b(t_k) f(t_k, \cdots, t_1, t)\, dt_k \cdots dt_1 \\ &\leq \gamma(t)^k \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-1}} b(t_k) f(t_k | t_{k-1} \cdots, t_1, t) f(t_{k-1} \cdots, t_1, t)\, dt_k \cdots dt_1 \\ &\leq \gamma(t)^k \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-2}} f(t_{k-1} \cdots, t_1, t)\, dt_{k-1} \cdots dt_1 \\ &\leq \gamma(t)^k \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-2}} \prod_{i=1}^{k-1} f(t_i | t_{i-1})\, dt_{k-1} \cdots dt_1 \quad (t_0 = 0) \end{aligned}$$

For the last equality we have used the Markovian property of $(Y_{t-s})_{s\geq 0}$ conditionally on Y_t which is a direct consequence of lemma 3.3.2. We also use this lemma again to find the conditional density $f(t_i|t_{i-1})$ (here note that $t_i \leq t_{i-1}$).

$$f(t_i|t_{i-1}) = \frac{1}{\sqrt{2\pi t_i(1 - ti/t_{i-1})}} e^{-\frac{(a(t_i)-a(t_{i-1})t_i/t_{i-1})^2}{t_i(1-ti/t_{i-1})}}$$

So we get:

$$|r_k(t)| \leq \gamma(t)^k (2\pi)^{-(k-1)/2} \int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-2}} \prod_{i=1}^{k-1} \frac{1}{\sqrt{t_i(1 - \frac{t_i}{t_{i-1}})}} dt_{k-1} \cdots dt_1 \tag{3.3.7}$$

Let us now compute the sequence of integrals. Fist put $x = \frac{t_i}{t_{i-1}}$. We have:

$$\int_0^{t_{k-2}} \frac{1}{\sqrt{t_{k-1}(1-\frac{t_{k-1}}{t_{k-2}})}} dt_{k-1} = \sqrt{t_{k-2}} \int_0^1 \frac{1}{\sqrt{x(1-x)}}\, dx = \pi\sqrt{t_{k-2}}$$

We then substitute this expression in the integral w.r.t t_{k-2}, and get:

$$\begin{aligned}\pi \int_0^{t_{k-3}} \sqrt{t_{k-2}} \frac{1}{\sqrt{t_{k-2}(1-\frac{t_{k-2}}{t_{k-3}})}}\, dt_{k-2} &= \pi t_{k-3} \int_0^1 \frac{1}{\sqrt{(1-x)}}\, dx \\ &= 2\pi t_{k-3}\end{aligned}$$

We can continue this reduction integral after integral and we will always get an expression of the type:

$$\begin{aligned}\pi \int_0^{t_{i-1}} \sqrt{t_i^{k-i-2}} \frac{1}{\sqrt{t_{k-2}(1-\frac{t_i}{t_{i-1}})}}\, dt_i &= t_{i-1}^{(k-i)/2} \int_0^1 \frac{1}{\sqrt{x^{k-i-2}(1-x)}}\, dx \\ &= B\left(\frac{k-i}{2}, \frac{1}{2}\right) t_{i-1}^{(k-i)/2} \\ &= \frac{\Gamma(\frac{k-i}{2})\Gamma(\frac{1}{2})}{\Gamma(\frac{k-i+1}{2})} t_{i-1}^{(k-i)/2}\end{aligned}$$

for all $i = (k-1), \ldots, 1$.

Finally we have :

$$\begin{aligned}&\int_0^t \int_0^{t_1} \cdots \int_0^{t_{k-2}} \prod_{i=1}^{k-1} \frac{1}{\sqrt{t_i(1-\frac{t_i}{t_{i-1}})}} dt_{k-1} \cdots dt_1 \\ &\qquad = \prod_{i=1}^{k-1} \frac{\Gamma(\frac{k-i}{2})}{\Gamma(\frac{k-i+1}{2})} (\pi t)^{(k-i)/2} = \frac{\pi^{k/2}}{\Gamma(\frac{k}{2})} t^{(k-1)/2}\end{aligned}$$

And finally substituting in (3.3.7) we have :

$$|r_k(t)| \leq \gamma(t)^k 2^{-(k-1)/2} \sqrt{\pi} \frac{1}{\Gamma(\frac{k}{2})} t^{(k-1)/2} \tag{3.3.8}$$

And we conclude using Stirling's formula stating that $\Gamma(\frac{k}{2})$ increases much more rapidly than any kth power of a finite quantity as $k \to \infty$, thus $|r_k(t)| \xrightarrow[k\to\infty]{} 0$, and the series expansion converge, and

$$p(t) = \sum_{j=1}^{\infty} (-1)^{j-1} q_j(t) \tag{3.3.9}$$

□

Remark 4. The truncated series of (3.3.9) is an approximation of the pdf $p(t)$, but we don't have any information on the rate of convergence of the series.

3.3.2 An Iterative Approximation

In this section we use the fixed point expression (3.2.24) to get an iterative approximation of the pdf $p(t)$.

Recall that:

$$p(t) = \left(a(t) + \frac{s-t}{t} a(t)\right) q(t, 0, a(t)) + \int_0^t \left(\frac{a(t) - a(u)}{t-u} - a'(t)\right) p(u) q(t-u, a(u), a(t))\, du \tag{3.3.10}$$

Here $p(t)$ is a $\mathbb{L}^1(\mathbb{R}^+, dt)$ function since it is a probability density with respect to Lebesgue's measure. $\mathbb{L}^1(\mathbb{R}^+, dt)$ is a Banach space.

Let us denote $T : \mathbb{L}^1 \to \mathbb{L}^1$ the operator defined for all f in $\mathbb{L}^1$ by:

$$Tf(t) := \left(a(t) + \frac{s-t}{t} a(t)\right) q(t, 0, a(t)) + \int_0^t \left(\frac{a(t) - a(u)}{t-u} - a'(t)\right) f(u) q(t-u, a(u), a(t))\, du \tag{3.3.11}$$

Let us denote for the sake of simplicity

$$A(t) := \left(a(t) + \frac{s-t}{t} a(t)\right) q(t, 0, a(t))$$
$$\Phi(t, u) := \left(\frac{a(t) - a(u)}{t-u} - a'(t)\right) q(t-u, a(u), a(t))$$

So the operator T reads:

$$Tf(t) := A(t) + \int_0^t \Phi(t, u) f(u)\, du \tag{3.3.12}$$

which is known as a linear integral operator (or a linear Volterra integral operator).

The pdf we search is a fixed point of T, i.e. $p = Tp$.

The method of approximation (refered as Picard's method) consists in defining a sequence of $\mathbb{L}^1$ functions defined by recurrence, and prove that this sequence converge to the fixed point

Let $f \in \mathbb{L}^1$ be the initial condition of the sequence. Put $p_0 := f$. We defined by induction the sequence p_n by:

$$p_{n+1} = Tp_n \tag{3.3.13}$$

Let us now recall the classical definitions for an operator in a Banach space K. For more details on this subject we refer to [4].

Definition 3.3.1. For an operator $T : K \to K$, we say it is :

1. contractive with contractivity constant $\alpha \in [0, 1)$ if
$$\|T(u) - T(v)\|_K \leq \alpha \|u - v\|_K \ \ \forall\, u, v, \in K$$
2. non expansive if
$$\|T(u) - T(v)\|_K \leq \|u - v\|_K \ \ \forall\, u, v, \in K$$
3. Lipschitz continuous if $\exists L \geq 0$ such that:
$$\|T(u) - T(v)\|_K \leq L\|u - v\|_K \ \ \forall\, u, v, \in K$$

Theorem 3.3.3. [Banach fixed-point theorem] *Assume that K is a non-empty closed set in a Banach space V and that $T : K \to K$ is a contractive mapping with contractivity constant $\alpha \in [0, 1)$. Then the following results hold:*

1. Existence and uniqueness: *There exists a unique $u \in K$ such that*
$$u = T(u).$$

2. Convergence and error estimates of the iteration: *For any $u_0 \in K$ the sequence $\{u_n\} \subset K$ defined by $u_{n+1} = T(u_n)$ is a Cauchy sequence and converges to u:*
$$\|u_n - u\| \xrightarrow[n\to\infty]{} 0$$
For the error, the following bounds are valid:

$$\begin{aligned}
\|u_n - u\|_V &\leq \frac{\alpha^n}{1-\alpha}\|u_0 - u_1\|_V \\
\|u_n - u\|_V &\leq \frac{\alpha}{1-\alpha}\|u_{n-1} - u_n\|_V \\
\|u_n - u\|_V &\leq \alpha\|u_{n-1} - u\|_V
\end{aligned}$$

The proof of this theorem is very classical and we will not reproduce it here. It is based on proving that the sequence u_n is a Cauchy sequence. The unicity is given by the contractance of the operator and the existence by the convergence of u_n.

In the representation of the pdf of the first hitting time, we have a linear integral equation. For instance if we assume that $u \in C([a,b],[a,b])$ for fixed reals a and b (wich is not the case in general) and with the uniform norm, the operator T is Lipschitz continuous with Lipschitz constant α:

$$\alpha := \max_{a \leq x \leq b} \int_a^b |\Phi(t,u)| du$$

So the operator is contractant if $\alpha \in [0,1)$.

This approach has not been studied yet, but is a way of approximating the pdf p without any assumption on the convexity (or concavity) of the boundary a. This will allow us to study a sinusoïdal entry for a neuron, which is often the case of study in customary neuroscience model experiments. This is also the case studied in the publication for the NeuroComp conference [18] using the Durbin expansion (where we do not have any proof of the convergence of the series) and the Monte-Carlo method.

3.4 Application to some simple cases

In this section we show that the first term of Durbin's development (i.e. putting $I \equiv 1$) gives the real pdf of the hitting time, in the case of the Brownian motion crossing a constant boundary,

3.4.1 Hitting time of the Brownian Motion to a linear boundary

In its article [16], Durbin proves that the equation (3.2.6) where he replaces the indicator function by the constant function 1 gives directly the true pdf of the Brownian motion crossing a linear boundary, wich is well known analytically (see 4.2.1 where we compute this formula).

This idea is exploited by the author to provide an approximation of the hitting time when the boundary becomes increasingly remote.

In the following section we show for a more complex problem that omitting the indicator function in Durbin's function $b(t)$ give us the true pdf for the Ornstein-Uhlenbeck process crossing the constant frontier 0.

3.4.2 Hitting time of the Brownian Motion to an constant boundary

In this section we consider an Ornstein-Uhlenbeck process X. Let σ and α be two postive numbers and $B := (B_t)_t$ be a standard Brownian motion. The associated Ornstein-

Ulhenbeck process $(X_t)_t$ is defined to be the unique solution of the stochastic differential equation:

$$\begin{cases} dX_t = -\alpha X_t dt + \sigma dB_t \\ X_0 = x_0 \quad > 0 \end{cases} \tag{3.4.1}$$

We know that the probability density function of the hitting time of the constant barrier 0 can be computed ([1, 29]) directly. Note that this is a very particular frontier (it is the "equilibrium state" of the process). For any other frontier there is no closed form for this density function.

The formula of this pdf is given by:

$$p(t) = \frac{x_0}{\sigma\sqrt{2\pi}} \exp\left\{-\frac{x_0^2 \alpha e^{-\alpha t}}{2\sigma^2 sh(\alpha t)} + \frac{\alpha t}{2}\right\} \left(\frac{\alpha}{sh(\alpha t)}\right)^{\frac{3}{2}} \tag{3.4.2}$$

We prove that this result is the first Durbin approximation of this pdf.

First of all, using the notations of Durbin's theorem about the gaussian processes, we recall that:

$$X_t = x_0 e^{-\alpha t} + \sigma \int_0^t e^{-\alpha(t-s)dW_s} \tag{3.4.3}$$

From this equation we can state that:

- X_t is a gaussian process and for all fixed $t \geq 0$, we have:

$$X_t \sim \mathcal{N}(x_0 e^{-\alpha t}, \sigma^2(1 - e^{-2\alpha t}),$$

- the covariance function is given by:

$$\rho(s,t) = \sigma^2 \left[e^{-\alpha|t-s|} - e^{-\alpha(t+s)}\right] \tag{3.4.4}$$

Proof. Let $s \leq t$. we have:

$$\begin{aligned} \rho(s,t) &= \sigma^2 \mathbb{E}\left[\int_0^t \int_0^s e^{-\alpha(t+s)} e^{-\alpha(u+v)} dW_u dW_v\right] \\ &= 2\sigma^2 e^{-\alpha(t+s)} \int_0^s e^{-2\alpha u} du \\ &= \frac{\sigma^2}{\alpha}(e^{-\alpha|t-s|} - e^{-\alpha(t+s)}) \end{aligned}$$

□

- it admits the stationnary distribution $\mathcal{N}(0, \sigma^2)$. (apply Kolmogorov -or Focker-Planck - equation).

So this is a Gaussian process. To get into the framework of Durbin's theorem we will not consider the process X_t (because it is not centered) but the process $X_t - x_0 e^{-\alpha t}$. This process is centered, starts form 0 and has to reach the frontier $-x_0 e^{-\alpha t}$, so the crossing will occur from above. To have a process crossing the frontier from below, let us define the gaussian process Y such that $Y_t = x_0 e^{-\alpha t} - X_t$. This is a centered Gaussian process, and we are searching the hitting time of the barrier $a(t) x_0 e^{-\alpha t}$ which is stricly above 0 at $t = 0$ so the process Y will cross $a(t)$ from below. The hitting time of Y_t to $a(t)$ has the same law as the hitting time of X to 0.

Now, we show that what we will call the "first approximation" of Durbin, i.e Durbin's formula replacing the indicator function by one, gives us the real pdf of this process (3.4.2).

Proposition 3.4.1. Let b_1 be the "first" approximation of Durbin's function $b(t)$, defined by:

$$b_1(t) := \lim_{s \nearrow t} \frac{1}{t-s} \mathbb{E}\left[(a(s) - Y_s) | Y_t = a(t)\right] \tag{3.4.5}$$

$$= \frac{a(t)}{\rho(t,t)} \left. \frac{\partial \rho(s,t)}{\partial s} \right|_{s=t} - a'(t) \tag{3.4.6}$$

Then we have

$$p(t) = b_1(t) f(t) \tag{3.4.7}$$

Proof. Recall that:

$$Y_t := x_0 e^{-\alpha t} - X_t$$

The process Y is a centered gaussian process of covariance function ρ starting from 0. The boundary we consider now is the function $a(t) := x_0 e^{-\alpha t}$. We can easily see that assumptions A.1 and A.2 of theorem 3.2.1 are satisfied :

1. the boundary function $a(t) = x_0 e^{-\alpha t}$ is continuous on $[0, t)$ and left differentiable at t
2. The covariance function is given by (3.4.4), and it is clear that it is positive definite with continuous first-order derivatives.
3. The assumption A.3 can be shown using:

$$\lim_{s \nearrow t} \left[\frac{\partial \rho(s,t)}{\partial s} - \frac{\partial \rho(s,t)}{\partial t} \right] = 2\sigma^2$$

Let us now compute the function b_1: we have:

- $\rho(t,t) = \frac{\sigma^2}{\alpha}(1 - e^{-2\alpha t})$
- $\frac{\partial \rho(s,t)}{\partial s}\Big|_{s=t} = \sigma^2 \alpha (1 + e^{-2\alpha t})$
- $a'(t) = -\alpha x_0 e^{-\alpha t}$

So

$$\begin{aligned}
b_1(t) &= \lim_{s \nearrow t} \frac{1}{t-s} \mathbb{E}\left[(a(s) - Y_s)|Y_t = a(t)\right] \\
&= \lim_{s \nearrow t} \left(a(s) - \frac{\rho(s,t)}{\rho(t,t)} a(t) \right) \\
&= \lim_{s \nearrow t} \left(a(s) - a(t) + \frac{\rho(t,t) - \rho(s,t)}{\rho(t,t)} a(t) \right) \\
&= -a'(t) + \frac{1}{\rho(t,t)} \frac{\partial \rho(s,t)}{\partial s}|_{s=t} a(t) \\
&= 2\alpha x_0 \frac{e^{-\alpha t}}{1 - e^{-2\alpha t}} \qquad\qquad = x_0 \frac{\alpha}{sh(\alpha t)}
\end{aligned}$$

Let us now compute the function $f(t)$ (distribution of Y on the barrier):

$$\begin{aligned}
f(t) &= \frac{1}{\sqrt{2\pi\rho(t,t)}} e^{-\frac{a(t)^2}{2\rho(t,t)}} \\
&= \frac{1}{\sigma\sqrt{2\pi(1 - e^{-2\alpha t}/\alpha}} exp\left\{ -\frac{x_0^2 e^{-2\alpha t}}{2sigma^2(1 - e^{-2\alpha t})/\alpha} \right\} \\
&= \frac{\sqrt{\alpha} e^{\frac{\alpha}{2}t}}{\sigma\sqrt{2\pi sh(\alpha t)}} exp\left\{ -\frac{x_0^2 e^{-2\alpha t}}{2sigma^2(1 - e^{-2\alpha t})/\alpha} \right\}
\end{aligned}$$

So eventually we get:

$$\begin{aligned}
p_1(t) &= b_1(t) f(t) \\
&= x_0 \left(\frac{\alpha}{sh(\alpha t)} \right)^{\frac{3}{2}} \frac{1}{\sigma\sqrt{2\pi}} exp\left\{ -\frac{x_0^2 e^{-2\alpha t}}{2sigma^2(1 - e^{-2\alpha t})/\alpha} + \frac{\alpha}{2} t \right\} \\
&= p(t) \quad \text{using formula as (3.4.2)}
\end{aligned}$$

So here replacing the indicator by 1 does not change anything and we still get the good formula.

□

Chapter 4

Computing the Laplace transform of the first hitting time

In this chapter we give some formulas and proof for computing the Laplace transforms of some hitting times for diffusion process to a constant or moving boundary. We refer to these formulas as Feynman-Kac formulas.

Then we apply this technique to compute the Laplace transforms of Hitting times for some classical processes (Brownian motion, Brownian motion with drift and Ornstein-Uhlenbeck process. We also use this characterization to prove the convergence in law and almost surely of those hitting time of a constant barrier when the starting point of the process tends to the barrier.

