Activity Report 2017

Team MATHNEURO

Mathématiques pour les Neurosciences

Inria teams are typically groups of researchers working on the definition of a common project, and objectives, with the goal to arrive at the creation of a project-team. Such project-teams may include other partners (universities or research institutions).

RESEARCH CENTER
Sophia Antipolis - Méditerranée

THEME
Computational Neuroscience and Medicine

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Team MATHNEURO

Creation of the Team: 2016 January 01

Keywords:

Computer Science and Digital Science:

A6.1.1. - Continuous Modeling (PDE, ODE)
A6.1.2. - Stochastic Modeling (SPDE, SDE)
A6.1.4. - Multiscale modeling
A6.2.1. - Numerical analysis of PDE and ODE
A6.2.2. - Numerical probability
A6.2.3. - Probabilistic methods
A6.3.4. - Model reduction

Other Research Topics and Application Domains:

B1.2. - Neuroscience and cognitive science
B1.2.1. - Understanding and simulation of the brain and the nervous system
B1.2.2. - Cognitive science

1. Personnel

Research Scientists

Mathieu Desroches [Team leader, Inria, Researcher, HDR]
Fabien Campillo [Inria, Senior Researcher, HDR]
Pascal Chossat [CNRS, Emeritus, HDR]
Olivier Faugeras [Inria, Emeritus, HDR]
Maciej Krupa [Université Côte d'Azur (UCA), Senior Researcher, from Sep 2017, HDR]
Romain Veltz [Inria, Researcher]

Post-Doctoral Fellows

Benjamin Aymard [Inria, from Sep 2017]
Elif Köksal Ersöz [Inria]
Émilie Soret [Inria, from Sep 2017]

PhD Student

Axel Dolcemascolo [CNRS]

Interns

Leila Bekri [Inria, until Mar 2017]
Raphael Forquet [CNRS, until Jan 2017]
Anna Song [Ecole Normale Supérieure Paris, from Feb 2017 until Jun 2017]

Administrative Assistant

Marie-Cecile Lafont [AI, Inria]

External Collaborators

Daniele Avitabile [School of Mathematical Sciences of the University of Nottingham]
Maciej Krupa [until Sep 2017]
Alexandre Richard [Ecole Polytechnique, until Aug 2017]
Audric Drogoul [Thales]

2. Overall Objectives

2.1. Overall Objectives

MATHNEURO focuses on the applications of multi-scale dynamics to neuroscience. This involves the modelling and analysis of systems with multiple time scales and space scales, as well as stochastic effects. We look both at single-cell models, microcircuits and large networks. In terms of neuroscience, we are mainly interested in questions related to synaptic plasticity and neuronal excitability, in particular in the context of pathological states such as epileptic seizures and neurodegenerative diseases such as Alzheimer.

Our work is quite mathematical but we make heavy use of computers for numerical experiments and simulations. We have close ties with several top groups in biological neuroscience. We are pursuing the idea that the "unreasonable effectiveness of mathematics" can be brought, as it has been in physics, to bear on neuroscience.

Modeling such assemblies of neurons and simulating their behavior involves putting together a mixture of the most recent results in neurophysiology with such advanced mathematical methods as dynamical systems theory, bifurcation theory, probability theory, stochastic calculus, theoretical physics and statistics, as well as the use of simulation tools.

We conduct research in the following main areas:

1. Neural networks dynamics
2. Mean-field and stochastic approaches
3. Neural fields
4. Slow-fast dynamics in neuronal models
5. Modeling neuronal excitability
6. Synaptic plasticity

3. Research Program

3.1. Neural networks dynamics

The study of neural networks is certainly motivated by the long term goal to understand how brain is working. But, beyond the comprehension of brain or even of simpler neural systems in less evolved animals, there is also the desire to exhibit general mechanisms or principles at work in the nervous system. One possible strategy is to propose mathematical models of neural activity, at different space and time scales, depending on the type of phenomena under consideration. However, beyond the mere proposal of new models, which can rapidly result in a plethora, there is also a need to understand some fundamental keys ruling the behaviour of neural networks, and, from this, to extract new ideas that can be tested in real experiments. Therefore, there is a need to make a thorough analysis of these models. An efficient approach, developed in our team, consists of analysing neural networks as dynamical systems. This allows to address several issues. A first, natural issue is to ask about the (generic) dynamics exhibited by the system when control parameters vary. This naturally leads to analyse the bifurcations [52] [53] occurring in the network and which phenomenological parameters control these bifurcations. Another issue concerns the interplay between neuron dynamics and synaptic network structure.

3.2. Mean-field and stochastic approaches

Modeling neural activity at scales integrating the effect of thousands of neurons is of central importance for several reasons. First, most imaging techniques are not able to measure individual neuron activity (microscopic scale), but are instead measuring mesoscopic effects resulting from the activity of several hundreds to several hundreds of thousands of neurons. Second, anatomical data recorded in the cortex reveal the existence of structures, such as the cortical columns, with a diameter of about $50\mu m$ to $1mm$, containing of the order of one hundred to one hundred thousand neurons belonging to a few different species. The description of this collective dynamics requires models which are different from individual neurons models. In particular, when the number of neurons is large enough averaging effects appear, and the collective dynamics is well described by an effective mean-field, summarizing the effect of the interactions of a neuron with the other neurons, and depending on a few effective control parameters. This vision, inherited from statistical physics requires that the space scale be large enough to include a large number of microscopic components (here neurons) and small enough so that the region considered is homogeneous.

Our group is developing mathematical and numerical methods allowing on one hand to produce dynamic mean-field equations from the physiological characteristics of neural structure (neurons type, synapse type and anatomical connectivity between neurons populations), and on the other so simulate these equations. These methods use tools from advanced probability theory such as the theory of Large Deviations [45] and the study of interacting diffusions [35].

3.3. Neural fields

Neural fields are a phenomenological way of describing the activity of population of neurons by delayed integro-differential equations. This continuous approximation turns out to be very useful to model large brain areas such as those involved in visual perception. The mathematical properties of these equations and their solutions are still imperfectly known, in particular in the presence of delays, different time scales and noise.

Our group is developing mathematical and numerical methods for analysing these equations. These methods are based upon techniques from mathematical functional analysis, bifurcation theory [54], equivariant bifurcation analysis, delay equations, and stochastic partial differential equations. We have been able to characterize the solutions of these neural fields equations and their bifurcations, apply and expand the theory to account for such perceptual phenomena as edge, texture [37], and motion perception. We have also developed a theory of the delayed neural fields equations, in particular in the case of constant delays and propagation delays that must be taken into account when attempting to model large size cortical areas [55]. This theory is based on center manifold and normal forms ideas.

3.4. Slow-Fast Dynamics in Neuronal Models

Neuronal rhythms typically display many different timescales, therefore it is important to incorporate this slow-fast aspect in models. We are interested in this modeling paradigm where slow-fast point models (using Ordinary Differential Equations) are investigated in terms of their bifurcation structure and the patterns of oscillatory solutions that they can produce. To insight into the dynamics of such systems, we use a mix of theoretical techniques — such as geometric desingularisation and centre manifold reduction [50] — and numerical methods such as pseudo-arclength continuation [43]. We are interested in families of complex oscillations generated by both mathematical and biophysical models of neurons. In particular, so-called *mixed-mode oscillations (MMOs)* [41], [49], which represent an alternation between subthreshold and spiking behaviour, and *bursting oscillations* [42], [47], also corresponding to experimentally observed behaviour [39].

3.5. Modeling neuronal excitability

Excitability refers to the all-or-none property of neurons [44], [48]. That is, the ability to respond nonlinearly to an input with a dramatic change of response from “none” — no response except a small perturbation that returns to equilibrium — to “all” — large response with the generation of an action potential or spike before the neuron returns to equilibrium. The return to equilibrium may also be an oscillatory motion of small amplitude;

in this case, one speaks of resonator neurons as opposed to integrator neurons. The combination of a spike followed by subthreshold oscillations is then often referred to as mixed-mode oscillations (MMOs) [41]. Slow-fast ODE models of dimension at least three are well capable of reproducing such complex neural oscillations. Part of our research expertise is to analyse the possible transitions between different complex oscillatory patterns of this sort upon input change and, in mathematical terms, this corresponds to understanding the bifurcation structure of the model. Furthermore, the shape of time series of this sort with a given oscillatory pattern can be analysed within the mathematical framework of dynamic bifurcations; see the section on slow-fast dynamics in Neuronal Models. The main example of abnormal neuronal excitability is hyperexcitability and it is important to understand the biological factors which lead to such excess of excitability and to identify (both in detailed biophysical models and reduced phenomenological ones) the mathematical structures leading to these anomalies. Hyperexcitability is one important trigger for pathological brain states related to various diseases such as chronic migraine, epilepsy or even Alzheimer's Disease. A central central axis of research within our group is to revisit models of such pathological scenarios, in relation with a combination of advanced mathematical tools and in partnership with biological labs.

3.6. Synaptic Plasticity

Neural networks show amazing abilities to evolve and adapt, and to store and process information. These capabilities are mainly conditioned by plasticity mechanisms, and especially synaptic plasticity, inducing a mutual coupling between network structure and neuron dynamics. Synaptic plasticity occurs at many levels of organization and time scales in the nervous system [36]. It is of course involved in memory and learning mechanisms, but it also alters excitability of brain areas and regulates behavioral states (e.g., transition between sleep and wakeful activity). Therefore, understanding the effects of synaptic plasticity on neurons dynamics is a crucial challenge.
Our group is developing mathematical and numerical methods to analyse this mutual interaction. On the one hand, we have shown that plasticity mechanisms, Hebbian-like or STDP, have strong effects on neuron dynamics complexity, such as dynamics complexity reduction, and spike statistics

4. New Results

4.1. Neural Networks as dynamical systems

4.1.1. Latching dynamics in neural networks with synaptic depression

Participants: Elif Köksal Ersöz, Carlos Aguilar [Université de Nice - BCL], Pascal Chossat [Université de Nice - LJAD, Inria MathNeuro], Martin Krupa [UCA, Inria MathNeuro], Frédéric Lavigne [Université de Nice - BCL].

Prediction is the ability of the brain to quickly activate a target concept in response to a related stimulus (prime). Experiments point to the existence of an overlap between the populations of the neurons coding for different stimuli, and other experiments show that prime-target relations arise in the process of long term memory formation. The classical modelling paradigm is that long term memories correspond to stable steady states of a Hopfield network with Hebbian connectivity. Experiments show that short term synaptic depression plays an important role in the processing of memories. This leads naturally to a computational model of priming, called latching dynamics; a stable state (prime) can become unstable and the system may converge to another transiently stable steady state (target). Hopfield network models of latching dynamics have been studied by means of numerical simulation, however the conditions for the existence of this dynamics have not been elucidated. In this work we use a combination of analytic and numerical approaches to confirm that latching dynamics can exist in the context of a symmetric Hebbian learning rule, however lacks robustness and imposes a number of biologically unrealistic restrictions on the model. In particular our work shows that the symmetry of the Hebbian rule is not an obstruction to the existence of latching dynamics, however fine tuning of the parameters of the model is needed.