4.1 Feynman-Kac formulas and Laplace transforms of Hitting Times

Let $X := (X_t, t \geq 0)$ be a multi-dimensional diffusion process of infinitesimal generator $\mathcal{L}$ and $B := ((B_t^{(i)})_{t\geq 0})_{i=1,\ldots,d}$ be a multi-dimensionnal Brownian motion. The aim of this section is to prove a link between some functionals of X and PDEs. For more details on diffusion processes we refer to [23, 5, 36]. The diffusion process studied here satisfies the equation:

$$dX_t = b(X_t)dt + \sigma(X_t)dB_t \tag{4.1.1}$$

We assume that b and σ are bounded and at least $\mathcal{C}^1$. Let $\mathcal{L}$ be the diffusion operator associated to the diffusion process (4.1.1)

$$\mathcal{L}f(x) := \frac{1}{2}\sum_{i,j=1}^{d} a_{i,j}(x)\frac{\partial^2}{\partial x_i \partial x_j}f(x) + (b(x)\cdot\nabla)f(x) \tag{4.1.2}$$

where $a(x) = (a_{i,j}(x))_{i,j} \in \mathcal{M}_d$ is the symmetrical matrix defined by $a(x) = \sigma(x)\sigma^T(x)$. In all this section we assume that the operator $\mathcal{L}$ is uniformly elliptic, i.e.

$$\exists \Lambda > 0 \quad \sum_{i,j=1}^{d} a_{i,j}(x)\xi_i\xi_j \geq \Lambda \sum_{i=1}^{d} \xi_i^2 \qquad \forall x, \xi \in \mathbb{R}^d \tag{4.1.3}$$

In all the section, we'll use a real function, denoted q, and called potential, in reference with the Schrödinger theory.

We consider the operator, called *Schrödinger operator*, defined by :

$$\mathcal{G}u(x) := \mathcal{L}u(x) + q(x)u(x) \tag{4.1.4}$$

The goal of the section is to characterize solutions of PDEs involving the operator $\mathcal{G}$ of (4.1.4) in terms of X, and eventually to characterize using this method the Laplace transforms of hitting times of a one dimensional diffusion process. The formulas obtained this way are called Feyman-Kac formulas.

4.1.1 Some Feynman-Kac formulas

In this section we state and prove some Feynman-Kac formulas linking solution of some PDEs and the diffusion process X.

Theorem 4.1.1. *Let D be a smooth bounded domain, q a $\mathcal{C}^2$ function on $\bar{D}$, f a continuous function on ∂D. Let τ_D be the first hitting time of the border of D (∂D) by the process X :*

$$\tau_D := \inf\{t > 0; X_t \in \partial D\} = \inf\{t > 0; X_t \in \partial D\}$$

Let u be the solution of the PDE equation with Dirichlet condition :

$$\begin{cases} \mathcal{L}u(x) + q(x)u(x) & = 0 \quad \forall x \in D \\ u(x) = f(x) \quad \forall x \in \partial D \end{cases} \tag{4.1.5}$$

If q is such that :

$$\mathbb{E}_x\left[e^{\int_0^{\tau_D} q^+(X_s)ds}\right] < \infty \tag{4.1.6}$$

where $q^+(x) := max(q(x), 0)$.

Then u solution of (4.1.5) *can be written :*

$$u(x) = \mathbb{E}_x \left[f(X_{\tau_D}) e^{\int_0^{\tau_D} q(X_s)ds} \right] \tag{4.1.7}$$

Proof. Let $Y_t := \int_0^t q(X_s)ds$ and consider the stochastic process $e^{Y_t}u(X_t)$. Itô's formula gives the following expression for this process :

$$\begin{aligned} e^{Y_t}u(X_t) &= u(X_0) + \int_0^t e^{Y_s}u(X_s)dY_s + M_t + \int_0^t e^{Y_s}\mathcal{L}u(X_s)ds \\ &= u(X_0) + M_t + \int_0^t e^{Y_s}(\mathcal{L}u(X_s) + q(X_s)u(X_s))ds \\ &= u(X_0) + M_t + \int_0^t e^{Y_s}\mathcal{G}u(X_s)ds \qquad (4.1.8) \\ & \qquad (4.1.9) \end{aligned}$$

where M_t denotes a local martingale associated, which reads :

$$M_t = \sum_{i=1}^d \int_0^t e^{Y_s} b_i(X_s) \frac{\partial u}{\partial x_i}(X_s)ds$$

Then let stop the process under consideration at the stopping time τ_D. Let $S_n := \inf\{t; \mathrm{dist}(X_t, \partial D) < 1/n\}$. We clearly have $S_n \underset{n\to\infty}{\nearrow} \tau_D$. Then since $u \in \mathcal{C}^2(\bar{D})$ we have $M_{t\wedge S_n}$ is a martingale for all $n \in \mathbb{N}$. Let us take the expectation and apply the optimal stopping theorem to (4.1.8). Stopping the process at time S_n ensures us that $\mathcal{G}u(X_s)$ is 0 because X_s is always inside the domain D.

$$\begin{aligned} e^{Y_{t\wedge S_n}}u(X_{t\wedge S_n}) &= u(X_0) + M_{t\wedge S_n} \quad \text{and taking the expectation} \\ \mathbb{E}_x \left[e^{Y_{t\wedge S_n}}u(X_{t\wedge S_n}) \right] &= u(x) \end{aligned}$$

Finally, letting $n \to \infty$ and using Lebesgue's theorem (the function u is bounded inside the domain D and the hypothesis (4.1.6) ensures us to have a $\mathbb{L}^1$ bound) we get :

$$\mathbb{E}_x \left[e^{Y_{t\wedge\tau_D}}u(X_{t\wedge\tau_D}) \right] = u(x) \quad \forall t > 0$$

We can conclude letting $t \to \infty$, since the expectation converges by Lebesgue's theorem. □

Theorem 4.1.2. *Under suitable conditions on q, D and g , the solution of*

$$\begin{cases} \mathcal{L}u(x) + q(x)u(x) & = -g(x) \quad \forall x \in D \\ u|_{\partial D} & = 0 \end{cases} \tag{4.1.10}$$

is given by

$$u(x) = \mathbb{E}_x \left[\int_0^{\tau_D} g(X_s) e^{\int_0^s q(X_r)dr} \, ds \right] \tag{4.1.11}$$

Theorem 4.1.3. *Under suitable conditions on q, f and D , the solution of*

$$\begin{cases} \frac{\partial u}{\partial t} & = \mathcal{L}u(x) + q(x)u(x) \quad \forall x \in \mathbb{R}^d \\ u(x,0) & = f(x) \end{cases} \tag{4.1.12}$$

is given by

$$u(x,t) = \mathbb{E}_x \left[f(X_t) e^{\int_0^t q(X_s)ds} \right] \tag{4.1.13}$$

The proofs of theorems 4.1.2 and 4.1.3 are very similar to that of theorem 4.1.1, thus left to the reader.

4.1.2 Application : Characterization of hitting times for constant boundaries

Let $X = (X_t;\ t > 0)$ be a one-dimensional diffusion process given by the equation :

$$dX_t = b(X_t)dt + \sigma(X_t)dB_t \tag{4.1.14}$$

where $B = (B_t)_{t \geq 0}$ is a standard one-dimensional Brownian motion.

Let T_{x_0} be the first passage-time of X to the fixed barrier x_0 and let $u_\lambda(x)$ be the Laplace transform of T_{x_0} conditionally on the fact that $X_0 = x$.

$$T_{x_0} := \inf\{t > 0; X_t = x_0\}$$

$$u_\lambda(x) := \mathbb{E}_x \left[e^{-\lambda T_{x0}} \right] \quad , \ \lambda \geq 0 \tag{4.1.15}$$

Theorem 4.1.4. *Assume that $x < x_0$. The Laplace transform $u_\lambda(x)$ is solution of the following PDE together with limit conditions :*

$$\begin{cases} \mathcal{L}u_\lambda(x) - \lambda u_\lambda(x) = 0 \\ u_\lambda(x_0) = 1 \\ \lim\limits_{x \to -\infty} u_\lambda(x) = 0 \end{cases} \tag{4.1.16}$$

Remark 5. The case $x > x_0$ can be treated in the same way with only a few changes as stated in the beginning of the section.

Proof. In the book of Bass [5, Theorem IV.3.4], a proof totally based on theorem 4.1.1 ([5, Theorem II.4.1]) is given, taking $D = (-\infty, x_0)$. But obviously, this domain in not bounded so we need further elements.

With the notations of the proof of theorem 4.1.1, we have $Y_t = -\lambda t$.

Necessary condition:

We assume that the solution of equation (4.1.16) exists and is regular. Let us denote

$$\tau_{x_0}^n := \inf\{t > 0; X_t = x_0 \text{ or } X_t = -n\}$$

Then using Itô's formula stopped at time $\tau_{x_0}^n$ together with the existence assumption of a regular solution, we get that the local martingale of Itô's extension is a real martingale, so when we take the expectation it holds :

$$\mathbb{E}_x\left[e^{-\lambda t\wedge\tau_{x_0}^n} u(X_{t\wedge\tau_{x_0}^n})\right] = u_\lambda(x)$$

We assumed the existence of a solution u to equation (4.1.16), so by definition u is regular on $(-\infty, x_0)$ and tends to 0 in $-\infty$, and to 1 at x_0 so is bounded on its definition domain. Therefore we can apply Lebesgue's convergence theorem to let $t \to \infty$:

$$\begin{array}{ccc}
t\wedge\tau_{x_0}^n & \xrightarrow{a.s.} & \tau_{x_0}^n \\
X_{t\wedge\tau_{x_0}^n} & \xrightarrow[\text{(path continuity)}]{a.s.} & X_{\tau_{x_0}^n} = x_0 Y - n(1-Y) \\
u_\lambda(X_{t\wedge\tau_{x_0}^n}) & \xrightarrow[\text{(regularity of } u_\lambda)]{a.s.} & u_\lambda(X_{\tau_{x_0}^n}) = u_\lambda(x_0)Y + u_\lambda(-n)(1-Y)
\end{array}$$

where $Y = \mathbb{1}_{\tau_{x_0}<\tau_{-n}}$.

So we have:

$$\mathbb{E}_x\left[e^{-\lambda\tau_{x_0}} u_\lambda(x_0)\mathbb{1}_{\tau_{x_0}<\tau_{-n}}\right] + \mathbb{E}_x\left[e^{-\lambda\tau_{-n}} u_\lambda(-n)\mathbb{1}_{\tau_{x_0}>\tau_{-n}}\right] = u_\lambda(x) \tag{4.1.17}$$

We know from eq.(4.1.16) that $u_\lambda(x) \xrightarrow[x\to\infty]{} 0$. So the term

$$\mathbb{E}_x\left[e^{-\lambda\tau_{-n}} u_\lambda(-n)\mathbb{1}_{\tau_{x_0}>\tau_{-n}}\right]$$

of eq. (4.1.17), which is clearly bounded by $u_\lambda(-n)$, vanishes when $n \to \infty$.

Moreover, we know that the diffusion will not explode as soon as the coefficients of the diffusion operator are Lipschitz. So $\tau_{-n} \xrightarrow[n\to\infty]{} \infty$ and the indicative function $\mathbb{1}_{\tau_{x_0}<\tau_{-n}}$ tends to $\mathbb{1}_{\tau_{x_0}<\infty}$ when $n \to \infty$. We recall that $u_\lambda(x_0) = 1$, so the term inside the expectation is bounded by 1 and we can apply Lebesgue's theorem and we get the result:

$$\begin{aligned}
\mathbb{E}_x\left[e^{-\lambda T_{x_0}}\right] &= \mathbb{E}_x\left[e^{-\lambda T_{x_0}}\mathbb{1}_{T_{x_0}<\infty}\right] + \mathbb{E}_x\left[e^{-\lambda T_{x_0}}\mathbb{1}_{T_{x_0}=\infty}\right] \\
&= \mathbb{E}_x\left[e^{-\lambda T_{x_0}}\mathbb{1}_{T_{x_0}<\infty}\right] \\
&= u_\lambda(x)
\end{aligned}$$

which ends the proof of the necessary condition.
So if a regular solution of (4.1.16) exists, then it is equal to the Laplace transform of T_{x_0}.
Sufficient condition:
We still need to prove that this equation (4.1.16) admits regular solutions. This problem is not solved here, and in the cases treated later we'll exhibit solutions of this equation.

□

Theorem 4.1.5. *The Laplace transform of the hitting time of a diffusion with generator $\mathcal{L}$ can be written:*

$$\mathbb{E}_x\left[e^{-\lambda T_{x0}}\right] = \frac{\Psi_\lambda(x)}{\Psi_\lambda(x_0)} \tag{4.1.18}$$

where $\Psi_\lambda(\cdot)$ is proportional to the unique increasing positive solution of

$$\mathcal{L}\Psi_\lambda = \lambda\Psi_\lambda$$

(i.e. the eigen value of the diffusion operator $\mathcal{L}$ associated to the eigen value λ).

Proof. The proof is not very difficult but introduce some new lemmas, we won't reproduce it here and refer for instance to the excellent book of Itô and McKean [23, Chapt. 4.6]. □

4.1.3 Application : Characterization of hitting times for moving boundaries

We still consider in this section a one-dimensional diffusion process $X = (X_t;\ t > 0)$ given by the equation :

$$X_t = b(X_t)dt + \sigma(X_t)dB_t \tag{4.1.19}$$

where $B = (B_t)_{t\geq 0}$ is a standard one-dimensional Brownian motion.

Let $a(t)$ be the boundary, and $\tau^a(X)$ the first passage time of X to the boundary. We have already seen Durbin's method to characterize those hitting times. In this section we provide a parabolic differential equation with boundary and limit conditions governing the Laplace transform of this hitting time.

We denote $u_\lambda(x)$ be the Laplace transform of $\tau^a(X)$ conditionally on the fact that $X_0 = x$.

$$\tau^a(X) := \inf\{t > 0; X_t = a(t)\}$$

$$u_\lambda(x) := \mathbb{E}_x\left[e^{-\lambda\tau^a(X)}\right] \quad , \lambda \geq 0 \tag{4.1.20}$$

Theorem 4.1.6. *Assume that $x < a(0)$. Then the Laplace transform $u_\lambda(x) = v_\lambda(0,x)$ where $v_\lambda(t,x)$ is solution of the following PDE together with limit conditions :*

$$\begin{cases} \partial_t v_\lambda(t,x) + \mathcal{L}v_\lambda(t,x) - \lambda v_\lambda(t,x) = 0 \\ v_\lambda(t,a(t)) = 1 \\ \lim\limits_{x\to-\infty} v_\lambda(t,x) = 0 \end{cases} \tag{4.1.21}$$

Proof. The proof of the necessary condition, i.e. assuming that a regular solution ($C^{1,2}$), the proof is very similar to the one of theorem 4.1.4.

To prove this theorem we only have to use Itô's formula to the (assumed) $C^{1,2}$ function $e^{-\lambda t}v(t,X_t)$. The local martingale will be a real martingale (it is necessary to bound the process X also to get a martingale, as we did in the last proof), and the optimal stopping theorem will apply and we will eventually get:

$$\mathbb{E}_x\left[e^{-\lambda\tau^a(X)}\right] = v_\lambda(0,x)$$

□

4.2 Applications

In this section we study some properties of the hitting times appearing in section 6.2, useful in the sequel. The problem of hitting times of Brownian motion and Ornstein-Ulhenbeck process has been widely studied. In this section, we only revisit and prove some useful properties for the network we will study in section 6.2.

4.2.1 Brownian Motion Hitting Times

In the section 6.2.1 we have written the probability density of the hitting time of a constant boundary of the Brownian motion. In this section, we derive this formula for the Brownian motion and the Brownian motion with drift, and obtain the expectation of this hitting time is infinite. We establish that this hitting time is almost surely finite, except in a special case of the Brownian motion with drift where we show that there is a strictly positive probability of never hitting the boundary.

Standard Brownian motion

Theorem 4.2.1. *Let $(B_t)_{t\geq 0}$ be a standard Brownian motion, starting from 0. Let T^a be the hitting time of a, i.e. the first time the Brownian motion B_t is equal to a, namely :*

$$T^a := \inf\{t \geq 0; B_t = a\}$$

Then its Laplace transform reads :

$$\mathbb{E}\left[e^{-\lambda T^a}\right] = e^{-\sqrt{2\lambda}a} \quad \forall\lambda \geq 0 \tag{4.2.1}$$

which is known to be the Laplace transform of the inverse Gaussian $\frac{a^2}{B_1^2}$. *So* T^a *is absolutely continuous w.r.t. Lebesgue's measure. We denote* $p(t)$ *its probability density (i.e.* $\mathbb{P}[T^a \in dt] =: p(t)\,dt$ *). We can write:*

$$p(t) = \frac{|a|}{\sqrt{2\pi t^3}} e^{-a^2/2t} \quad t > 0 \tag{4.2.2}$$

So with this expression we can see that T^a *is almost surely finite and*

$$\mathbb{E}[T^a] = \infty \tag{4.2.3}$$

Proof. First of all let's compute the Laplace transform. It's easily done using the exponential martingale and the optional sampling theorem [26]. T^a is clearly a stopping time since it's the first passage time of a continuous process.

It's well known that the process $e^{\theta B_t - \frac{\theta^2}{2}t}$ is a martingale. Then we see that $e^{\theta B_{t\wedge T^a} - \frac{\theta^2}{2}t\wedge T^a}$ is a bounded martingale so a uniformly integrable martingale. The optional sampling theorem applies, so we have :

$$\forall t \geq 0 \;\; \mathbb{E}\left[e^{\theta B_{t\wedge T^a} - \frac{\theta^2}{2}t\wedge T^a}\right] = 1$$

Then letting $t \to \infty$ and using Lebesgue's theorem we have :

$$\mathbb{E}\left[e^{-\frac{\theta^2}{2}T^a}\right] = e^{-\theta a}$$

So that we obtain the formula (4.2.1).