This work has been published in PLoS one and is available as [13].

A natural follow-up of the work which has lead to the article [13] has been initiated through the postdoc project of Elif Köksal Ersöz. The objective is to extend the previous results in several ways. First, to gain more robustness in the heteroclinic chains sustained by the network model. Second, to be able to simulate much larger networks and exhibit heteroclinic dynamics in them. Third, to link with experimental data. The postdoc of Elif Köksal Ersöz is funded by the “tail” of the ERC Advanced Grant NerVi held by Olivier Faugeras.

4.1.2. Special issue for Martin Golubitsky

Participants: Pietro-Luciano Buono University Of Ontario Institute Of Technology, Canada „ Martin Krupa [UCA, Inria MathNeuro], Ian Stewart [University of Warwick, UK].

The work is the introducion of this special issue, co-edited by Martin Krupa. It has been published in Dynamical Systems: An International Journal and is available as [17].

4.1.3. Consecutive and non-consecutive heteroclinic cycles in Hopfield networks

Participants: Pascal Chossat [Université de Nice - LJAD, Inria MathNeuro], Martin Krupa [UCA, Inria MathNeuro].

We review and extend the previous work [38] where a model was introduced for Hopfield-type neural networks, which allows for the existence of heteroclinic dynamics between steady patterns. This dynamics is a mathematical model of periodic or aperiodic switching between stored information items in the brain, in particular, in the context of sequential memory or cognitive tasks as observed in experiments. The basic question addressed in this work is whether, given a sequence of steady patterns, it is possible by applying classical learning rules to build a matrix of connections between neurons in the network, such that a heteroclinic dynamics links these patterns. It has been shown previously that the answer is positive in the case where the sequence is a so-called simple consecutive cycle. We show that on the contrary the answer is negative for a non-simple cycle: heteroclinic dynamics does still exist; however, it cannot follow the sequence of patterns from which the connectivity matrix was derived.

This work has been published in Dynamical Systems: An International Journal and is available as [21].

4.1.4. Asymptotic stability of pseudo-simple heteroclinic cycles in $\mathbb{R}^4$

Participants: Pascal Chossat [Université de Nice - LJAD, Inria MathNeuro], Olga Podvigina [Institute of Earthquake Prediction Theory and Mathematical Geophysics, Russia].

Robust heteroclinic cycles in equivariant dynamical systems in $\mathbb{R}^4$ have been a subject of intense scientific investigation because, unlike heteroclinic cycles in $\mathbb{R}^3$, they can have an intricate geometric structure and complex asymptotic stability properties that are not yet completely understood. In a recent work [51], we have compiled an exhaustive list of finite subgroups of $O(4)$ admitting the so-called simple heteroclinic cycles, and have identified a new class which we have called pseudo-simple heteroclinic cycles. By contrast with simple heteroclinic cycles, a pseudo-simple one has at least one equilibrium with an unstable manifold which has dimension 2 due to a symmetry. Here, we analyze the dynamics of nearby trajectories and asymptotic stability of pseudo-simple heteroclinic cycles in $\mathbb{R}^4$.

This work has been published in Journal of Nonlinear Science and is available as [26].

4.1.5. The period adding and incrementing bifurcations: from rotation theory to applications

Participants: Albert Granados [Polytechnic University of Catalonia, Barcelona, Spain], Lluís Alsedà [Autonomous University of Barcelona, Spain], Martin Krupa [UCA, Inria MathNeuro].

This survey article is concerned with the study of bifurcations of piecewise-smooth maps. We review the literature in circle maps and quasi-contractions and provide paths through this literature to prove sufficient conditions for the occurrence of two types of bifurcation scenarios involving rich dynamics. The first scenario consists of the appearance of periodic orbits whose symbolic sequences and "rotation" numbers follow a Farey tree structure; the periods of the periodic orbits are given by consecutive addition. This is called the *period adding* bifurcation, and its proof relies on results for maps on the circle. In the second scenario, symbolic sequences are obtained by consecutive attachment of a given symbolic block and the periods of periodic orbits are incremented by a constant term. It is called the *period incrementing* bifurcation, in its proof relies on results for maps on the interval. We also discuss the expanding cases, as some of the partial results found in the literature also hold when these maps lose contractiveness. The higher dimensional case is also discussed by means of *quasi-contractions*. We also provide applied examples in control theory, power electronics and neuroscience where these results can be applied to obtain precise descriptions of their dynamics.

This work has been published in SIAM Review and is available as [24].

4.1.6. *Inverse correlation processing by neurons with active dendrites*

Participants: Tomasz Górski [UNIC, CNRS, France], Romain Veltz, Mathieu Galtier [UNIC, CNRS, France], Helissande Fragnaud [UNIC, CNRS, France], Bartosz Teleńczuk [UNIC, CNRS, France], Alain Destexhe [UNIC, CNRS, France].

In many neuron types, the dendrites contain a significant density of sodium channels and are capable of generating action potentials, but the significance and role of dendritic sodium spikes are unclear. Here, we use simplified computational models to investigate the functional effect of dendritic spikes. We found that one of the main features of neurons equipped with excitable dendrites is that the firing rate of the neuron measured at soma decreases with increasing input correlations, which is an inverse relation compared to passive dendrite and single-compartment models. We first show that in biophysical models the collision and annihilation of dendritic spikes causes an inverse dependence of firing rate on correlations. We then explore this in more detail using excitable dendrites modeled with integrate-and-fire type mechanisms. Finally, we show that the inverse correlation dependence can also be found in very simple models, where the dendrite is modeled as a discrete-state cellular automaton. We conclude that the cancellation of dendritic spikes is a generic mechanism that allows neurons to process correlations inversely compared to single-compartment models. This qualitative effect due to the presence of dendrites should have strong consequences at the network level, where networks of neurons with excitable dendrites may have fundamentally different properties than networks of point neuron models.

This work has been submitted for publication and is available as [33].

4.2. Mean field theory and stochastic processes

4.2.1. *Emergence of collective phenomena in a population of neurons*

Participants: Benjamin Aymard, Fabien Campillo, Romain Veltz.

In this work, we propose a new model of biological neural network, combining a two-dimensional integrate-and-fire neuron model with a deterministic model of electrical synapse, and a stochastic model of chemical synapse. We describe the dynamics of a population of neurons in interaction as a piecewise deterministic Markov process. We prove the weak convergence of the associated empirical process, as the population size tends to infinity, towards a McKean-Vlasov type process and we describe the associated PDE. We are also interested in the simulation of these dynamics, in particular by comparing "detailed" simulations of a finite population of neurons with a simulation of the system with infinite population. Benjamin Aymard has the adapted toolkit to attack these questions numerically. The mean field equations studied by Benjamin are of transport type for which numerical methods are technical. However, they are the domain of expertise of Benjamin. His postdoc is funded by the Flagship Human Brain Project.

4.2.2. *Off-line numerical Bayes identification of dynamical systems for life sciences*

Participants: Fabien Campillo, Vivien Rossi [CIRAD].

In this project, we develop Monte Carlo algorithms for the identification of parameters and hidden components for dynamic systems used in the life sciences. The peculiarity of these systems and they do not require online processing and they call for data of various natures and sometimes low quality. We use particle filtering techniques so that we try to improve the prediction phases using MCMC techniques.

4.2.3. *On the variations of the principal eigenvalue with respect to a parameter in growth-fragmentation models*

Participants: Fabien Campillo, Nicolas Champagnat [Inria, project-team TOSCA, Nancy], Coralie Fritsch [Inria, project-team TOSCA, Nancy].

We study the variations of the principal eigenvalue associated to a growth-fragmentation-death equation with respect to a parameter acting on growth and fragmentation. To this aim, we use the probabilistic individual-based interpretation of the model. We study the variations of the survival probability of the stochastic model, using a generation by generation approach. Then, making use of the link between the survival probability and the principal eigenvalue established in a previous work, we deduce the variations of the eigenvalue with respect to the parameter of the model.

This work has been published in Communications in Mathematical Sciences and is available as [18].

4.2.4. *Hopf bifurcation in a nonlocal nonlinear transport equation stemming from stochastic neural dynamics*

Participants: Audric Drogoul [Thales, France], Romain Veltz.

In this work, we provide three different numerical evidences for the occurrence of a Hopf bifurcation in a recently derived mean field limit of a stochastic network of excitatory spiking neurons [40], [46]. The mean field limit is a challenging nonlocal nonlinear transport equation with boundary conditions. The first evidence relies on the computation of the spectrum of the linearized equation. The second stems from the simulation of the full mean field. Finally, the last evidence comes from the simulation of the network for a large number of neurons. We provide a “recipe” to find such bifurcation which nicely complements the works in [40], [46]. This suggests in return to revisit theoretically these mean field equations from a dynamical point of view. Finally, this work shows how the noise level impacts the transition from asynchronous activity to partial synchronization in excitatory globally pulse-coupled networks.

This work has been published in Chaos and is available as [22].

4.2.5. *Mathematical statistical physics applied to neural populations*

Participants: Émilie Soret, Olivier Faugeras, Étienne Tanré [Inria, project-team TOSCA, Sophia-Antipolis].

This project focuses on Mean-Field descriptions or thermodynamics limits of large populations of neurons. They study a system of Stochastic Differential Equations (SDEs) which describes the evolution of membrane potential of each neuron over the time when the synaptic weights are random variables (not assumed to be independent). This setup is well suited to Émilie, who has worked during her PhD and first postdoc on mathematical statistical physics and stochastic processes. Her postdoc is funded by the Flagship Human Brain Project.

4.2.6. *A numerical approach to determine mutant invasion fitness and evolutionary singular strategies*

Participants: Coralie Fritsch [Inria, project-team TOSCA, Nancy], Fabien Campillo, Otso Ovaskainen [University of Helsinki, Finland].

We propose a numerical approach to study the invasion fitness of a mutant and to determine evolutionary singular strategies in evolutionary structured models in which the competitive exclusion principle holds. Our approach is based on a dual representation, which consists of the modelling of the small size mutant population by a stochastic model and the computation of its corresponding deterministic model. The use of the deterministic model greatly facilitates the numerical determination of the feasibility of invasion as well as the convergence-stability of the evolutionary singular strategy. Our approach combines standard adaptive dynamics with the link between the mutant survival criterion in the stochastic model and the sign of the eigenvalue in the corresponding deterministic model. We present our method in the context of a mass-structured individual-based chemostat model. We exploit a previously derived mathematical relationship between stochastic and deterministic representations of the mutant population in the chemostat model to derive a general numerical method for analyzing the invasion fitness in the stochastic models. Our method can be applied to the broad class of evolutionary models for which a link between the stochastic and deterministic invasion fitnesses can be established.