To find the actual probability density we can use the inverse laplace transform or use the reflection principle. This principle states that

$$\begin{aligned}
\mathbb{P}[T^a < t] &= \mathbb{P}[T^a < t; B_t > a] + \mathbb{P}[T^a < t; B_t < a] \\
&= \mathbb{P}[B_t > a] + \mathbb{P}[T^a < t; B_t < a] \\
&= \mathbb{P}[B_t > a] + \mathbb{E}[\mathbb{1}_{T^a<t}\mathbb{P}[B_t < a|\mathcal{F}_{T^a}]] \\
&= \mathbb{P}[B_t > a] + \mathbb{E}[\mathbb{1}_{T^a<t}\mathbb{P}[B_{t-Ta+T_a} - B_{T_a} < 0|\mathcal{F}_{T^a}]] \\
&= \mathbb{P}[B_t > a] + \mathbb{E}\left[\mathbb{1}_{T^a<t}\mathbb{P}\left[\widetilde{B}_{t-T^a} < 0|\mathcal{F}_{T^a}\right]\right] \quad \text{(Strong Markov property)} \\
&= \mathbb{P}[B_t > a] + \frac{1}{2}\mathbb{P}[T^a < t]
\end{aligned}$$

So we have the repartition function of T^a

$$\mathbb{P}[T^a < t] = \sqrt{\frac{2}{\pi}} \int_{a/\sqrt{t}}^{\infty} e^{-x^2/2}\,dx$$

and differentiating w.r.t. t we get the p.d.f. of T^a (4.2.2).

Now with this probability density function, we can see that the expectation is infinite, because the expectation is the integral of a function equivalent to $\frac{C}{\sqrt{t}}$ when $t \to \infty$.

□

Proposition 4.2.2. The hitting time of the constant barrier x of the Brownian motion starting form 0 tends in distribution and in probability to 0 when x tends to 0.

Proof. The convergence in distribution comes from the convergence of the Laplace transform of T^a to 1 when $a \to 0$ (see theorem 4.2.6 and section A.2).

Let us now prove the convergence in probability. Let ε be a positive real. We consider the probability of the event $\{T^a > \varepsilon\}$:

$$\mathbb{P}\left[T^a > \varepsilon\right] = \int_{\varepsilon}^{\infty} \frac{|a|}{\sqrt{2\pi t^3}} e^{-a^2/2t}\, dt$$

The integrand tends almost surely to 0 when $a \to 0$ and has the upper bound :

$$\forall t > 0, \;\; \forall a > 0, \frac{|a|}{\sqrt{2\pi t^3}} e^{-a^2/2t} \leq \frac{|a|}{\sqrt{2\pi t^3}}$$

which is integrable on $[\varepsilon, \infty)$ so we can apply Lebesgue's theorem and we conclude that

$$\forall \varepsilon > 0 \quad \mathbb{P}\left[T^a > \varepsilon\right] \xrightarrow[a \to 0]{} 0$$

which is the definition of the convergence in probability.

□

Brownian motion with drift

The key concept to study the Brownian motion with drift is the Girsanov's theorem (or the particular case of the Cameron-Martin formula). Details on the Girsanov theorem are not given here, we refer to [26, Chapter 3.5]). Let $W := (W_t)_t$ be a standard Brownian motion and $\gamma \neq 0$ a real number. We consider the process $X_t := W_t - \gamma t$. By the Girsanov's theorem, the process X is a Brownian motion under the measure

$$Q_\gamma|_{\mathcal{F}_t} = e^{\gamma U_t - \frac{\gamma^2}{2} t} \mathbb{W}|_{\mathcal{F}_t}$$

where U_t is the canonical process.

This means that $\forall A \in \mathcal{F}_t$

$$Q_\gamma(A) = \mathbb{E}\left[\mathbb{1}_A e^{\gamma W_t - \frac{\gamma^2}{2} t}\right]$$

Under this new probability Q_γ, X_t is a standard Brownian motion, so $W_t = X_t + \gamma t$ is a Brownian motion with drift γ.

$$\begin{aligned}
Q_\gamma\left[T_b \le t\right] &= \mathbb{E}\left[\mathbb{1}_{T_b\le t} e^{\gamma W_t - \frac{\gamma^2}{2}t}\right] \\
&= \mathbb{E}\left[\mathbb{1}_{T_b\le t} e^{\gamma W_{t\wedge T_b} - \frac{\gamma^2}{2}t\wedge T_b}\right] \quad \text{because} \{T_b \le t\} \in \mathcal{F}_{T_b\wedge t} \\
&= \mathbb{E}\left[\mathbb{1}_{T_b\le t} e^{\gamma b - \frac{\gamma^2}{2}T_b}\right] \\
&= \int_0^t e^{\gamma b - \frac{\gamma^2}{2}t}\mathbb{P}\left[T_b \in dt\right] \qquad (4.2.4)
\end{aligned}$$

Now, recalling from (4.2.2) the probability density function of T_b yields the density of T_b under Q_γ :

$$Q_\gamma(T_b \in dt) = \frac{|b|}{\sqrt{2\pi t^3}}\exp\left[-\frac{(b-\gamma t)^2}{2t}\right]dt, \quad t > 0 \qquad (4.2.5)$$

Finally, letting $t \to \infty$ in equation (4.2.4), we can write :

$$Q_\gamma(T_b < \infty) = e^{\gamma b}\mathbb{E}\left[e^{-\frac{1}{2}\gamma^2 T_b}\right]$$

and so we obtain from (4.2.1) :

$$Q_\gamma(T_b < \infty) = e^{\gamma b - |\gamma b|} \qquad (4.2.6)$$

In particular, a Brownian motion with drift $\gamma \neq 0$ reaches the level $b \neq 0$ with probability one *if and only if* γ and b have the same sign. If γ and b have opposite signs, the density is defective in the sense that $Q_\gamma(T_b < \infty) < 1$. In this case, the probability of never crossing the barrier b is equal to (4.2.6). This differs a lot from the behavior of the standard Brownian motion. Nevertheless, one can prove again the regularity of these hitting time w.r.t. b, as stated in proposition 4.2.3

Proposition 4.2.3. The hitting time of the constant barrier x of the Brownian motion with drift γ starting form 0 tends in distribution and in probability to 0 when x tends to 0.

Proof. The proof is very similar to the proof of theorem 4.2.2. Here we haven't computed the Laplace transform of Hitting times so we will use the convergence in probability to prove the convergence in law.

Here again the only argument to use is Lebesgue's theorem : $\frac{|b|}{\sqrt{2\pi t^3}}\exp\left[-\frac{(b-\gamma t)^2}{2t}\right] \le \frac{|b|}{\sqrt{2\pi t^3}}$ which is integrable on the intervals of the type $[\varepsilon, \infty)$ with $\varepsilon > 0$. On the other hand, the expression (4.2.5) tends obviously to 0 when $b \to 0$ for all $t > 0$ so Lebesgue's theorem gives us the convergence in probability of the hitting time sequence to 0 when $b \to 0$.

Then we know that the convergence in probability implies the convergence in law so finally the proposition is proved. □

Remark 6. We have proved in theorems 4.2.2 and 4.2.3 that the hitting times converge in probability to 0. This means also that there is a subsequence which converges to 0 almost surely. Let us now show that this sequence of hitting times tends to 0 almost surely.

Proposition 4.2.4. The family of hitting times $(T_b)_{b\geq 0}$ tends to 0 almost surely when $b \to 0$.

Proof. The definition of the convergence almost sure of a sequence of random variables X_n to a random variable X means that there exist $\widetilde{\Omega} \subset \Omega$ such that $\mathbb{P}\left[\widetilde{\Omega}\right] = 1$ and :

$$\forall \omega \in \widetilde{\Omega},\ \ \forall \varepsilon > 0,\ \ \exists N \ \text{ such that } \ n \geq N \Rightarrow |X_n(\omega) - X(\omega)| \leq \varepsilon$$

Let Ω_ε denote the subset $\bigcup\limits_{N\geq 0} \bigcap\limits_{n\geq N} \{|X_n - X| \leq \varepsilon\}$. We have $\widetilde{\Omega} = \bigcap\limits_{\varepsilon > 0} \Omega_\varepsilon$. We have $\varepsilon \to \Omega_\varepsilon$ is increasing, so taking the intersection over $\varepsilon > 0$ is equivalent to taking the intersection: $\widetilde{\Omega} = \bigcap\limits_{p\geq 1} \Omega_{1/p}$. So finally the convergence almost sure is equivalent to the property:

$$\forall \varepsilon > 0,\ \ \mathbb{P}\left[\bigcup_{N\geq 0} \bigcap_{n\geq N} \{|X_n - X| \leq \varepsilon\}\right] = 1 \tag{4.2.7}$$

We will prove this property in our case. The sequence is indexed by $\mathbb{R}$ but this same argument is still valid, because the sequence of hitting times of the Brownian motion starting from 0 to reach b is monotonous.

We are interested in the sequence $X_n := T_{1/n}$. and $X = 0$.

We have:

$$\begin{aligned} \bigcup_{k\geq n} \{|X_k - X| > \varepsilon\} &= \bigcup_{k\geq n} \{T_{1/k} > \varepsilon\} \\ &= \{T_{1/n} > \varepsilon\} \end{aligned}$$

And we have:

$$\begin{aligned} \mathbb{P}\left[T_{1/n} > \varepsilon\right] &\leq \tfrac{1}{n} \textstyle\int_\varepsilon^\infty \tfrac{1}{\sqrt{2\pi t^3}} dt \\ &\leq \tfrac{1}{n} \left[-\tfrac{1}{2\sqrt{2\pi t}}\right]_\varepsilon^\infty \\ &\leq \tfrac{1}{2n} \tfrac{1}{\sqrt{2\pi\varepsilon}} \xrightarrow[n\to\infty]{} 0 \end{aligned}$$

which ends the proof.

□

4.2.2 Ornstein-Ulhenbeck hitting times

General properties of Ornstein-Ulhenbeck processes

Let $B := (B_t)_{t\geq 0}$ be a standard Brownian motion. The associated Ornstein Ulhenbeck (OU) process $U := (U_t)_{t\geq 0}$ with parameter $\lambda \in \mathbb{R}$ is defined to be the unique solution of the equation

$$\begin{cases} dU_t = -\lambda U_t dt + dB_t \\ U_0 = x \in \mathbb{R} \end{cases} \tag{4.2.8}$$

This linear equation when integrated gives the following expression for U :

$$U_t = x\, e^{-\lambda t} + \int_0^t e^{\lambda(s-t)} dB_s \quad \forall t \geq 0 \tag{4.2.9}$$

By the Dubins-Schwarz theorem, there is a Brownian motion $W := (W_t)_{t\geq 0}$ defined on the same probability space, such that

$$\int_0^t e^{\lambda s} dB_s = W_{\tau(t)}, \quad t \geq 0 \tag{4.2.10}$$

where $\tau(t) = \frac{1}{2\lambda}(e^{2\lambda t} - 1)$. Hence, the representation $U_t = e^{-\lambda t}(x + W_{\tau(t)})$ holds. This representation was first introduced by Doob in [15] to study some path properties of U. With this representation we can see that U has almost surely continuous paths which are nowhere differentiable. Assume that $\lambda > 0$. In this case U is positive recurrent and its semigroup has a unique invariant measure which is the law of a centered Gaussian random variable with variance $\frac{1}{2\lambda}$.

The process U is a Feller process (c.f. for instance Revuz [31, section I.5] for definition and properties), with infinitesimal generator denoted $\mathcal{L}$, given on $\mathcal{C}_b^2$ by:

$$\mathcal{L}f(x) = \frac{1}{2}\frac{\partial^2 f}{\partial x^2}(x) - \lambda x \frac{\partial f}{\partial x}(x), \quad x \in \mathbb{R} \tag{4.2.11}$$

Next, denote by $\mathbb{P}_x^{(\lambda)}$ the law of U when $U_0 = x \in \mathbb{R}$. Then thanks to Girsanov's theorem, for any fixed $t > 0$, the following absolute continuity relationship holds :

$$d\mathbb{P}_x^{(\lambda)}|\mathcal{F}_t = \exp\left(-\frac{\lambda}{2}(B_t^2 - x^2 - t) - \frac{\lambda^2}{2}\int_0^t B_s^2 ds\right) d\mathbb{W}_x|\mathcal{F}_t \tag{4.2.12}$$

where $\mathbb{W}_x$ stands for the law of a Brownian motion starting at x.

Remark 7. Note that the Radon-Nikodym derivative (4.2.12) is a true martingale.

Hitting times of a constant barrier of the Ornstein-Ulhenbeck process

The properties of hitting times of the OU process has been widely studied. For instance, in [1], the authors give three representations of the probability density of these processes, and in [32] we have an explicit expression of the moments of those hitting times. In this section we focus on the regularity properties of those hitting times. The main results of this section is the convergence in law (which is more general as stated in remark 8) and the convergence almost sure of the hitting time of the constant threshold x starting from y when $y \to x$.

Let $a \in \mathbb{R}$ be a given fixed real number and introduce the first passage time of the process U and B :

$$H^a := \inf\{t \geq 0; U_t = a\} \tag{4.2.13a}$$

$$T^a := \inf\{t \geq 0; B_t = a\} \tag{4.2.13b}$$

The law of H^a (resp T^a) is absolutely continuous w.r.t. the Lebesgue measure and its density will be denoted $p^{(\lambda)}_{x\to a}(\cdot)$ (resp $p_{x\to a}(\cdot)$). We focus in this chapter on the case $x < a$, i.e. the process starts below the barrier. The symmetric case $x > a$ can be treated in the same way changing U by $-U$ (which is also an OU process), x in $-x$ and a in $-a$.

First of all let us compute the Laplace transform of H^a, well known since Siegert [34] and Breiman [7]. We'll give here an elementary proof of this.

Proposition 4.2.5. For $x < a$ the Laplace transform of H^a is given by

$$\mathbb{E}_x\left[e^{-\alpha H^a}\right] = \frac{\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})}{\mathcal{H}_{-\alpha/\lambda}(-a\sqrt{\lambda})} = \frac{e^{\lambda x^2/2}\mathcal{D}_{-\alpha/\lambda}(-x\sqrt{2\lambda})}{e^{\lambda a^2/2}\mathcal{D}_{-\alpha/\lambda}(-a\sqrt{\lambda})} \tag{4.2.14}$$

where $\mathcal{H}_\nu$ stands for Hermite function and $\mathcal{D}_{-\alpha/\lambda}$ for the parabolic cylinder functions respectively (see Lebedev [27, chapter 10] for a precise study of those functions or the section A.1).

Proof. We use the hitting time characterization given by Feynman-Kac equations, proved in section 4.1.2. The Laplace transform of the first passage time is given by theorem 4.1.4 as the unique solution of the boundary value problem :

$$\begin{cases} \mathcal{L}u(x) & = \alpha u(x), \text{ for } x < a \\ u(a) & = 1 \\ \lim\limits_{x\to-\infty} u(x) & = 0 \end{cases} \tag{4.2.15}$$

Here the theory applies since the coefficients of the diffusion operator $\mathcal{L}$ are $\mathcal{C}^\infty$. This is a singular value problem since the interval is not bounded. Nevertheless one can prove that the solution to the above problem takes the form :

$$\mathbb{E}_x\left[e^{-\alpha H^a}\right] = \frac{\psi_\alpha(x)}{\psi_\alpha(a)}$$

where $\psi_\alpha(\cdot)$ is up to some multiplicative constant, the unique increasing positive solution of the equation $\mathcal{L}\psi_\alpha = \alpha\psi_\alpha$. By definition of Hermite functions, see A.1, we get $\psi_\alpha(x) = \mathcal{H}_{-\alpha/\lambda}(x\sqrt{\lambda})$, which completes the proof of the first equality. Indeed, the equation (4.1.16) reads :

$$\begin{cases} \frac{1}{2}\frac{\partial^2 u}{\partial x^2}(x) - \lambda x \frac{\partial u}{\partial x}(x) - \alpha u(x) = 0 \\ u(x_0) = 1 \\ \lim\limits_{x\to-\infty} u(x) = 0 \end{cases}$$

The differential equation satisfied by $\mathcal{H}_\nu$ is

$$f'' - 2zf'(z) + \nu f(z) = 0$$

Let $g(x) = \mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})$. We have :

$$\begin{aligned} g'(x) &= \sqrt{\lambda}\,\mathcal{H}'_{-\alpha/\lambda}(-x\sqrt{\lambda}) \\ g''(x) &= \lambda\,\mathcal{H}''_{-\alpha/\lambda}(-x\sqrt{\lambda}) \end{aligned}$$

$$\begin{aligned} \frac{1}{2}g''(x) - \lambda x g'(x) - \alpha g(x) &= \frac{1}{2}\lambda\mathcal{H}''_{-\alpha/\lambda}(-x\sqrt{\lambda}) - x\lambda\sqrt{\lambda}\mathcal{H}'_{-\alpha/\lambda}(-x\sqrt{\lambda}) - \alpha\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda}) \\ &= \frac{\lambda}{2}\left(\mathcal{H}_{-\alpha/\lambda}"(z) - 2z\mathcal{H}'_{-\alpha/\lambda}(z) - \frac{\alpha}{\lambda}\mathcal{H}_{-\alpha/\lambda}(z)\right)|_{z=x\sqrt{\lambda}} \\ &= 0 \end{aligned}$$

The two fundamental solutions of the linear differential equations are $\mathcal{H}_{-\alpha/\lambda}(x\sqrt{\lambda})$ and $\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})$. The function ψ_α is up to a positive constant the one that is increasing. With the series expansion of Hermite's functions (A.1.2), it's clear that the increasing function researched $\psi_\alpha = \mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})$. The second equality relies on the relation between $\mathcal{H}_\nu$ and $\mathcal{D}_\nu$.

□

We are now concerned with the regularity of $\tau_y^x := \inf\{t > 0; X_t = x | X_0 = y\}$. The two following theorems give us the convergence in law and almost surely of the random variables τ_y^x when $y \to x$.

Theorem 4.2.6. *The sequence of random variables $(\tau_y^x)_{y\le x}$ converges in law (in distribution) to 0 when y tends to x :*

$$\boxed{\tau_y^x \xrightarrow[y\to x]{\mathcal{L}} 0}$$

Proof. Here we prove and use a classical result of stochastic process analysis. The proof relies on the fact that the Laplace transform of the random variable τ_y^x converges to the Laplace transform of 0.

Indeed, the Laplace transform of τ_y^x reads, according to (4.2.14) :

$$\mathbb{E}_x\left[e^{-\alpha\tau_y^x}\right] = \frac{\mathcal{H}_{-\alpha/\lambda}(-y\sqrt{\lambda})}{\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})}$$

It's clear with the series expansion of the Hermite functions (A.1.2) that the Hermite function is strictly positive for any real negative argument and is continuous, so here the Laplace transform is defined and continuous for all $y \leq x$. When $y \to x$, the Laplace transform tends to 1 which is the Laplace transform of the random variable identically 0. We know that the Laplace transform completely determines a probability distribution. We can prove that when a sequence of probability measures $\mathbb{P}_n$ has their Laplace transforms converging to the same Laplace transform of a distribution, then the sequence is tight (see A.2 for a proof of this or the book of Billingsley [6]), so the sequence is relatively compact. Any limit point of the sequence has the same Laplace transform so the limit is unique and the sequence converges weakly (or in distribution/law).

Eventually, the theorem is proved. □

Remark 8. This result is much more general than the particular case of the Ornstein-Ulhenbeck process. This proof can be driven without major change for any diffusion process, provided the regularity of the Laplace transform. For instance it is the case of the Brownian motion hitting time to a constant barrier, which has the Laplace transform given by (4.2.1).

We now prove that the sequence of hitting times $(\tau_y^x)_{y\leq x}$ of the Ornstein-Ulhenbeck process converges also almost surely to 0 when $y \to x$. To do this we use the expectation of this hitting time, differentiating the Laplace transform of H^a with respect to the parameter. So first we need the expression of the differential of the Laplace transform (4.2.14). To have more simple expressions of this Laplace transform, let us write, using together (4.2.14) and the expression of the Hermite function (A.1.1):

$$\begin{aligned} u(\alpha) &:= \mathbb{E}_x\left[e^{-\alpha H^a}\right] \\ &= \frac{\mathcal{H}_{-\alpha/\lambda}(-x\sqrt{\lambda})}{\mathcal{H}_{-\alpha/\lambda}(-a\sqrt{\lambda})} \\ &= \frac{\varphi(-\alpha/\lambda, -x\sqrt{\lambda})}{\varphi(-\alpha/\lambda, -a\sqrt{\lambda})} \end{aligned} \tag{4.2.16}$$

where

$$\varphi(\nu, z) = \phi(-\frac{\nu}{2}, \frac{1}{2}; z^2) - 2\sqrt{2}z\frac{\Gamma(\frac{1-\nu}{2})}{\Gamma(\frac{-\nu}{2})}\phi(\frac{1-\nu}{2}, \frac{3}{2}; z^2) \tag{4.2.17}$$

This formula is straightforward using $\Gamma(-\frac{1}{2}) = -2\Gamma(\frac{1}{2})$.

Lemma 4.2.7. The function $\varphi(\nu, z)$ is differentiable w.r.t. ν and its derivative reads :

$$\frac{\partial\varphi}{\partial\nu}(\nu,z) = -\frac{1}{2}\phi^{(1)}\left(-\frac{\nu}{2},\frac{1}{2};z^2\right) - \sqrt{2}z\left(-\frac{\Gamma'(\frac{1-\nu}{2})}{\Gamma(-\frac{\nu}{2})} + \frac{\Gamma(\frac{1-\nu}{2})\Gamma'(-\frac{\nu}{2})}{\Gamma(-\frac{\nu}{2})^2}\right)$$
$$\phi\left(\frac{1-\nu}{2},\frac{3}{2};z^2\right) + \sqrt{2}z\frac{\Gamma(\frac{1-\nu}{2})}{\Gamma(\frac{-\nu}{2})}\phi^{(1)}\left(\frac{1-\nu}{2},\frac{3}{2};z^2\right) \quad (4.2.18)$$

where $\phi^{(1)}(\alpha,\beta;z)$ denotes the derivative w.r.t. the first argument of the confluent hypergeometric function :

$$\phi^{(1)}(\alpha,\beta;z) = \frac{\partial\phi}{\partial\alpha}(\alpha,\beta;z) = \sum_{n=0}^{\infty}\frac{d(\alpha)_n}{d\alpha}\frac{1}{(\beta)_n}\frac{z^n}{n!}$$

which is continuous and differentiable.

The differential of $\varphi(\cdot,\cdot)$ is continuous and its value at $\nu = 0$ is :

$$\frac{\partial\varphi}{\partial\nu}(\nu,z)|_{\nu=0} = -\frac{1}{2}\phi^{(1)}(0,\frac{1}{2};z^2) - \sqrt{2\pi}z\phi(\frac{1}{2},\frac{3}{2};z^2) \quad (4.2.19)$$

Proof. The first expression is straightforward, differentiating the expression (4.2.17). We obtain (4.2.19) taking the limit of (4.2.18) at $\nu = 0$. To find this limit we use the well known limit :

$$|\Gamma(z)| \xrightarrow[z\to 0]{} \infty$$

together with the representation of the one over Gamma function used in [40] to conclude.

$$\frac{1}{\Gamma(z)} = z\exp\left(\gamma z - \sum_{k=2}^{\infty}(-1)^k\zeta(k)z^k/k\right)$$

where $\zeta(\cdot)$ is the Riemann zeta function and γ is the Euler-Mascheroni constant[1].

Differentiating this expression gives us :

$$\frac{\Gamma'(z)}{\Gamma(z)^2} = e^{\gamma z - \sum_{k=2}^{\infty}\frac{(-1)^k\zeta(k)z^k}{k}} + (\gamma - \sum_{k=2}^{\infty}(-1)^k\zeta(k)z^{k-1})\frac{1}{\Gamma(z)}$$

The first term tends to 1 when $z \to 0$ and the second one tends to 0, so $\frac{\Gamma'(z)}{\Gamma(z)^2} \xrightarrow[z\to 0]{} 1$ and we have (4.2.19) □

Theorem 4.2.8. *The sequence of hitting times $(\tau_y^x)_{y\leq x}$ tends to 0 almost surely when $y \nearrow x$:*

$$\boxed{\tau_y^x \xrightarrow[y\nearrow x]{almost\ surely} 0}$$

[1] $\zeta(n) = \sum_{n=1}^{\infty} n^{-k}$ and $\gamma = lim\, n \to \infty \left(\sum_{k=1}^{n}\frac{1}{k} - \log(n)\right)$

Proof. We use the representation of the Laplace transform of the hitting times $(\tau_y^x)_{y\leq x}$ given by (4.2.16). We show that the expectation of these hitting times exists, and converges to 0 when $y \to x$, which gives us the almost sure. The expectation of a random variable, if it exists, is the derivative in 0 of the Laplace transform w.r.t. the argument of the transform

$$\begin{aligned}
\mathbb{E}\left[\tau_y^x\right] &= \left.\frac{du(\alpha)}{d\alpha}\right|_{\alpha=0} \\
&= -\frac{1}{\lambda}\left(\frac{\frac{\partial\varphi}{\partial\nu}(0,-x\sqrt{\lambda})}{\varphi(0,-a\sqrt{\lambda})} - \frac{\frac{\partial\varphi}{\partial\nu}(0,-a\sqrt{\lambda})\varphi(0,-x\sqrt{\lambda})}{\varphi(0,-a\sqrt{\lambda})^2}\right) \\
&= -\frac{1}{\lambda}\left(\frac{\partial\varphi}{\partial\nu}(0,-x\sqrt{\lambda}) - \frac{\partial\varphi}{\partial\nu}(0,-a\sqrt{\lambda})\right) \qquad (4.2.20)
\end{aligned}$$

Now we use the expressions of $\frac{\partial\varphi}{\partial\nu}$ given in the lemma 4.2.7, and use the continuity of these function to conclude that the expectation of τ_y^x tends to 0 uniformly, so the (positive) hitting time τ_y^x tends to 0 almost surely when $y \nearrow x$.

□

Remark 9. Note that this theorem is not as general as theorem 4.2.6, because we need some properties of regularity on the function ψ_α appearing in the proof of proposition 4.2.5. For instance we have already proved that for the hitting times of the Brownian motion, we could not apply the same technique, since the expectation of the hitting times is always infinite. In this particular case, the function ψ_α is null when $\alpha = 0$.

Chapter 5

Numerical Approximation of the pdf for some simple types of neuron models

In this chapter we apply the results of chapter 3 for some simple types of neuron models. Numerical approximation has been done with the help of Theodore Papadopoulo[1] who implemented in C++ the equations, and with the help of Etienne Tanrï¿½footnoteINRIA, Sophia-Antipolis, Omega project for the Monte-Carlo Simulations.

This chapter is also the contents of a future oral communication at the NeuroComp conference which will take place in Pont-ï¿½Mousson on November 23-24 of this year. It has been done together with Olivier Faugeras, Theodore Papadopoulo, Denis Talay, Etienne Tanrï¿½Mireille Bossy and me.

5.1 Introduction

The dynamics of the discharge of neurons in vivo is greatly influenced by noise. It is generally agreed that a large part of the noise experienced by a cortical neuron is due to the intensive and random excitation of synaptic sites. The impact of noise on neuronal dynamics can be studied in detail in a simple spiking neuron model, the integrate-and-fire (IF) neuron [37]. For more complicated models the authors usually make use of the framework of the Fokker-Planck equation associated to a set of stochastic differential equations describing the dynamics of the neuron membrane potential in the presence of synaptic noise [33]. Since this equation cannot in general be solved analytically, the authors resort to various plausible approximations to obtain analytical results in various extreme case [10, 20]. In this paper

[1] INRIA, Sophia-Antipolis, Odyssï¿½ project

we outline a method that can produce the statistics of the inter-spikes time intervals for any input current and for a variety of synaptic noise types.

5.2 Monte-Carlo Method

A method used in this study to have an approximation of the hitting time is the Monote-Carlo Method. We will not explain in details this very classical method here, but just recall the principle of this method, since we show some numerical simulations based on Monte-Carlo.

This method consists in simulating the trajectories of the process using independent Brownian increments. The time is discretised, and we simulate a large number of independent trajectories. We consider that the process has crossed the boundary either if the simulation point is other the boundary, or we can compute the probability of crossing the boundary when two consecutive points are underneath the boundary.

5.3 Integrate and fire with instantaneous synaptic conductances

The simplest model we consider is the integrate and fire where the membrane potential u follows the stochastic differential equation

$$\tau du = (\mu - u(t))dt + I_e(t)dt + \sigma dW,$$

with initial condition $u(0) = 0$, where τ is the time constant of the membrane, μ a reversal potential, $I_e(t)$ the injected current and $W(t)$ a Brownian process representing synaptic input. The neuron emits a spike each time its membrane potential reaches a threshold θ. The membrane potential is then reinitialized to the initial value, i.e. 0. We are interested in characterizing the sequence $\{t_i\}$, $i = 1, \cdots$, $t_i > 0$, $t_{i+1} > t_i$ when the neuron emits spikes.

5.3.1 The time of the first spike

The problem of characterizing the first time t_1 when the membrane potential reaches the threshold θ is defined as

$$t_1 = inf\{t : t > 0, u(t) = \theta\},$$

where $u(t)$ is given by the following expression

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \frac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\, ds + \frac{\sigma}{\tau}\int_0^t e^{\frac{s-t}{\tau}} dW(s)$$

The condition $u(t) = \theta$ can be rewritten as

$$\int_0^t e^{\frac{s}{\tau}} dW = \frac{\tau}{\sigma}\left[(\theta - \mu)e^{\frac{t}{\tau}} + \mu - \frac{1}{\tau}\int_0^t e^{\frac{s}{\tau}} I_e(s)\, ds\right] \equiv b(t) \tag{5.3.1}$$

In order to characterize t_1 we need the following

Lemma 5.3.1. Let $X(t) = \int_0^t e^{\frac{s}{\tau}} dW(s)$ The stochastic process $X(t)$ is a Brownian motion if we change the time scale: $X(t) = W\left(\frac{\tau}{2}\left(e^{2\frac{t}{\tau}} - 1\right)\right)$.

Proof. This lemma is in fact a direct consequence of the Dubins-Schwarz theorem [26]. We provide an elementary proof for completeness. Let $r = \frac{\tau}{2}\left(e^{2\frac{t}{\tau}} - 1\right)$, it is a monotonously increasing function of t equal to 0 for $t = 0$. For all times $0 < r_1 < r_2 < \cdots < r_n$, the random variables $X(r_1)$, $X(r_2) - X(r_1)$, $\ldots X(r_n) - X(r_{n-1})$ are independent because W is a Brownian motion. Finally, it is easy to see that $X(t_2) - X(t_1)$ is distributed as $N(0, \int_{t_1}^{t_2} e^{2\frac{s}{\tau}}\, ds)$ which implies that $X(r_2) - X(r_1)$ is distributed as $N(0, r_2 - r_1)$. □

We can now rewrite the threshold crossing condition above as

$$W(r) = \frac{\tau}{\sigma}\left[(\theta - \mu)\sqrt{\frac{2}{\tau}r + 1} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\, ds\right],$$

where

$$\tilde{I}_e(s) = \frac{I_e(\frac{\tau}{2}\log\left(\frac{2}{\tau}s + 1\right))}{\sqrt{\frac{2}{\tau}s + 1}}$$

The time t_1 at which the membrane potential reaches the threshold θ is obtained from the time r_1 at which the Brownian motion W reaches for the first time the curve $a(r)$ defined by the equation

$$y = a(r) = \frac{\tau}{\sigma}\left[(\theta - \mu)\sqrt{\frac{2}{\tau}r + 1} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\, ds\right],$$

by the formula

$$t_1 := \frac{\tau}{2}\log(\frac{2}{\tau}r_1 + 1)$$

The corresponding problem has been studied in particular by Durbin [16, 17] who provides an integral equation for the probability density function (pdf) of r_1. From this integral equation he deduces a series approximation of the pdf and proves convergence when the curve is concave or convex.

This result is summarized in the next theorem.

Theorem 5.3.2 (Durbin)**.** *Let $W(\tau)$ be a standard Brownian motion for $\tau \geq 0$ and $y = a(\tau)$ be a boundary such that $a(0) > 0$ and $a(\tau)$ is continuously differentiable for $\tau \geq 0$. The first-passage density $p(t)$ of $W(\tau)$ to $a(t)$ can be written as*

$$p(t) = \sum_{j=1}^{k}(-1)^{j-1}q_j(t) + r_k(t),$$

where

$$q_j(t) = \int_0^t q_{j-1}(s)(\frac{a(t)-a(s)}{t-s} - a'(t))f(t|s)\,ds \quad j \geq 1.$$

$a'(t)$ is the derivative of $a(t)$ and q_0 is given by

$$q_0(t) = (\frac{a(t)}{t} - a'(t))f_0(t),$$

where $f_0(t)$ is the density of $W(t)$ on the boundary, i.e.

$$f_0(t) = (2\pi t)^{-1/2}\exp(-a(t)^2/2t),$$

and $f(t|s)$ is the joint density of $W(s)$ and $W(t) - W(s)$ on the boundary, i.e.

$$f(t|s) = f_0(s)(2\pi(t-s))^{-1/2}\exp(-(a(t)-a(s))^2/(2(t-s))).$$

The remainder $r_k(t)$ goes to 0 if $a(\tau)$ is convex or concave.

As an application of the above, we consider two examples.

Constant intensity

In this case the membrane potential is the realization of an Ornstein-Uhlenbeck process. The function $a(r)$ is convex, hence the hypotheses of Durbin's theorem are satisfied. Moreover some analytical results have been obtained for the first moment of the law of the first passage time. In table 5.1, we show the successive approximations of the values of the integral of the law (which should be equal to 1); the mean value is found to be equal to 1.93 (which is the value found by the analytical formula found in, e.g., [32]). The values of the parameters are $\theta = \sigma = 2$, $\mu = \tau = 1$.

time-terms	3	5	7	9
10^3	0.86	0.86	0.86	0.86
10^5	0.98	0.95	0.95	0.95
10^7	1.12	0.97	0.98	0.98
10^9	1.44	1.01	0.99	0.99

Table 5.1: Values of the integral of the estimated pdf for $I_e = 0$. The left column indicates the range of the values of r, the first line the number of terms in the series approximation.

Periodic intensity

We choose $I_e(t) = \sin(2\pi f t)$. Table 5.2 is similar to 5.1. The parameters are the same as in the previous example, $f = 1$. It is seen that Durbin's series converges very quickly. Figure

time-terms	3	5	7	9
10^3	0.86	0.88	0.88	0.88
10^5	0.86	0.97	0.96	0.96
10^7	0.82	1.00	0.98	0.98
10^9	0.88	0.97	1.00	0.99

Table 5.2: Values of the integral of the estimated pdf for $I_e = \sin(2\pi t)$.

5.1 shows the shape of the pdf of the first passage time and the first four terms in the series approximation. Tables 5.1 and 5.2 indicate that a very good approximation of the pdf can be obtained with only 5 terms in the series. The total computation time is 8 seconds on a 2GHz computer for 800 sample points.

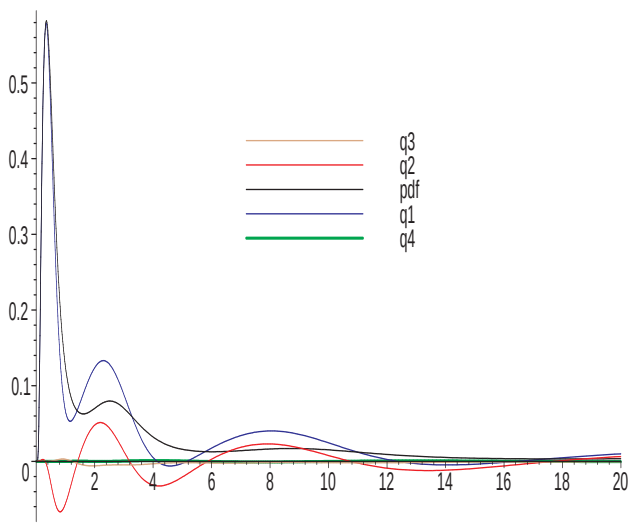


Figure 5.1: Four terms of the series approximation of the pdf when $I_e(t) = \sin(2\pi t)$ and the resulting pdf (the horizontal scale is in r units).