This work has been published in Theoretical Population Biology and is available as [23].

4.3. Neural fields theory

4.3.1. Spatiotemporal canards in neural field equations

Participants: Daniele Avitabile [University of Nottingham, UK], Mathieu Desroches, Edgar Knobloch [University of California Berkeley, USA].

Canards are special solutions to ordinary differential equations that follow invariant repelling slow manifolds for long time intervals. In realistic biophysical single-cell models, canards are responsible for several complex neural rhythms observed experimentally, but their existence and role in spatially extended systems is largely unexplored. We identify and describe a type of coherent structure in which a spatial pattern displays temporal canard behavior. Using interfacial dynamics and geometric singular perturbation theory, we classify spatiotemporal canards and give conditions for the existence of folded-saddle and folded-node canards. We find that spatiotemporal canards are robust to changes in the synaptic connectivity and firing rate. The theory correctly predicts the existence of spatiotemporal canards with octahedral symmetry in a neural field model posed on the unit sphere.

This work has been published in Physical Review E and is available as [14].

4.3.2. Standing and travelling waves in a spherical brain model: the Nunez model revisited

Participants: Sid Visser [University of Nottingham, UK], Rachel Nicks [University of Nottingham, UK], Olivier Faugeras, Stephen Coombes [University of Nottingham, UK].

The Nunez model for the generation of electroencephalogram (EEG) signals is naturally described as a neural field model on a sphere with space-dependent delays. For simplicity, dynamical realisations of this model either as a damped wave equation or an integro-differential equation, have typically been studied in idealised one dimensional or planar settings. Here we revisit the original Nunez model to specifically address the role of spherical topology on spatio-temporal pattern generation. We do this using a mixture of Turing instability analysis, symmetric bifurcation theory, centre manifold reduction and direct simulations with a bespoke numerical scheme. In particular we examine standing and travelling wave solutions using normal form computation of primary and secondary bifurcations from a steady state. Interestingly, we observe spatio-temporal patterns which have counterparts seen in the EEG patterns of both epileptic and schizophrenic brain conditions.

This work has been published in Physica D and is available as [27].

4.4. Slow-fast dynamics in Neuroscience

4.4.1. Ducks in space: from nonlinear absolute instability to noise-sustained structures in a pattern-forming system

Participants: Daniele Avitabile [University of Nottingham, UK], Mathieu Desroches, Edgar Knobloch [University of California Berkeley, USA], Martin Krupa [UCA, Inria MathNeuro].

A subcritical pattern-forming system with nonlinear advection in a bounded domain is recast as a slow-fast system in space and studied using a combination of geometric singular perturbation theory and numerical continuation. Two types of solutions describing the possible location of stationary fronts are identified, whose origin is traced to the onset of convective and absolute instability when the system is unbounded. The former are present only for non-zero upstream boundary conditions and provide a quantitative understanding of noise-sustained structures in systems of this type. The latter correspond to the onset of a global mode and are present even with zero upstream boundary conditions. The role of canard trajectories in the nonlinear transition between these states is clarified and the stability properties of the resulting spatial structures are determined. Front location in the convective regime is highly sensitive to the upstream boundary condition, and its dependence on this boundary condition is studied using a combination of numerical continuation and Monte Carlo simulations of the partial differential equation. Statistical properties of the system subjected to random or stochastic boundary conditions at the inlet are interpreted using the deterministic slow-fast spatial dynamical system.

This work has been published in Proceedings of the Royal Society A and is available as [15].

4.4.2. *Canard dynamics and anticipated synchronisation in spiking models*

Participants: Elif Köksal Ersöz, Mathieu Desroches, Claudio Mirasso [University of the Balearic Islands, Palma, Spain], Serafim Rodrigues [Ikerbasque, BCAM, Bilbao, Spain].

This project is on the phenomenon of anticipated synchronisation, studied theoretically in a number of models of excitable systems over the past fifteen years or so, and observed experimentally in laser systems. The idea is that when coupling two identical excitable system unidirectionally from a "master" system to a "slave" system with a delayed term of the slave's signal in its own differential equation, one may observe that the slave reacts to an external stimulus before the master, and this is referred to as *anticipation* or *anticipated synchronisation*. Even though a number of studies have reported and analysed this effect in various systems, its main underpinning mechanisms remain elusive. In the current project, we show that in the case where the systems have an explicit slow-fast nature, then the canard regime can induce anticipation and explain its feature. Our objective is to go beyond the theoretical explanation, on which we are currently preparing an article, and to propose an electrophysiological protocol so as observe this phenomenon in real neurons. This is very much related to the PhD work of Elif Köksal Ersöz on the synchronisation properties of canard oscillators, in particular to the paper [25] (see Section 4.4.5 below). This postdoc is funded by the "tail" of the ERC Advanced Grant NerVi held by Olivier Faugeras.

4.4.3. *Spike-adding in a canonical three time scale model: superslow explosion & folded-saddle canards*

Participants: Mathieu Desroches, Vivien Kirk [University of Auckland, New-Zealand].

We examine the origin of complex bursting oscillations in a phenomenological ordinary differential equation model with three time scales. We show that bursting solutions in this model arise from a Hopf bifurcation followed by a sequence of spike-adding transitions, in a manner reminiscent of spike-adding transitions previously observed in systems with two time scales. However, the details of the process can be much more complex in this three-time-scale context than in two-time-scale systems. In particular, we find that spike-adding can involve canard explosions occurring on two different time scales and is associated with passage near a folded-saddle singularity. We show that the form of spike-adding transition that occurs depends on the geometry of certain singular limit systems, specifically the relative positions of the critical and superslow manifolds. We also show that, unlike the case of spike-adding in two-time-scale systems, the onset of a new spike in our model is not typically associated with a local maximum in the period of the bursting oscillation.

This work has been submitted for publication and is available as [31].

4.4.4. *Piecewise-linear (PWL) canard dynamics: Simplifying singular perturbation theory in the canard regime using piecewise-linear systems*

Participants: Mathieu Desroches, Soledad Fernández-García [University of Sevilla, Spain], Martin Krupa [UCA, Inria MathNeuro], Rafel Prohens [University of the Balearic Islands, Spain], Antonio Teruel [University of the Balearic Islands, Spain].

In this chapter we gathered recent results on piecewise-linear (PWL) slow-fast dynamical systems in the canard regime. By focusing on minimal systems in $\mathbb{R}^2$ (one slow and one fast variables) and $\mathbb{R}^3$ (two slow and one fast variables), we proved the existence of (maximal) canard solutions and show that the main salient features from smooth systems is preserved. We also highlighted how the PWL setup carries a level of simplification of singular perturbation theory in the canard regime, which makes it more amenable to present it to various audiences at an introductory level. Finally, we presented a PWL version of Fenichel theorems about slow manifolds, which are valid in the normally hyperbolic regime and in any dimension, which also offers a simplified framework for such persistence results.

This work has been accepted for publication as a chapter in a book titled *Nonlinear Systems; Vol. 1: Mathematical Theory and Computational Methods* (Springer, in press) and is available as [28].

4.4.5. Synchronization of weakly coupled canard oscillators

Participants: Elif Köksal Ersöz, Mathieu Desroches, Martin Krupa [UCA, Inria MathNeuro].

Synchronization has been studied extensively in the context of weakly coupled oscillators using the so-called phase response curve (PRC) which measures how a change of the phase of an oscillator is affected by a small perturbation. This approach was based upon the work of Malkin, and it has been extended to relaxation oscillators. Namely, synchronization conditions were established under the weak coupling assumption, leading to a criterion for the existence of synchronous solutions of weakly coupled relaxation oscillators. Previous analysis relies on the fact that the slow nullcline does not intersect the fast nullcline near one of its fold points, where canard solutions can arise. In the present study we use numerical continuation techniques to solve the adjoint equations and we show that synchronization properties of canard cycles are different than those of classical relaxation cycles. In particular, we highlight a new special role of the maximal canard in separating two distinct synchronization regimes: the Hopf regime and the relaxation regime. Phase plane analysis of slow-fast oscillators undergoing a canard explosion provides an explanation for this change of synchronization properties across the maximal canard.

This work has been published in Physica D and is available as [25].

4.5. Models of neural excitability

4.5.1. Modeling cortical spreading depression induced by the hyperactivity of interneurons

Participants: Mathieu Desroches, Olivier Faugeras, Martin Krupa [UCA, Inria MathNeuro], Massimo Mantegazza [IMPC, Sophia Antipolis].

Cortical spreading depression (CSD) is a wave of transient intense neuronal firing leading to a long lasting depolarization block of neuronal activity. It is a proposed pathological mechanism of migraine with aura. Some molecular/cellular mechanisms of migraine with aura and of CSD have been identified studying a rare mendelian form: familial hemiplegic migraine (FHM). FHM type 1 & 2 are caused by mutations of the CaV2.1 Ca^{2+} channel and the glial Na^+ / K^+ pump, respectively, leading to facilitation of CSD in mouse models mainly because of increased glutamatergic transmission/extracellular glutamate build-up. FHM type 3 mutations of the SCN1A gene, coding for the voltage gated sodium channel NaV1.1, cause gain of function of the channel and hyperexcitability of GABAergic interneurons. This leads to the counterintuitive hypothesis that intense firing of interneurons can cause CSD ignition. To test this hypothesis in silico, we developed a computational model of an E-I pair (a pyramidal cell and an interneuron), in which the coupling between the cells in not just synaptic, but takes into account also the effects of the accumulation of extracellular potassium caused by the activity of the neurons and of the synapses. In the context of this model, we show that the intense firing of the interneuron can lead to CSD. We have investigated the effect of various biophysical parameters on the transition to CSD, including the levels of glutamate or GABA, frequency of the interneuron firing and the efficacy of the KCC2 co-transporter. The key element for CSD ignition in our model was the frequency of interneuron firing and the related accumulation of extracellular potassium, which induced a depolarization block of the pyramidal cell. Our model can be used to study other types of activities in microcircuits and of couplings between excitatory and inhibitory neurons.

This work has been submitted for publication and is available as [30].

5. Partnerships and Cooperations

5.1. European Initiatives

5.1.1. FP7 & H2020 Projects

5.1.1.1. HBP

Title: The Human Brain Project

Programm: FP7

Duration: October 2013 - March 2016 (first part) and then : April 2016 - March 2018 (second part)

Coordinator: EPFL

Partners:
see the webpage of the project.