5.3.2 Validation of these approximations

In the case when the intensity is constant, we can compute using the Laplace transform of the Ornstein-Ulhenbeck process the moments of the law of the first hitting time. Then using those simulations we can compute the empirical first, second and third moments of the law. The validation here was meant to compare those three values and to see wether the simulations were stable or not.

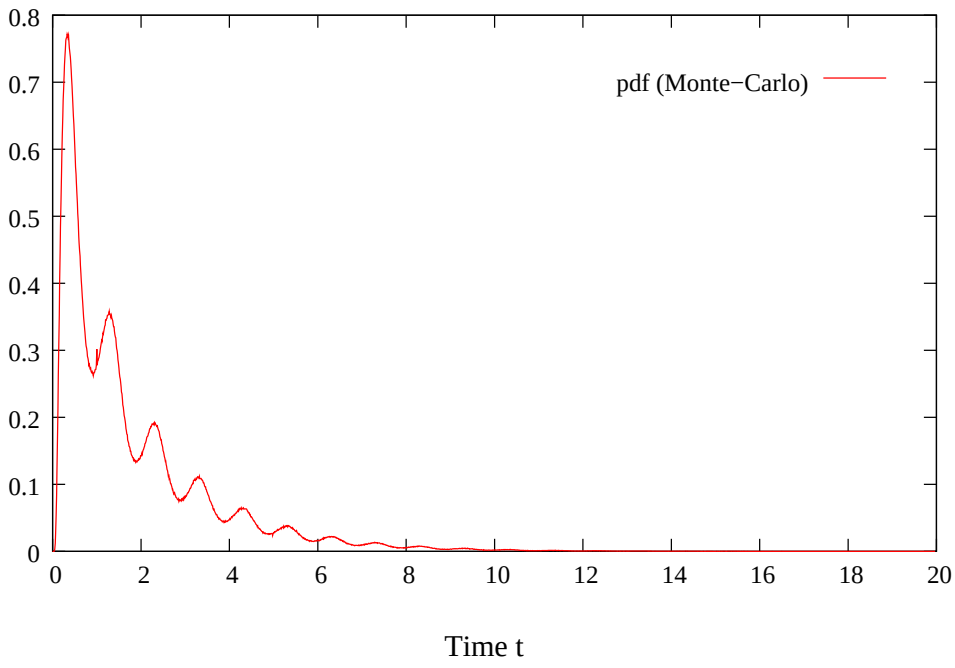


Figure 5.2: Monte-Carlo approximation of the pdf when $I_e(t) = \sin(2\pi t)$

To compute the moments of the law, I refer to the article of Ricciardi and Sato [32]. In this article the authors give a rather complicated method to compute the moments of the Ornstein-Ulhenbeck process.

In our case, we are only interested in the first three moments, so we give here the explicit formulae of those moments:

Theorem 5.3.3. *We denote* $\alpha := \frac{\mu}{\sigma}$ *and* $\beta := \frac{\sigma}{\theta\sqrt{\tau}}$.

Let us define the three following functions:

$$\Phi_1(z) := \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n$$

$$\Phi_2(z) := \frac{1}{2}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})\left(\Psi(\frac{n}{2})-\Psi(1)\right)(z-\alpha)^n$$

$$\Phi_1(z) := \frac{3}{8}\sum_{n=1}^{\infty}\left(\frac{2}{\beta}\right)^n \frac{1}{n!}\Gamma(\frac{n}{2})(z-\alpha)^n\rho_n^{(3)}$$

where Γ *is the gamma function,* $\Psi(z) = \frac{\Gamma'(z)}{\Gamma(z)}$ *is the digamma function, and*

$$\rho_n^{(3)} = \left(\Psi(\frac{n}{2})-\Psi(1)\right)^2 + \left(\Psi'(\frac{n}{2})-\Psi'(1)\right)$$

Then let X *be our OU process starting from 0. Let* T *be the hitting time of this process to the barrier* θ*. We have:*

$$\mathbb{E}\left[T\right] = \tau(\Phi_1(1)-\Phi_1(0)) \tag{5.3.2}$$

$$\mathbb{E}\left[T^2\right] = \tau^2(2\Phi_1(1)^2 - \Phi_2(1) - 2\Phi_1(1)\Phi_1(0) + \Phi_2(0)) \tag{5.3.3}$$

$$\begin{aligned}\mathbb{E}\left[T^3\right] = \tau^3\big\{&6\Phi_1(1)^3 - 6\Phi_1(1)\Phi_2(1) + \Phi_3(1)\\ &-6(\Phi_1(1)^2 - 3\Phi_2(1))\Phi_1(0) + 3\Phi_1(1)\Phi_2(0) - \Phi_3(0)\big\}\end{aligned} \tag{5.3.4}$$

With the variables we chose in our simulations, we obtain, using maple and truncating the series appearing in the definitions of Φ_i the reference values. Then we compute the empirical expectation, first and second moment for different parameters. The results are in the table 5.3.

5.3.3 The times of the next spikes

The previous analysis and results can be extended to the times $t_2, \dots t_n$ of the next spikes. We discuss how to determine t_n given t_{n-1}, i.e. how to compute $p(t_n|t_{n-1})$. The scenario is similar to the one used to compute t_1.

method	$\mathbb{E}[T]$	$\mathbb{E}[T^2]$	$\mathbb{E}[T^3]$
theoretical values	1.9319289	7.1356162	40.0830265
Durbin, 30 terms, $T_max = 10^{36}$, step $= 10^{-2}$	1.9292822	7.1269290	39.8541918
Monte-Carlo, 10^6 realizations, step $= 10^{-4}$	1.932180	7.139402	40.079556

Table 5.3: Values of the first 3 moments of the Ornstein-Ulhenbeck process and the empirical values, for the parameters: $\theta = \sigma = 2$, $\mu = \tau = 1$

We know that the process u_t is strongly Markovian (diffusion process with Lipschitz coefficients, see [26, 36]). Conditionally on the stopping time t_{n-1}, determining the interspike interval reduces to the problem of determining the first stopping time t_1. The only difference is that the random time shift t_{n-1} appears in the input I_e (but the conditioning allows us to apply the same method as before).

More precisely, we have for $r \geq 0$

$$u(t_{n-1}+r) = \mu(1-e^{-\frac{r}{\tau}}) + \frac{1}{\tau}\int_0^r e^{\frac{s-r}{\tau}} I_e(s+t_{n-1})\,ds + \frac{\sigma}{\tau}\int_0^r e^{\frac{s-t}{\tau}} dW(s). \tag{5.3.5}$$

Let r_n be the nth interspike interval. We have $t_n = t_{n-1} + r_n$. The same local martingale as in section 5.3.1 can be used. The Dubins-Schwarz' theorem yields the same change of variables and eventually the crossing condition reads :

$$\tilde{W}_r = \frac{\tau}{\sigma}\left\{(\theta-\mu)\sqrt{\frac{2}{\tau}r+1} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e^{(n)}(s)ds\right\},$$

where

$$\tilde{I}_e^{(n)}(s) = \frac{I_e(\frac{\tau}{2}\log\left(\frac{2}{\tau}s+1\right)+t_{n-1})}{\sqrt{\frac{2}{\tau}s+1}}.$$

Finally, the problem of finding the sequence of stopping times $(t_n)_{n\geq 1}$ is equivalent to the problem of finding the first stopping time. Furthermore, we can see that the sequence (t_n) is a Markov chain, and that if the input is constant, the interspike intervals are independent and identically distributed.

5.4 Integrate and fire with exponentially decaying synaptic conductances

We modify the model of section 5.3 to include exponentially decaying synaptic conductances.

$$\begin{cases} \tau du &= (\mu - u(t))dt + I_e(t)dt + I_s(t)dt \\ \tau_s dI_s &= -I_s(t)dt + \sigma dW \end{cases}$$

We can integrate this system of stochastic differential equations as follows. The first equation yields

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\,ds + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_s(s)\,ds,$$

the second equation can be integrated as

$$I_s(t) = I_s(0)e^{-\frac{t}{\tau_s}} + \frac{\sigma}{\tau_s}\int_0^t e^{\frac{s-t}{\tau_s}} dW(s),$$

where $I_s(0)$ is a given random variable. We define $\frac{1}{\alpha} = \frac{1}{\tau} - \frac{1}{\tau_s}$. Replacing in the first equation $I_s(t)$ by its value in the second equation we obtain

$$u(t) = \mu(1 - e^{-\frac{t}{\tau}}) + \tfrac{1}{\tau}\int_0^t e^{\frac{s-t}{\tau}} I_e(s)\,ds + \tfrac{I_s(0)}{1-\frac{\tau}{\tau_s}}(e^{-\frac{t}{\tau_s}} - e^{-\frac{t}{\tau}}) + \frac{\sigma}{\tau\tau_s}e^{-\frac{t}{\tau}}\int_0^t e^{\frac{s}{\alpha}}\left(\int_0^s e^{\frac{s'}{\tau_s}} dW(s')\right) ds$$

5.4.1 The time of the first spike

We prove the following

Lemma 5.4.1. Let $X(t) = \int_0^t e^{\frac{s}{\alpha}}\left(\int_0^s e^{\frac{s'}{\tau_s}} dW(s')\right) ds$, the stochastic process $X(t)$ is a Brownian motion if we change the time scale:

$$X(t) = W\left((\tau - \tau_s)^2 e^{2\frac{t}{\tau}} - \tau_s(\tau + \tau_s)e^{2\frac{t}{\alpha}} + 4\tau\tau_s e^{\frac{t}{\alpha}} - \tau(\tau + \tau_s)\right)$$

.

Proof. This result is also a consequence of the Dubins-Schwarz' theorem. We provide a short elementary proof. By exchanging the order of integration in the definition of $X(t)$ (Fubini's theorem, which here is equivalent to an integration by parts) we obtain

$$X(t) = \int_0^t e^{\frac{s'}{\tau_s}}\left(\int_{s'}^t e^{\frac{s}{\alpha}} ds\right) dW(s') = \alpha\int_0^t e^{\frac{s'}{\tau_s}}(e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}})\,dW(s'),$$

and the result follows from the computation of $f(t) = \alpha^2\int_0^t e^{2\frac{s'}{\tau_s}}(e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}})^2\,ds'$. □

In the same line of idea as in section 5.3, we can express the problem of characterizing the time t_1 at which the membrane potential reaches the threshold θ as that at which

$$X(t) + \frac{\alpha\tau_s}{\sigma}I_s(0)(e^{\frac{t}{\alpha}} - 1) = \frac{\tau\tau_s}{\sigma}\left[(\theta - \mu)e^{\frac{t}{\tau}} + \mu - \frac{1}{\tau}\int_0^t e^{\frac{s}{\tau}} I_e(s)\,ds\right],$$

or equivalently at which

$$W(r) + \frac{\alpha\tau_s}{\sigma} I_s(0)(e^{\frac{f^{-1}(r)}{\alpha}} - 1) = \frac{\tau\tau_s}{\sigma}\left[(\theta-\mu)e^{\frac{f^{-1}(r)}{\tau}} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\,ds\right],$$

where f is the function defined in the proof of lemma 5.4.1 and

$$\tilde{I}_e(s) = e^{\frac{f^{-1}(s)}{\tau}} \frac{I_e(f^{-1}(s))}{f'(f^{-1}(s))}$$

It is easy to verify that if $\tau > \tau_s$, f is monotonously increasing. The time t_1 at which the membrane potential reaches the threshold θ for the first time is therefore obtained, conditionally on the random variable $I_s(0)$, from the time r_1 at which the Brownian motion reaches for the first time the curve $a(r)$ defined by the equation

$$y = a(r) = \frac{\tau\tau_s}{\sigma}\left[(\theta-\mu)e^{\frac{f^{-1}(r)}{\tau}} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e(s)\,ds\right] - \frac{\alpha\tau_s}{\sigma} I_s(0)(e^{\frac{f^{-1}(r)}{\alpha}} - 1)$$

by Durbin's theorem and the formula

$$t_1 = f^{-1}(r_1)$$

5.4.2 The times of the next spikes

As in the case of instantaneous synaptic conductances, we can extend our analysis and compute the conditional probabilities $p(t_n|t_{n-1})$, or rather $p(t_n|t_{n-1}, I_s(0))$, as follows. For $t > t_{n-1}$, let us denote $r = t - t_{n-1}$. We know that the process I_s is Markovian, hence conditionally on t_{n-1} and by the uniqueness of I_s we obtain:

$$I_s(t_{n-1}+r) = I_s(t_{n-1})e^{-\frac{r}{\tau_s}} + \frac{\sigma}{\tau_s}\int_0^r e^{\frac{s-r}{\tau_s}}\,dW(s).$$

Conditionally on t_{n-1} we can integrate the equation from this origin, and we obtain the following expression for the membrane potential:

$$u(t) = u(t_{n-1}+r) = \mu(1-e^{-\frac{r}{\tau}}) + \tfrac{1}{\tau}\int_0^r e^{\frac{s-r}{\tau}} I_e(s+t_{n-1})\,ds + \tfrac{I_s(t_{n-1})}{1-\frac{\tau}{\tau_s}}(e^{-\frac{r}{\tau_s}} - e^{-\frac{r}{\tau}}) + \frac{\sigma}{\tau\tau_s}e^{-\frac{r}{\tau}}\int_0^r e^{\frac{s}{\alpha}}\left(\int_0^s e^{\frac{s'}{\tau_s}}\,dW(s')\right)ds$$

Here again the problem is exactly the same as finding the first spike time. The only difference is that we condition on t_{n-1}, and this only amounts to change $I_s(0)$ to $I_s(t_{n-1})$ and $I_e(\cdot)$ by $I_e(\cdot + t_{n-1})$. The time t_n at which the membrane potential reaches the threshold θ for the

first time after t_{n-1} is therefore obtained, conditionally on the random variables $I_s(0)$ and t_{n-1}, from the time r_n at which the Brownian motion reaches for the first time the curve $a(r)$ defined by the equation

$$y = a(r) = \frac{\tau\tau_s}{\sigma}\left[(\theta-\mu)e^{\frac{f^{-1}(r)}{\tau}} + \mu - \frac{1}{\tau}\int_0^r \tilde{I}_e^{(n)}(s)\,ds\right] - \frac{\alpha\tau_s}{\sigma}I_s(t_{n-1})(e^{\frac{f^{-1}(r)}{\alpha}} - 1),$$

where $f(t) = \alpha^2 \int_0^t e^{2\frac{s'}{\tau_s}}(e^{\frac{t}{\alpha}} - e^{\frac{s'}{\alpha}})^2\,ds'$ is the change of time scale used in the proof of lemma 5.4.1, and

$$\tilde{I}_e^{(n)}(s) = e^{\frac{f^{-1}(s)}{\tau}}\frac{I_e(f^{-1}(s)+t_{n-1})}{f'(f^{-1}(s))}.$$

Finally we obtain t_n by Durbin's theorem and the formula

$$t_n = t_{n-1} + f^{-1}(r_n)$$

Again, we can state that conditionally on the random variable $I_s(0)$ the sequence $(t_n)_{n\geq 0}$ is a Markov chain.

5.5 Conclusion

We have outlined a method for computing the pdf's of the spikes times of two variations of the integrate and fire neuron model with synaptic conductances. The method is based upon representing the membrane potential as the sum of a deterministic function and a local martingale. Due to a theorem by Dubins and Schwarz, by changing the time scale we can turn the local martingale into a Brownian motion and the problem of computing the pdfs of the spikes times into that of computing the first-passage density of the Brownian motion to a curved boundary. This particular problem can be solved through a method due to Durbin [17] which provides a series approximation of the pdf. Numerical experiments show that the series converges rapidly. The method can be extended to more complex neuron models [24] [8]

Conclusion

This study has opened a large number of issues, I will try to list now. Addressing those problem would probably be the first part of my thesis work I will follow jointly in the Odyssée laboratory and in the Omega Laboratory.

First we would like to extand the method presented in the chapter 5 for some other types of neurons and of inputs. The problem is that we do not have any proof of the convergence of Durbin's expansion when the frontier is not concave or convex. So it would be interesting to extand the proof of convergence of the Durbin's series to a wider range of processes.

It would also be interesting to study inside Durbin's or Feynman-Kac's frameworks some other types of neurons.

We could also try to get some informations about the pdf of some hitting times using Durbin's fixed-point equation, which is more general than the series expansion and which has not been studied yet, so far as we know.

For the network, we are working to extend the results of Cottrell and Philippe Robert to our problems, and we may have a chance to prove it using Lyapunov functions, but we have no formal proof so far.

Part III

A stochastic network of biological neurons

Chapter 6

Dynamics of Noisy Inhibitory Networks of Integrate-and Fire Neuron: A Stochastic Network Theory Approach

In this chapter we construct a network model of noisy integrate-and-fire neurons. The aim of this section is to prove that a wide range of neuron models fit into a general mathematical framework.

We still have to study some more the mathematical framwork we define here.

Nevertheless, some mathematical results are already known, and have been proved in the past ten years by some authors such as Marie Cottrell, Philippe Robert and Tatiana Turova. We will state these results in the section 7, but it does not apply directly to our network model. All my future work will consist in extending these results to a more general case where the biological networks lie.

6.1 Introduction : Basic definitions

In this paper we build a bridge between a wide range of biological networks models and a general mathematical framework.

The networks studied consist in a set of N noisy integrate-and-fire models. Every neuron of the networks has the same dynamics (the parameters of the model can change, such as the spiking threshold, the time constants, the noise level, ...).

The interactions between the neurons are inhibitory: when a postsynaptic neuron receives a spike, it prevent it from spiking immediately. The connectivity map is arbitrary. In the sequel, the set of neighbors of the neuron i is denoted $\mathcal{V}(i)$.

6.1.1 Integrate-and-fire neurons

In the classical neuron models, the state of a neuron is described by its membrane potential, which we will denote $V^{(i)}$ in the following.

During the time intervals when no neuron spike, the states of all neurons evolve as independent stochastic processes, following one of the different evolution equation as detailed in section 6.2.