Inria contact: Olivier Faugeras (first part) and then : Romain Veltz (second part)

Understanding the human brain is one of the greatest challenges facing 21st century science. If we can rise to the challenge, we can gain profound insights into what makes us human, develop new treatments for brain diseases and build revolutionary new computing technologies. Today, for the first time, modern ICT has brought these goals within sight. The goal of the Human Brain Project, part of the FET Flagship Programme, is to translate this vision into reality, using ICT as a catalyst for a global collaborative effort to understand the human brain and its diseases and ultimately to emulate its computational capabilities. The Human Brain Project will last ten years and will consist of a ramp-up phase (from month 1 to month 36) and subsequent operational phases.
This Grant Agreement covers the ramp-up phase. During this phase the strategic goals of the project will be to design, develop and deploy the first versions of six ICT platforms dedicated to Neuroinformatics, Brain Simulation, High Performance Computing, Medical Informatics, Neuromorphic Computing and Neurorobotics, and create a user community of research groups from within and outside the HBP, set up a European Institute for Theoretical Neuroscience, complete a set of pilot projects providing a first demonstration of the scientific value of the platforms and the Institute, develop the scientific and technological capabilities required by future versions of the platforms, implement a policy of Responsible Innovation, and a programme of transdisciplinary education, and develop a framework for collaboration that links the partners under strong scientific leadership and professional project management, providing a coherent European approach and ensuring effective alignment of regional, national and European research and programmes. The project work plan is organized in the form of thirteen subprojects, each dedicated to a specific area of activity.
A significant part of the budget will be used for competitive calls to complement the collective skills of the Consortium with additional expertise.

5.2. International Research Visitors

5.2.1. Visits of International Scientists

Invitation of Antoni Guillamon (as part of a sabbatical semester), Polytechnic University of Catalonia (Spain), March-April 2017

Invitation of Vivien Kirk, University of Auckland (New Zealand), April 2017

Invitation of Jeff Moehlis, University of California Santa Barbara (USA), April 2017

Invitation of Martin Wechselberger, University of Sydney (Australia), August 2017

Invitation of Cian O'Donnell, University of Bristol (UK), September 2017

invitation of Moritz Helias and Tobias Kuehn, University of Aachen and Juelich Research Center (Germany), September 2017

Invitation of David Terman (as part of a sabbatical semester), Ohio State University (USA), October 2017

Invitation of Zack Kilpatrick, University of Colorado Boulder (USA), November 2017

5.2.1.1. Internships

Leila Bekri, co-supervised by Romain Veltz and Hélène Marie (IPMC), Feb.-Apr. 2017

Raphael Forquet, co-supervised by Romain Veltz and Hélène Marie (IPMC), until Jan. 2017

Anna Song, supervised by Olivier Faugeras, Feb.-June 2017

5.2.2. Visits to International Teams

Visit of Mathieu Desroches to Mirela Domijan (University of Liverpool, UK) in March 2017

Visit of Mathieu Desroches to Daniele Avitabile (University of Nottingham, UK) in August 2017

Visit of Fabien Campillo & Mathieu Desroches to Serafim Rodrigues (BCAM, Bilbao, Spain) in September 2017

Visit of Mathieu Desroches to Serafim Rodrigues (Basque Center for Applied Mathematics, Bilbao, Spain) in December 2017

5.2.2.1. Research Stays Abroad

One-month research stay of Mathieu Desroches at BCAM (Bilbao, Spain) on an invited professor scholarship to work with Serafim Rodrigues, June 2017

6. Dissemination

6.1. Promoting Scientific Activities

6.1.1. Scientific Events Organisation

6.1.1.1. Member of the Organizing Committees

Olivier Faugeras and Romain Veltz were on the Advisory Board of the 3rd International Conference on Mathematical Neuroscience, held in Boulder Colorado (USA), May 30 - June 2, 2017.

Mathieu Desroches organised a special session on "Dynamical Systems and Dysfunctions: modeling and neuronal dynamics' interpretation in both healthy and pathological brain states" at the C@UCA workhop (Fréjus, France), June 6-8, 2017.

Mathieu Desroches co-organised together with Daniele Avitabile (University of Nottingham, UK) and Vivien Kirk (University of Auckland, New Zealand) a two-part mini-symposium on "Recent Advances in Slow-Fast Dynamics" at the SIAM Conference on Applications of Dynamical Systems (Snowbird, Utah, USA), May 21-25, 2017.

Romain Veltz co-organised with Stéphane Barland (ILNL, Sophia Antipolis) the workshop Computational Neuroscience and Optical Dynamics held at the Institut Nonlinéaire de Nice (INLN, Sophia Antipolis), May 18-19, 2017.

6.1.2. Scientific Events Selection

6.1.2.1. Member of the Conference Program Committees

Pascal Chossat and Martin Krupa were on the Program Committee of the 3rd International Conference on Mathematical Neuroscience, held in Boulder Colorado (USA) May 30 - June 2 2017.

6.1.3. Journal

6.1.3.1. Member of the Editorial Boards

Olivier Faugeras is the co-editor in chief of the open access Journal of Mathematical Neuroscience.

6.1.3.2. Reviewer - Reviewing Activities

Fabien Campillo acts as a reviewer for Journal of Mathematical Biology, for the conference TAMTAM 2017 *Tendances dans les Applications Mathématiques en Tunisie, Algérie et Maroc*.

Mathieu Desroches acts as a reviewer for Physica D, SIAM Journal on Applied Dynamical Systems (SIADS), PLoS Computational Biology, Dynamical Systems: An International Journal, IEEE Transactions on Cognitive and Developmental Systems, Discrete and Continuous Dynamical Systems Series B.

Olivier Faugeras acts as a reviewer for the Journal of Mathematical Neuroscience, the Journal of Computational Neuroscience, the SIAM Journal on Applied Dynamical Systems (SIADS).