When the membrane potential $V^{(i)}(t)$ of some neuron, say i, reaches a deterministic threshold value θ at time t_0 (i.e. $V^{(i)}(t_0^-) = \theta$), then a spike is produced, and subsequently we have :

- the membrane potential $V^{(i)}$ reset : ($V^{(i)}(t_0) = V_r$)
- the states of the target neurons j connected to the neuron i (i.e. $j \in \mathcal{V}(i)$) are modified. The effect of a pre-synaptic spike received by a neuron can be instantaneous (i.e. $V^{(j)}(t_0) = V^{(j)}(t_0^-) + w_{i,j}$ where $w_{i,j} < 0$ denotes the synaptic efficiency of the connection $i \to j$) or more complicated (via synaptic current, synaptic pulses, etc.). Many examples are treated in the following sections 6.2 and 6.3. Figure 6.1.1 illustrates the dynamics of the network, showing the structure of the network in 6.1(a) and the dynamics of the membrane potential in 6.1(b)

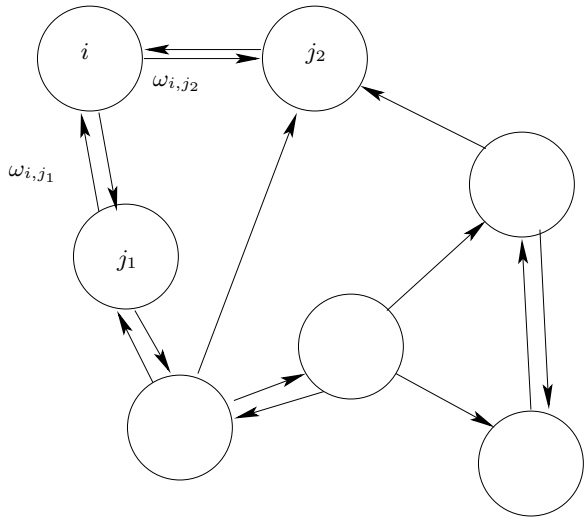
This type of model was studied for instance by Brunel and Hakim [9] with the use of the Fokker-Planck equation. Assuming that the network is sparsely connected, they found that in the limit $N \to \infty$ the network exhibited a sharp transition between two regimes: a stationnary regime and a weakly synchronized oscillatory regime. Each neuron is an integrate-and-fire neuron, and is randomly connected to C neurons of the network, and to C_{ext} external neurons. The sparse connectivity assumption is $\varepsilon = \frac{C}{N} \ll 1$. Interactions between external and internal neurons are delayed by a constant delay δ (i.e. when a spike is emitted by a neuron of the network, it decreases or increases the membrane potential after a time δ, see section 6.3). This delay plays a crucial role in the generation of global oscillations.

We wish to re-express the dynamics from an event-driven point of view (see for example Reutimann et al [30]), and to consider the noise in the dynamics of each individual neuron.

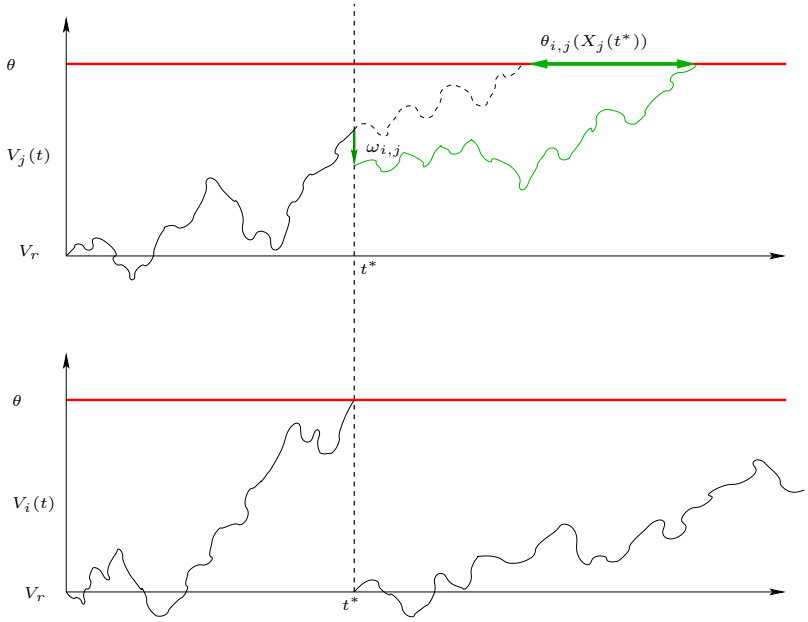
6.1.2 Mathematical Framework: The Hourglass Model

Independently, in the field of stochastic networks and queue theory and Markov processes, a network model has been developed during the last 10 years. It is referred for instance as the *hourglass model* by Turova [3, 12, 38, 39]. This model has been introduced for the first time by Marie Cottrell in [11], and the variable taken into account was initially called the *inhibition process*, which is a rather confusing term in the neuroscience field, so we will use in the sequel the term of *countdown process*.

Consider a N nodes network. This model has two types of parameter:



(a) Oriented Network



(b) Sample traces for two connected neurons $i \to j$

- The random variables $(Y_i)_{i=1\dots N}$ which describe the interspike interval distribution for the neuron i.
- $(\eta_{i,j})_{i\neq j}$ describing the interaction of $i \to j$.

Let the state of the network be described by a N-dimensional vector $(X_t)_{t\geq 0} = \left((X_t^{(i)})_{i=1\dots N}\right)_{t\geq 0}$ having the following dynamics: let $t > 0$,

1. if $\forall i \in \{1\dots N\}$, $X_i(t) > 0$ then each component of X decreases linearly with slope -1 in time.
2. if $\exists i \in \{1\dots N\}$, $X_i(t^-) = 0$, subsequently we have:
   - X_i is reset to a random variable independent of all the history of the process and with distribution Y_i.
   - $\forall j \in \mathcal{V}(i)$, a positive random variable $\eta_{i,j}$ is added to X_j:

$$X_j(t) = X_j(t^-) + \eta_{i,j}$$

Our study will lead us to extend this model to other types of random variables. The only difference we have from the initial hourglass model defined here is in the random variable of interaction $\eta_{i,j}$. In the cases we study, this random variable can depend on $X_j(t^-)$, t and a N^2-dimensional process H defined by:

Definition 6.1.1. Let $(H_t)_{t\geq 0} = ((h_{i,j}(t))_{t\geq 0}$, where $\forall t \geq 0$, $h_{i,j}(t) \in \mathbb{N}$ be the *past-interaction* matrix defined by:

1. $\forall i \in \{1,\dots,N\}$, $\forall t \geq 0$, $h_{i,i}(t) = 0$
2. if $j \neq i$, $h_{i,j}(t)$ is the number of spikes received by the neuron j from neuron i

Let us now assume that $\eta_{i,j}$ is no more a random variable but a random function of the variables (X, H, t).

Theorem 6.1.1. *Let $Y_t := (X_t, H_t, t)$ is a Markov jump process.*

- *The first jump after time t occur at time $\inf_{k=1\dots N} X_t^{(k)}$ and we denote i the neuron realizing this inf.*
- *At this time, say τ*
  - *$X^{(i)}(\tau)t$ is set to an independent copy of Y_i*
  - $h_{i,j}(\tau) = h_{i,j}(\tau^-) + \mathbb{1}_{j\in\mathcal{V}(i)}$, $\forall j \in \{1,\dots N\}$
  - $h_{j,i}(\tau) = 0$, $\forall j \in \{1,\dots N\}$
  - *All the over components of H are unchanged.*
  - $\forall j \in \mathcal{V}(i)$, $X^{(j)}(\tau) = X_{\tau^-}^{(j)} + \eta_{i,j}(X^{(j)}(\tau^-), H_{\tau^-}, \tau)$

6.1.3 From Biological networks to the Hourglass model

Let us now consider a network such as those defined in section 6.1.1.

Definition 6.1.2. *[Countdown process]* For each neuron i, let us define $X^{(i)}(t) \geq 0$ the duration of time (after time t) till the first firing moment of this neuron, if no interaction takes place meanwhile. We will call this stochastic process the *countdown process* of the neurons.

Remark 10. This process is called *countdown* because of its dynamics, but in fact at any time, its value gives us the time to wait till the next spike, so it can be also seen as a *clock*. It can be seen as a countdown set at the instant of reception of the last spike or just after the spike, to the time to wait for the next spike to occur if no interaction takes place meanwhile.

Proposition 6.1.2. The dynamics of the variable X^i is linear and decreasing in the intervals of time where no spike is received or produced:

$$\frac{dX^{(i)}}{dt} = -1 \tag{6.1.1}$$

At time t, the next spike will occur in neuron $i = \underset{j \in 1 \ldots N}{\operatorname{Arg\,Min}} X^{(j)}(t)$ at time $t + X^{(i)}(t)$ (t is the absolute time). In most of the case (for instance in the case where all the random variables have a density with respect to Lebesgue's measure), the probability for two neurons to spike exactly at the same time is null since the network is inhibitory so we will neglect this case and assume that only one neuron spikes at a given time. At spike time, $X^{(i)}(t)$ is instantaneously reset by drawing the law of a random variable noted Y_i, which has the same distribution as the first hitting time of the stochastic process $(V_t^{(i)})_{t \geq 0}$ to θ (the distribution of the interspike interval in terms of neural models). The states of all neurons just before the spike are given by: $X^{(j)}\left((t + X^{(i)})^-\right) = X^{(j)}(t) - X^{(i)}(t)$. Finally, the states of all neurons j connected to neuron i are modified according to the spike produced by neuron i. Because the interaction is inhibitory, this amounts to postponing the spike produced by neuron j by an amount $\eta_{i,j} \geq 0$ (see Fig 6.1(b)), because the inhibition increases the time to the next spike.

In general, $\eta_{i,j}$ is a random variable depending on the membrane potential $V^{(j)}$ at time t. In most of the models considered in section 6.2, it depends in fact only on $X^{(j)}$, so that the update reads $X^{(j)}(t + X^{(i)}) = X^{(j)}(t) - X^{(i)}(t) + \eta_{i,j}(X^{(j)}(t) - X^{(i)}(t))$, where $\eta_{i,j}(x)$ is a random function.

In all our mathematical study we consider the process

$$X(t) := (X^{(i)}(t))_{1 \leq i \leq N} \tag{6.1.2}$$

Up to an additional Markov chain, this model will be a continuous time Markov process, as we will show in section 6.2.

Nevertheless, the process $(X_t)_t$ defined is piecewise continuous, so the analysis of Davis in [13] can be applied here. But our case is even more simple since the discontinuities are very simply related to the value of the process. This very particular property implies that studying the continuous time stochastic process is strictly equivalent to considering one of the two folloving discrete time Markov chain (6.1.3) and (6.1.4).

Proposition 6.1.3. Let (t_n) denote the time sequence of the spikes emitted by one of all the neurons, (Z_n) the sequence of the states just before each spike and (X_n) the vector of states just after each spike.

$$Z_n = X(t_n^-) \tag{6.1.3}$$
$$X_n = X(t_n) \tag{6.1.4}$$

Consider now the random variable $\eta_{i,j}$ to add to the state of a postsynaptic neuron j when receiving a spike from i at time t^*. This random variable is the delay caused by the inhibition, i.e. the additional time to wait for j to spike because of the reception of a presynaptic spike.

Example. In the case of instantaneous synaptic interactions, the inhibition applies to the membrane potential and the random variable to add to the state of the neuron $j \in \mathcal{V}(i)$ is:

$$\theta_{i,j}(X^{(j)}(t_0^-)) = (\tau^j_{V^{(j)}(t_0^-)+w_{i,j}} - \tau^j_{V^{(j)}(t_0^-)}|X^{(j)}) = (\tau^j_{V^{(j)}(t_0^-)+w_{i,j}} - X^{(j)}|X^{(j)}) \tag{6.1.5}$$

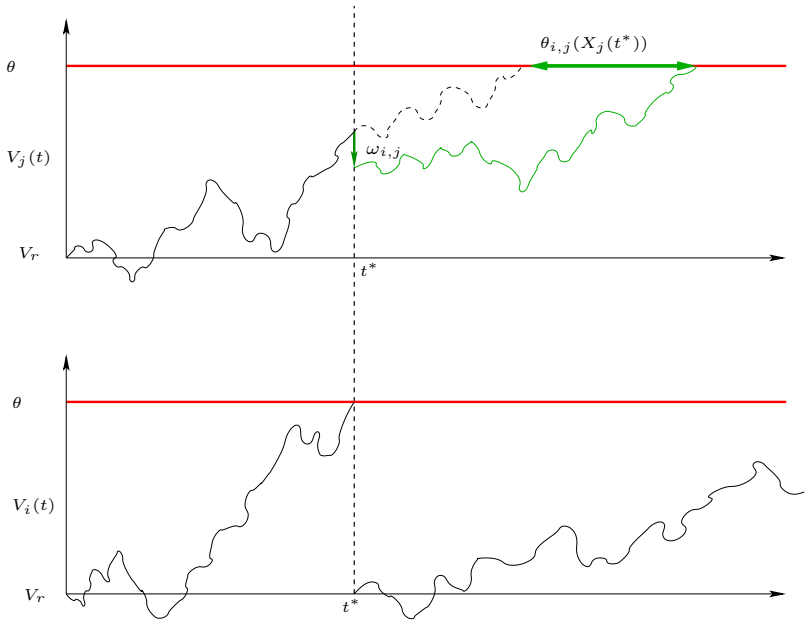
where τ^j_x denotes the first hitting time of the constant barrier θ starting from x of the stochastic process $V^{(j)}(t)$.

All the work done in the following sections 6.2 and 6.3 is aimed to show that many biological neuron models fit into the framework described in section 6.1.2 and to identify the parameters of the corresponding Hourglass model.

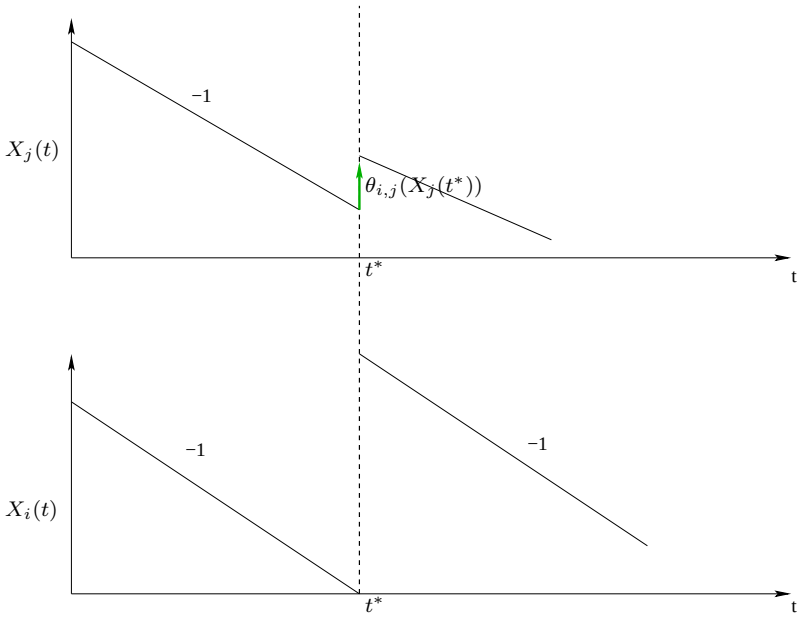
6.2 Single Neuron Biological Models

In this section we consider different types of models of integrate-and-fire neurons and different types of synaptic interactions, and up to a transformation show that the network model can be considered as an hourglass network, and identify the parameters of the model.

The first model we consider is a noisy integrate-and-fire neuron without leak current, which we refer as the perfect noisy integrate-and-fire neuron. We then add a leak current.



(c) membrane potential dynamics



(d) Corresponding *countdown process* : An inhibitory spike at time t^* postpones the next spike to time $X^{(j)}(t^*) + \theta_{i,j}(X^{(j)}(t^*))$

6.2.1 Perfect integrate-and-fire models

Model

We start by considering integrate-and-fire models driven by noise. The membrane potential of the neuron i, denoted $V^{(i)}(t)$, is driven by the following equation between two spikes:

$$\tau_i dV^{(i)}(t) = I_e^{(i)}(t)dt + \sigma_i dW_t^{(i)} \tag{6.2.1}$$

where τ_i is the membrane potential time constant, $I_e^{(i)}(t)$ is the input current, σ_i the standard deviation of the noise and $(W^{(i)})_{1\leq i\leq N}$ are independent Brownian motions, which represents external synaptic stimulations[1].

The neuron fires when its membrane potential reaches the threshold θ: the membrane potential is reset to a value V_r and a spike is emitted.

$$V^{(i)}(t^-) = \theta \Rightarrow V^{(i)}(t) = V_r \tag{6.2.2}$$

We refer to the case $I_e^{(i)} \equiv 0$ as the perfect integrate-and-fire model and $I_e^{(i)}(t) \equiv \mu_i \neq 0$ as the perfect integrate-and-fire with drift.

In the absence of interactions, $V^{(i)}(t)$ integrates the entry $I_e^{(i)}$ with an additive noise proportional to a Brownian motion, i.e. :

$$V^{(i)}(t) = \int_0^t I_e(i)(s)\, ds + \sigma_i W_t^{(i)} \tag{6.2.3}$$

The interactions are taken instantaneous: if neuron i spikes at time t^*, then:

$$\forall j \in \mathcal{V}(i) V^{(j)}(t^*) = V^{(j)}(t^{*-}) + \omega_{i,j} \tag{6.2.4}$$

Link with the Hourglass model and parameters

As in section 6.1.3, we define $X^{(i)}$ the corresponding countdown process, so we have to derive the two random parameters of this model.

In the general case, the threshold crossing condition happens at time:

$$\tau := \inf\left\{t > 0;\ \ W_t^{(i)} = \frac{1}{\sigma_i}(\theta - \int_0^t I_e(i)(s)\, ds)\right\} \tag{6.2.5}$$

[1] It could have been possible to replace the Brownian motions by instantaneous spikes ($V^{(i)} \to V^{(i)} + \delta$) triggered according to a Poisson process (the equation (6.2.1) would be the diffusion approximation of this type of excitation). This would change considerably the following study, since the process is no more continuous between two consecutive spikes

With a general entry I_e, this time can be approximated using for instance the methods of Durbins (see for instance [17, 16]), as stated in Faugeras, Papadopoulo and Touboul in [19].

Let us compute explicitly the probability density function of this hitting time in the case $I_e^{(i)} \equiv 0$ (Brownian motion) and in the case $I_e^{(i)} \equiv \mu_i \neq 0$ (drifted Brownian motion).

The expression of the distribution of the first hitting time to the boundary θ, which is the distribution of U_i, is well known analytically, see below equations (6.2.6) and (6.2.7).

Let us examine the effect of synaptic interactions in the two cases:

We consider that neuron j receives an inhibitory spike from neuron i at time t. The time of the next spike of neuron j is $t + X^{(j)}(t) + \eta_{i,j}$, where $\eta_{i,j}$ is the first hitting time of the drifted Brownian motion to θ, starting from $\theta + w_{i,j}$ (recall that $w_{i,j} \leq 0$, which is the first hitting time of a drifted Brownian motion starting from 0 to the constant barrier $w_{i,j}$ (because the stochastic process solution of (6.2.1) is a Lévy process).

For the Brownian motion without drift, the probability density function of this random variable is well known and can be computed by using the exponential martingale of the Brownian motion and the optional sampling theorem. Explicit computation of this hitting time is given in 4.2.1. This density reads :

$$p^{(j)}(t) = \frac{|w_{i,j}|}{\sqrt{2\pi t^3}} e^{-\frac{w_{i,j}^2}{2t}} \mathbb{1}_{\mathbb{R}_+^*}(t) \tag{6.2.6}$$

For the Brownian motion with drift, we can prove by means of the Girsanov's theorem [26] that this random variable is absolutely continuous with respect to (w.r.t.) Lebesgue's measure and has the density :

$$p^{(j)}(t) = \frac{|w_{i,j}|}{\sqrt{2\pi t^3}} e^{-\frac{(w_{i,j} - \mu_j\, t)^2}{2t}} \mathbb{1}_{\mathbb{R}_+^*}(t) \tag{6.2.7}$$

Thus in the case of the perfect integrate-and-fire (resp. perfect integrate-and-fire with drift) model, the effect of the reception of a spike is equivalent to adding an independent random variable with the probability density w.r.t. Lebesgue's measure given by (6.2.6) (resp. (6.2.7)).

6.2.2 Leaky integrate-and-fire models

Let us now consider leaky integrate-and-fire (LIF) models.

The general LIF equation with instantaneous synaptic and noisy input currents reads :

$$\begin{cases} \tau_i dV^{(i)} & = & f_i(V^{(i)}, t)dt + \sigma_i dW_t^{(i)} \\ V^{(i)}(t^-) & = & \theta \Rightarrow V^{(i)}(t) = V_r \end{cases} \tag{6.2.8}$$

Where $(W_t^i)_{1 \leq i \leq N}$ are independent Brownian motions.

For technical reasons we consider right-continuous sample paths. In all the following sections, we only consider

$$f_i(u, s) = -u + I_e^{(i)}(s) \tag{6.2.9}$$

So finally the evolution equation of the membrane potential during the time where no spike is emitted reads:

$$\left\{ \begin{array}{lcl} \tau_i dV^{(i)} & = & -V^{(i)}dt + I_e^{(i)}(t)dt + \sigma_i dW_t^{(i)} \\ V^{(i)}(t^-) & = & \theta \Rightarrow V^{(i)}(t) = V_r \end{array} \right. \tag{6.2.10}$$

Where $I_e^{(i)}$ is a current modeling the entries of the neuron i.

The aim of this section is to relate those type of neuron models to the Hourglass model. To do this, we consider the countdown process related to this

The random variable denoted Y_i in section 6.1.2 will be the same for all synaptic interactions. It is distributed as the hitting time of the threshold θ starting from V_r of the process defined by (6.2.10). The only difficulty arises from the current input I_e: if it depends on the time t, then this random variable has not the same law at each time but depends on the time of the spike.

If I_e is constant, then:

$$Y_i := \inf \left\{ t > 0;\ \ V_t^{(i)} = \theta | V_0^{(i)} = V_r \right\} \tag{6.2.11}$$

where $V^{(i)}$ is solution of (6.2.10).

If I_e is not constant, then assume that the neuron i spikes at time t^*. At this time, the process $X^{(i)}$ is reset by drawing an independent random variable having the law of (6.2.11) where $V^{(i)}$ is solution of (6.2.10) with the time-shifted input current $I_e^{(i)'}(t) = I_e^{(i)}(t + t^*)$.

Let us now specify the synaptic interactions and compute the other parameter of the Hourglass model, denoted $\eta_{i,j}$ in the section 6.1.2.

LIF model with instantaneous synaptic currents

We consider that the membrane potential follows the equation (6.2.10), together with the spiking condition:

$$V^{(i)}(t^-) = \theta \Rightarrow \left\{ \begin{array}{lcl} V^{(i)}(t) & = & V_r \\ V^{(j)}(t) & = & V^{(j)}(t^-) + w_{i,j} \mathbb{1}_{j \in \mathcal{V}(i)} \end{array} \right. \tag{6.2.12}$$

We compute the membrane potential with and without the reception of a spike. Let t^* be the time when the neuron j receives a spike, $V^{(j)}$ the membrane potential of the neuron j after reception of a spike, $\widetilde{V}^{(j)}$ the membrane potential of the neuron j without any interaction with other neurons, $V_{(j)}^* := V^{(j)}(t^{*-})$ and $X_{(j)}^* := X^{(j)}(t^{*-})$. We have :

$$\begin{aligned} V^{(j)}(t^* + t) =& (V_{(j)}^* + w_{i,j})e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{(s-t)/\tau} I_e^j(s + t^*)\, ds + \\ & \frac{1}{\tau}\int_0^t e^{(s-t)/\tau} \sigma\, dW_s \end{aligned}$$

$$\widetilde{V}^{(j)}(t^*+t) = V^*_{(j)}e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{(s-t)/\tau} I_e^j(s+t^*)\,ds + \frac{1}{\tau}\int_0^t e^{(s-t)/\tau}\sigma\,dW_s$$

From the two equations above we can easily see that :

$$V^{(j)}(t^*+t) = \widetilde{V}^{(j)}(t^*+t) + w_{i,j}e^{-t/\tau} \tag{6.2.13}$$

For $t = X^*_{(j)}$ we have $\widetilde{V}^{(j)}(t^*+X^*_{(j)}) = \theta$ and from (6.2.13) we have :

$$V^{(j)}(t^*+X^*_{(j)}+t) = (\theta + w_{i,j}e^{-X^*_{(j)}/\tau})e^{-t/\tau} + \frac{1}{\tau}\int_0^t e^{(s-t)/\tau} I_e^j(s+t^*+X^*_{(j)})\,ds + \frac{1}{\tau}\int_0^t e^{(s-t)/\tau}\sigma\,dW_s \tag{6.2.14}$$

Remark 11. To find this result we could have integrated the difference between V and $\widetilde{V}$. We keep this simple but longer proof because it is more general and applies to the other results we state in the sequel.

It is clear from equation (6.2.13) that the hitting time of the barrier θ by the process $V^{(j)}$, conditionally on the random variable $X^*_{(j)}$ is the sum of $X^*_{(j)}$ and an independent random variable whose law is equal to the hitting time of the barrier θ of the process (6.2.8) with initial condition $V^{(j)}(0) = \theta + w_{i,j}e^{-X^*_{(j)}/\tau}$ and with the time shifted input current $\tilde{I_e^j}(t) := I_e^j(t+t^*+X^*_{(j)})$.

$$\eta_{i,j}(u) := \inf\left\{t>0;\ \ U^{(j)}(t) = \theta | U^{(j)}(0) = \theta + w_{i,j}e^{-X^*_{(j)}/\tau}\right\} \tag{6.2.15}$$

where $U^{(j)}(t)$ is the solution of equation (6.2.10) with the time-shifted current specified.

Remark 12. We will show in section 4.2.2 that for some simple cases of the input current the Laplace transform of this random variable is known. In other cases, the methods developed in [19] will apply and we can approximate these hitting times.

Remark 13. We also show that this random variable tends to 0 in law and almost surely (a.s.), when $X^*_{(j)}$ tends to infinity. The influence of a spike received when the neuron is strongly inhibited is very small.

Remark 14. Finally, in this case the random variable to add depends on $X^*_{(j)}$. Conditionally to $X^*_{(j)}$, the random variable added is independent of the past of the process, so the sequence $X^{(j)}$ is Markovian.

LIF model with exponentially decaying synaptic conductances

The equations of the models are the following :

$$\left\{ \begin{array}{lcl} \tau_i dV^{(i)} & = & (\mu_i - V^{(i)}(t))dt + I_e^i(t)dt + I_s^i(t)dt \quad 1 \leq i \leq N \\ \tau_s dI_s^i & = & -I_s^i(t)dt + \sigma_i dW_t^i \end{array} \right. \tag{6.2.16}$$

The spike condition in this model is :

$$V^{(i)}(t^-) = \theta \Rightarrow \left\{ \begin{array}{lcl} V^{(i)}(t) & = & V_r \\ I_s^j(t) & = & I_s^j(t^-) + w_{i,j}\mathbb{1}_{j\in\mathcal{V}(i)} \end{array} \right. \tag{6.2.17}$$

Qualitatively, when a spike is received by a neuron, the synaptic current I_s integrates the spike and the effect on the membrane potential is smoother.

Driving the same type of calculus as in the previous section we obtain, for $j \in \mathcal{V}(i)$ and $\tau \neq \tau_s$ the relationship :

$$V^{(j)}(t^* + t) = \widetilde{V}^{(j)}(t^* + t) + e^{-t/\tau} w_{i,j} \frac{1 - e^{-\alpha t}}{\alpha} \tag{6.2.18}$$

where $\alpha = \frac{1}{\tau_s} - \frac{1}{\tau}$ and again $\widetilde{V}^{(j)}(t^* + t)$ the membrane potential of the neuron j without any interaction.

Eventually we can see that after the time $X^*_{(j)}$, the membrane potential of j is $\theta + w_{i,j}e^{-t/\tau}\frac{1-e^{-\alpha X^*_{(j)}}}{\alpha}$. The evolution of the potential $V^{(j)}$ after $t^* + X^*_{(j)}$ and conditionally on $X^*_{(j)}$ and $I_s(t^*)$ is independent of the past, so we have to wait for the process (6.2.17) to reach the threshold θ from the initial condition $\theta + w_{i,j}e^{-t/\tau}\frac{1-e^{-\alpha X^*_{(j)}}}{\alpha}$ and with the time shifted currents $\tilde{I_e^j}(t) := I_e^j(t + t^* + X^*_{(j)})$.

Remark 15. In this case we note that the process X_t itself is not a Markov process anymore, but the process $(X(t), I_s(t))_t$ is a Markov process.

Note that in the case $\tau = \tau_s$ we only have to replace the expression $\frac{1-e^{-\alpha X^*_{(j)}}}{\alpha}$ by $X^*_{(j)} w_{i,j} e^{-t/\tau}$. Here again, the random variable tends almost surely to 0, even if the effect of the spike is larger than in the case (6.2.12) because the spike is integrated by the synaptic current and affects the membrane potential for a longer time.

LIF model with general post-synaptic current pulse

In this section we consider a LIF neuron described by (6.2.8). Like presented in the section 4.1.3 of [22] each presynaptic spike generates a postsynaptic current pulse. More precisely, if the neuron i spikes at time t^* and $j \in \mathcal{V}(i)$ receives the spike, then this neuron feel an additional input current

$$I_{PSP}(t^* + t) = w_{i,j}\, \alpha(t) \tag{6.2.19}$$

Let's include this effect inside the input current $\widetilde{I}_e$ (i.e.

$$\widetilde{I}_e(t) = Ie(t) + \sum_{i \neq j} \sum_{t^j \leq t_i^j \leq t} w_{i,j}\, \alpha(t - t_i^j)$$

where t^j denotes the time of the last spike emitted by the neuron j and t_i^j the sequences of spikes emitted from the neuron i to the neuron j.

The same calculations drive to :

$$V^{(j)}(t^* + X^*_{(j)}) = \theta + w_{i,j} e^{-X^*_{(j)}/\tau} \int_0^{X^*_{(j)}} \alpha(s) e^{s/\tau} ds \tag{6.2.20}$$

So eventually the lasting time to spike for the neuron j is the time the stochastic process $V^{(j)}$, beginning from the value (6.2.20), reaches the threshold θ, with a new external current. The random variable here is again $(X(t), \widetilde{I}_e(t))_t$. Adding this new Markov process allows us to consider an extended model of the hourglass model in which one component is the countdown process.

LIF model with a potential-dependant post-synaptic current

The equation (6.2.18) is a reasonable model of interaction. Nevertheless in reality it is even more complicated. In fact the amplitude of the post-synaptic current pulse depends on the actual value of the membrane potential $V^{(j)}$. It has been proved that each presynaptic spike evokes a change in the conductance of the post-synaptic membrane with a certain time course $g(t - t^*)$. A post-synaptic current model taking in account this type of phenomenon can be written as :

$$\begin{cases} \tau dV^{(i)} & = & -V^{(i)}dt + I_e(t)dt + I_s(t)dt + \sigma dW_t^i \\ V^{(i)}(t^-) & = & \theta \Rightarrow V^{(i)}(t) = V_r \end{cases} \tag{6.2.21}$$

where I_s is null if the neuron i doesn't receive a pre-synaptic spike. If a neuron, say j, receives a spike from one of its neighbors i, we add to the current I_s the synaptic current $w_{i,j} g(t - t^*)(V^{(j)} - E_{\text{syn}})$ where E_{syn} is the reversal potential of the synapse.

In this case we can still have an explicit expression for the membrane potential, but we can't have an closed-form for the random variable of the delay induced by the reception of a spike.

$$V^{(j)}(t + t^*) = V^*_{(j)} e^{-\Phi(t)} + \int_0^t I_e^*(s) e^{\Phi(s) - \Phi(t)}\, ds + \int_0^t \sigma e^{\Phi(s) - \Phi(t)}\, dW_s \tag{6.2.22}$$

With $\Phi(t) := \frac{1}{\tau}\left(t + \int_0^t w_{i,j} g(s)\, ds\right)$ and $I_e^*(t) = I_e(t^* + t) + w_{i,j} g(t) E_{\text{syn}}$. This membrane potential is to compare to the potential without any spike received, which reads :

$$\widetilde{V}^{(j)}(t + t^*) = V^*_{(j)} e^{-t/\tau} + \int_0^t I_e(t^* + s) e^{(s-t)/\tau}\, ds + \int_0^t \sigma e^{(s-t)/\tau}\, dW_s \tag{6.2.23}$$

So we can't write a simple relation between (6.2.22) and (6.2.23) more explicit than (6.1.5). Again, X itself is no more a Markov process, it depends on the number of spikes received between the last spike emitted by the neuron j and t, like in the section of the LIF model with a potential dependant post-synaptic current.

This case seems very difficult to deal with so we won't discuss it any further.

6.3 Including Synaptic Delays and Refractory Period

In all the models of section 6.2 we have modeled different types of spike integration in the post-synaptic neuron, but we never considered the spike transmission in the axon and the behavior of a neuron after emitting a spike. In this section we discuss the effect of considering those types of phenomena in the models presented in the previous section.

6.3.1 Synaptic Delays and Refractory Period

In this section we build models of network including synaptic delays. Those synaptic delays model the transmission time of the spike in the axon. In terms of network interactions, we consider that spikes emitted by a neuron do not affect instantaneously the target neurons, but only after some delay $\Delta_{i,j}$ (c.f. Fig. 6.3.2).

The refractory period models the perturbation induced by the emission of a spike by a neuron, just after having triggered. More precisely, in most nerve cells, the action potential is followed by a transient hyperpolarization, called the *after-potential*. This phenomenon is closely linked with the ion channels behavior after a spike emission. During this transition period, the neuron is in a *refractory state*, and it is impossible to excite the cell, no matter how great the stimulating current applied is (see for instance [25], chapter 9, for a further biological discussion of the phenomenon and [22, 2] for a discussion on modelling this refractory period). In the rest of the section we denote the refractory period R_i.

If an incoming spike from neuron i acts on neuron j at time t, we distinguish two different cases, depending on wether $\Delta_{i,j} < X^{(j)}(t)$ or not.

If $\Delta_{i,j} < X^{(j)}(t)$, then the reception of a spike at time t influences the post-synaptic neuron at time $t + \Delta_{i,j}$ the same ways as discussed in the different models considered in section 6.2.

If $\Delta_{i,j} \geq X^{(j)}(t)$, the neuron j will spike before the incoming spike from the neuron i arrives. If $\Delta_{i,j} - X^{(j)}(t) \leq R$ then the spike is lost, since it arrives at neuron j during the refractory period. Otherwise it will influence the neuron j at time $t + \Delta_{i,j}$ (this case could be troublesome in our mathematical framework).

Finally, if the neuron j spikes at time t_0 and receives a spike from neuron i after having spiked at time $t_1 > t_0$, and if $(t_1 - t_0) + \Delta_{i,j} < R$ then again this spike is lost.

6.3.2 A special case of synaptic delays and refractory period

Assumption 6.3.1. In this case, we assume that the refractory period is equal to the synaptic delay (i.e. $R_j = Delta_{i,j} \ \forall (i,j) \in \{1,\dots,N\}^2$).

This an approximation of the global dynamics described. This assumption allows us to keep considering the same Markov process as before, since the neuron keeps "forgetting" the past events.

In reality we do not need such a strong assumption and we can assume the following property is fulfilled:

Assumption 6.3.2. When a neuron spikes, every incoming spike is lost, and will not affect the future dynamics of this neuron.

Those two assumptions are biologically relevant: we know that the probability for a spike to occur during the short critical period of time is very small and we can in a first model neglect this case, which is not fundamental in the studied phenomenon. On the other hand, it is known that refractory period and synaptic are of the same order, around 5ms [14, 22].

Under one of these assumptions, we have two types of interactions between two neighbor neurons. Assume that the neuron i emits a spike to its neighbor j. We can have have one of two effects:

1. If $\Delta_{i,j} < X^{(j)}(t)$, then the neuron j is affected like in the previous models if it received the spike at time $t + \Delta_{i,j}$.
2. If $\Delta_{i,j} > X^{(j)}$, then the spike would not influence the dynamics of $X^{(j)}$.

Let us now check how these synaptic delays affect the random variables to add in our network model, for the different types of models presented in the previous section.

First of all it is clear that since these events only affect the interactions between two neurons, the "private" random variable Y_i is in all the cases discussed already is the same that the one where no synaptic delay or refractory period was taken into account. The only change is that the cell cannot spike during the refractory period, which means that the new random variable Y_i is related to the random variable already computed $\widetilde{Y}_i$ by the following relation:

$$Y_i = \widetilde{Y}_i \mathbb{1}_{\widetilde{Y}_i \geq R_i}$$

Perfect Integrate-and-Fire

Including synaptic delays in the perfect integrate-and-fire model doesn't change very much the initial model. If the spike is received by the post-synaptic neuron (i.e. $\Delta_{i,j} < X^{(j)}(t)$) then we add the same random variable as in the later case, which was the hitting time of a Brownian motion (resp. drifted Brownian motion) with the constant barrier $w_{i,j}$, otherwise it has no effect on the post-synaptic neuron. So in this case we have a state-dependant interaction rather simple, instead of the state independent interaction we had in section

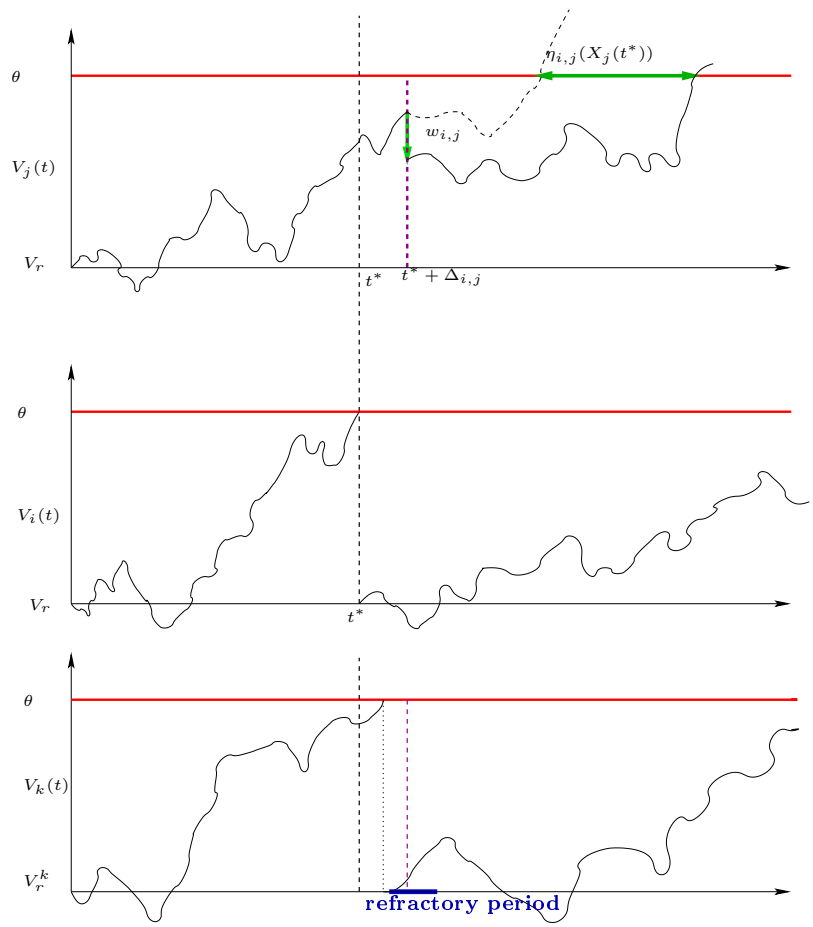


Figure 6.1: Synaptic delays and refractory period. Neuron i spikes at time t^*. Neuron j receives the spike during its classical behavior at time $t^* + \Delta_{i,j}$: it's inhibited after the synaptic delay. Neuron k receives the spike at time $t^* + \Delta_{i,k}$ but spiked during the interval of time $[t^*, t^* + \Delta_{i,k}]$, so the spike is received during its refractory period and the neuron is not inhibited.

6.2.1. Let $\widetilde{\eta}_{i,j}$ be a random variable describing the hitting time of a Brownian motion (resp. drifted Brownian motion) with the constant barrier $w_{i,j}$ and t^* the time when a spike from neuron i is sent to the neuron j. Then the random variable $\eta_{i,j}$ to add is now a random function depending on the state of the postsynaptic neuron j ($X_j(t^*)$) and has the law of the random variable :

$$\eta_{i,j}(X_j(t^*)) = \widetilde{\eta}_{i,j} \mathbb{1}_{X_j(t^*)>\Delta_{i,j}} \tag{6.3.1}$$

Leaky integrate-and-fire models

We compute like in section 6.2.2 the random variables to add in the various cases studied. In all the cases the computations are the same and they are straightforward. It consists in treating the two possible behaviors separately. Let i denote the presynaptic neuron, j the postsynaptic, and t^* the time of the spike. In the first case ($\Delta_{i,j} < X^{(j)}(t^*) =: X_j^*$) we refer to the results obtained in the section 6.2.2 including the delay information, and in the second case the random variable is 0. So we get the following results :

1. *LIF with instantaneous synaptic conductances:* We denote $\widetilde{\eta}_{i,j}(x,\tau)$ the hitting time of the constant θ of the process given by 6.2.9 starting from x, with the time-shifted input current function $I_e(\cdot+\tau)$. The random variable to add is :

$$\eta_{i,j}(X_j^*) = \widetilde{\eta}_{i,j}(\theta + w_{i,j}e^{\Delta_{i,j}}e^{-X_j(t^*)}\mathbb{1}_{X_j>\Delta_{i,j}}, t^* + \Delta_{i,j})\mathbb{1}_{X_j>\Delta_{i,j}} \tag{6.3.2}$$

   We can see in this equation appear an observed synaptic coefficient $w_{i,j}e^{\Delta_{i,j}}$ with is in absolute value larger than the real synaptic coefficient. It will appear in all the LIF models considered.

2. *LIF model with exponentially decaying synaptic conductances, synaptic delay and refractory period:* We still denote $Y_{i,j}(x,\tau)$ the random variable defined above, but for this new process. With the notations of section 6.2, if $\alpha \neq 0$, the random variable to add has the same distribution as :

$$\eta_{i,j}(X_j) = \widetilde{\eta}_{i,j}(\theta + w_{i,j}e^{\Delta_{i,j}}\frac{1-e^{\alpha(\Delta_{i,j}-X_j(t^*))}}{\alpha}e^{-X_j^*}, t^* + \Delta_{i,j})\mathbb{1}_{X_j>\Delta_{i,j}} \tag{6.3.3}$$

   If $\alpha = 0$, we have

$$\eta_{i,j}(X_j) = \widetilde{\eta}_{i,j}(\theta + w_{i,j}e^{\Delta_{i,j}}(X_j^* - \Delta_{i,j})e^{-X_j^*}, t^* + \Delta_{i,j})\mathbb{1}_{X_j>\Delta_{i,j}}$$

3. *LIF model with general post-synaptic current pulse:* With the same notations as before, we have:

$$\eta_{i,j}(X_j) = \widetilde{\eta}_{i,j}(\theta + w_{i,j}e^{\Delta_{i,j}}e^{-X_j^*}\int_0^{X_j^*-\Delta_{i,j}} \alpha(s)e^{s/\tau}\,ds, t^* + \Delta_{i,j})\mathbb{1}_{X_j>\Delta_{i,j}} \tag{6.3.4}$$

4. *LIF model with potential-dependant post-synaptic current, synaptic delays and refractory period:* In this case there is in the general case no explicit formula for the random variable to add, but if any, or a numerical approximation of its probability density function (pdf) then we could compute in the same way the new random variable : conditionally on X_j^*, if $\Delta_{i,j} < X_j^*$, then the random variable has the same distribution as the random variable to add at time $X_j^* - \Delta_{i,j}$, else it is 0.

Chapter 7

Mathematical Analysis of the Hourglass model

In this chapter we review and prove some of the main results obtained in the ergodicity analysis of the Hourglass model. First we will begin to prove the results of Marie Cottrell in the founding article of this network, [11]. In this article the interactions between the neurons are constant (i.e. $\forall i, j$, we have $\eta_{i,j}(u) \equiv \eta$ where η is a positive constant.

In her article, she proves the irreductibility and the aperiodicity of the Markov chain we consider, find a criterion for the positive recurrence of this chain and characterizes the ISI for a two neuron network. In the transient case she shows that some neuron will stop firing in a finite time, and study the pattern formed by the "dead" neurons.

Then we will review the article of Fricker, Robert et al [21], where the interaction variable $\eta_{i,j}$ is no more constant but is a random variable. Specifying the topology of the network, they obtain ergodicity conditions on the parameters of the model, for the fully connected network and for the linear network.

7.1 Constant Interactions

The first result obtained in [11] is the irreductibility and aperiodicity of the chain.

The proof of this property is rather simple. It consists in constructing a set of probability in which all the N neurons fire consecutively. The probability of this set is strictly postive, and we can show that every state is accessible after the Nth spike triggered by the last neuron. The same analysis can be done after the next spike, so at spike $N+1$, which proves that the embedded Markov chain X_n is irreductible and aperiodic.

Then the author proves the following theorem:

Theorem 7.1.1. *If* $\theta < \inf_{i=1,\dots,N} \frac{\mathbb{E}[Y]}{|\mathcal{V}(i)|}$ *and* $\mathbb{E}\left[Y_i^2\right] < \infty$*, then* $(X_t)_t$ *and* (X_n) *are ergodics, irreductibles, aperiodics and positive recurrents.*

7.2 IID Interactions

In the article of Fricker, Robert et al [21], the authors find necessary and sufficient conditions of ergodicity for the system when the variables of interations $\eta_{i,j}$ does not depend on the state of the variable, and are an iid sequence of random variables.

Assume that the network is fully connected, and that the reinitialisation random variables Y_i are exponentially distributed, with parameter λ_i, and that the interactions are the same for all the neighbors of a neuron (i.e. $\eta_{i,j} = \eta_i$ for all $j \in \mathcal{V}(i)$.

For the fully connected network, the authors prove that the network is stable if $\rho = max_i \rho_i := max_i \mathbb{E}[\eta_i]\,\mathbb{E}[Y_i] < 1$.

Under this stability ocndition, they give an explicit expression for the Laplace transform of the invariant measure of the Markov process associated to this model. Then they prove that if $\rho > 1$, then the network is not stable, and after a finite time, only one neuron would spike and all the other neuron are "dead" (i.e. will not fire anymore).

Then the authors examine the case of the linear network of size N. Now the random variables sent to the neighbors are no more the same, but independant and with the same law η_i, which is exponentially distributed (with parameter μ, and assume that $\forall i \lambda_i = \lambda$. Then the authors prove that:

1. if N is odd then the network is stable if $\rho = \frac{\lambda}{\mu} < 1/2$ and not stable if $\rho > 1/2$.
2. if N is even, then the network is stable if $\rho < \frac{1}{2cos(\pi/(N+1))}$ and not stable if $\rho > \frac{1}{2cos(\pi/(N+1))}$

Note that the proof of ergodicity is based on an adapted version of the *second vector field* associated to a Markov process. It was introduced by Malyshev and Menshikov in [28], and will be used by T. Turova to extand those results.

Appendix A

Mathematical Complements

A.1 Hermite Functions

The special functions used in previous sections are recalled below and we refer to [27] for most of the results and proofs.

Definition A.1.1. The Hermite function $\mathcal{H}_\nu$ is defined by :

$$\mathcal{H}_\nu(z) := \frac{2^\nu \Gamma(\frac{1}{2})}{\Gamma(\frac{1-\nu}{2})} \phi\left(-\frac{\nu}{2}, \frac{1}{2}; z^2\right) + \frac{2^{\nu+\frac{1}{2}} \Gamma(-\frac{1}{2})}{\Gamma(\frac{-\nu}{2})} z \phi\left(\frac{1-\nu}{2}, \frac{3}{2}; z^2\right) \tag{A.1.1}$$

where ϕ denotes the confluent hypergeometric function (or Kummer's function of the first kind) and Γ the gamma function.

$$\begin{aligned}\phi(a,b;z) &:= 1 + \frac{a}{b} z + \frac{a(a+1)}{b(b+1)} \frac{z^2}{2!} + \frac{a(a+1)(a+2)}{b(b+1)(b+2)} \frac{z^3}{3!} + \dots \\ &:= \sum_{k=0}^{\infty} \frac{(a)_k}{(b)_k} \frac{z^k}{k!}\end{aligned}$$

Proposition A.1.1. Hermite function satisfies the following relations :

i. The Hermite function has the following series representation :

$$\mathcal{H}_\nu(z) = \frac{1}{2\Gamma(-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu}{2}\right) (2z)^m, \quad |z| < \infty \tag{A.1.2}$$

ii. The following recurrence relations hold :

$$\frac{\partial \mathcal{H}_\nu(z)}{\partial z} = 2\nu \mathcal{H}_{\nu-1}(z) \tag{A.1.3}$$

$$\mathcal{H}_{\nu+1}(z) = 2z\mathcal{H}_\nu(z) - 2\nu\mathcal{H}_{\nu-1}(z) \tag{A.1.4}$$

iii. $\mathcal{H}_\nu(z)$ and $\mathcal{H}_\nu(-z)$ are fundamental solutions of the ordinary so called Hermite equation :

$$f''(z) - 2zf'(x) + 2\nu f = 0 \tag{A.1.5}$$

Proof. The series expansion of i. comes from the definition of the ϕ function.

The recurrence relations of ii. come from the fundamental relation on Γ : $\Gamma(1+z) = z\Gamma(z)$ and the series expansion (A.1.2) : on one hand we have

$$\begin{aligned}\frac{\partial \mathcal{H}_\nu(z)}{\partial z} &= \frac{1}{2\Gamma(-\nu)} \sum_{m=1}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu}{2}\right) 2m(2z)^{m-1} \\ &= \frac{-2}{2\Gamma(-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m+1-\nu}{2}\right) (2z)^m \quad \text{changing } m \text{ to } m+1\end{aligned}$$

On the other hand,

$$2\nu\mathcal{H}_{\nu-1}(z) = \frac{2\nu}{2\Gamma(1-\nu)} \sum_{m=0}^{\infty} \frac{(-1)^m}{m!} \Gamma\left(\frac{m-\nu+1}{2}\right) (2z)^m$$

And conclude with the relation $\Gamma(1-\nu) = -\nu\Gamma(-\nu)$.

The second recurrence relation comes also from those two relations. To check this relation we compare the coefficient of the power of $2z$ of the series expansion of the two sides of (A.1.4) and play with the fundamental relation of Γ.

Finally, the ordinary differential equation (A.1.5) is no more than (A.1.4), writing $\mathcal{H}_{\nu-1}$ and $\mathcal{H}_{\nu-2}$ in terms of derivatives of $\mathcal{H}_\nu$ using (A.1.3). □

A.2 Convergence of probability measures

Theorem A.2.1. *Let $(\mathbb{P}_n)_{n\geq 0}$ be a sequence of probability measures and let $\mathbb{P}$ be a probability measure. We denote $L_n(t)$ (resp $L(t)$) the Laplace transform of $\mathbb{P}_n$ (resp $\mathbb{P}$). Then the following equivalence holds:*

$$\boxed{\mathbb{P}_n \xrightarrow[n\to\infty]{\mathcal{L}} \mathbb{P} \quad \Leftrightarrow \quad L_n(t) \xrightarrow[n\to\infty]{pointwise} L(t) \quad \forall t \geq 0} \tag{A.2.1}$$

Proof. The direct direction of the equivalence is obvious, (it's a particular case of the functional definition of the weak convergence, using the exponential function).

Let us prove the converse. The only thing to prove is the tightness of the sequence, the uniqueness of limit points being clear. To prove the tightness of the sequence, we want to major uniformly for a given n_0 all the probabilities of the type $\mathbb{P}_n(A,\infty)$, for all $n \geq n_0$, with a bound going to 0. To do this we use the following relation between the Laplace transform and the probabilities of such events.

$$\begin{aligned}
\frac{1}{u}\int_0^u (1-L_n(t))dt &= \frac{1}{u}\int_{x\geq 0}\int_0^u (1-e^{-tx})dt\, d\mathbb{P}_n(x) \\
&\geq \frac{1}{u}\int_{x\geq 1/u}\int_0^u (1-e^{-tx})dt\, d\mathbb{P}_n(x) \\
&\geq \frac{1}{u}\int_{x\geq 1/u}\int_0^u (1-e^{-t/u})dt\, d\mathbb{P}_n(x) \\
&\geq e^{-1}\mathbb{P}_n(\frac{1}{u},\infty)
\end{aligned}$$

To bound uniformly the expression $\frac{1}{u}\int_0^u (1-L_n(t))dt$ we refer to L. $L(t)$ is continuous and $L(0)=1$.

Let $\varepsilon > 0$ a given real. There is a u such that $u^{-1}\int_0^u (1-L(t))dt < \frac{\varepsilon}{2e}$. Since $L_n(t) \underset{n\to\infty}{\to} L(t)$ for all t and the integration interval is bounded, Lebesgue's theorem ensures us that $u^{-1}\int_0^u (1-L_n(t))dt < \frac{\varepsilon}{e}$ for all n beyond some n_0. Let $A := u^{-1}$. We have :

$$\mathbb{P}_n[0;A] \geq 1-\varepsilon \qquad \forall n \geq n_0.$$

Therefore, $(\mathbb{P}_n)_n$ is tight.

By Prohorov theorem (cf for instance [6]), the sequence is relatively compact. Let Q be a limit point. Necessarily the Laplace transform of Q is L by the direct sense of the theorem, so $Q = \mathbb{P}$ in distribution. So eventually, the sequence is relatively compact with only one limit point so the sequence $\mathbb{P}_n$ converges weakly (i.e. in distribution) to $\mathbb{P}$ □

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