Martin Krupa acts as a reviewer for Nonlinearity, Proceedings of the National Academy of Sciences of the USA (PNAS), the SIAM Journal of Applied Dynamical Systems (SIADS).

Martin Krupa has edited together with Pietro-Luciano Buono (University of Ontario, Canada) and Ian Stewart (University of Warwick, UK) a special issue of the Journal *Dynamical Systems: An International Journal* titled “Equivariance and Beyond: M. Golubitsky’s 70th Birthday”.

Romain Veltz acts as a reviewer for Neural Computation, Elife, SIADS, Journal of the Royal Society Interface.

6.1.4. Invited Talks

Pascal Chossat, “Latching dynamics in neural networks with synaptic depression”, C@UCA workshop, Fréjus (France), June 2017.

Pascal Chossat, “Pourquoi le léopard est-il tacheté et le tigre rayé”, Café des Sciences d’Avignon, Avignon (France), December 2017.

Pascal Chossat, “Heteroclinic chains as a model of sequential activation of concepts in neural networks”, workshop Nice Nonlinearities, Nice (France), December 2017.

Mathieu Desroches, “Canards and spike-adding phenomena in neural bursters”, University of Liverpool (UK), March 2017.

Mathieu Desroches, “Canards and spike-adding in neural bursters”, University of The Balearic Islands (Palma, Spain), March 2017.

Mathieu Desroches, “Three-timescale dynamics: canards and spike-adding”, SIAM Conference on Applications of Dynamical Systems, Snowbird (Utah, USA), May 2017.

Mathieu Desroches, “Slow-fast transitions to seizure states in the Wendling-Chauvel neural mass model”, C@UCA workshop, Fréjus (France), June 2017.

Olivier Faugeras, “Describing the thermodynamic limit of networks of interacting neurons”, workshop *PDE and Probability Methods for Interactions*, Inria Sophia Antipolis, April 2017.

Olivier Faugeras, “Multiscale representations in mathematical neuroscience: deterministic and stochastic approaches”, C@UCA workshop, Fréjus (France), June 2017. [keynote lecture]

Olivier Faugeras, “Coping with correlations in the analysis of the thermodynamic limit of neuronal networks", HBP workshop *Theoretical Neuroscience in the Human Brain Project* and at the workshop *New advances in theoretical tools for the study of large scale neural systems* at the CNS Conference, Antwerp, the Netherlands, July 2017.

Olivier Faugeras, “On a certain McKean-Vlasov equation that arises in Neuroscience", workshop on *Singular McKean-Vlasov equations*, Inria Sophia Antipolis, September 2017.

Elif Köksal Ersöz, “Synchronization of weakly coupled canard oscillators”, mini-symposium on “Recent Advances in Slow-Fast Dynamics” at the SIAM Conference on Applications of Dynamical Systems (Snowbird, Utah, USA), May 21-25, 2017.

Elif Köksal Ersöz, “Canard mediated (de)synchronization in coupled phantom bursters”, C@UCA workshop, Fréjus (France), June 2017.

Martin Krupa, “Modeling cortical spreading depression induced by the hyperactivity of interneurons”, C@UCA workshop, Fréjus (France), June 2017. [joint talk with Massimo Mantegazza (IPMC, Sophia Antipolis)]

Romain Veltz, “Invariant manifolds in Mathematical Neurosciences”, winter school *Deterministic and Stochastic Models in Neurosciences*, Toulouse (France), December 2017.

Romain Veltz, “On a toy network of neurons interacting through nonlinear dendritic compartments”, workshop *Random Structures on the Brain*, Lorentz Center, Leiden (the Netherlands), December 2017.

Romain Veltz, “Oscillatory dynamics in a stochastic spiking neural network", workshop *Brain Dynamics and Statistics*, Banff (Canada), March 2017.

Romain Veltz, “Hopf bifurcation in the mean field of a stochastic spiking neural networks”, European Institute in Theoretical Neuroscience, Paris (France), April 2017.

Romain Veltz, “Study of a mean field model stemming from a neural network", Gdr NonLocal, Toulouse (France), April 2017.

6.1.5. Scientific Expertise

Pascal Chossat was on the Advisory Board of the Complex Systems Academy of the UCA$^{\text{JEDI}}$ Idex.

Fabien Campillo reviewed a grant proposal for the Swiss National Science Foundation. He is also member of the *Comité NICE* of the Projects Committee of Inria Sophia Antipolis - Méditerranée.

Mathieu Desroches reviewed grant proposals for the Agence Nationale de la Recherche (ANR).

Olivier Faugeras regularly reviews proposals to the European Research Council (ERC) in Mathematics, Computer Science and NeuroScience and he is a member of the ERC Panel 1 (Mathematics). He also reviewed a proposal in Mathematics for the Netherlands Organisation for Scientific Research (NWO).

6.2. Teaching - Supervision - Juries

6.2.1. Teaching

Chalk-learning

Master 2 MVA/UPMC: Romain Veltz, Mathematical Methods for Neurosciences, 20 hours, Paris, France.

Master 1 BIM/UPMC: Mathieu Desroches, Modèles Mathématiques et Computationnels en Neuroscience, 30 hours, Paris, France.

In-service education, Supagro & Inra: Fabien Campillo (in collaboration with Céline Casenave from Inra), Modélisation et contrôle de systèmes dynamiques en agronomie, 20 hours, Montpellier, France.

6.2.2. Supervision

PhD in progress: Axel Dolcemascolo, “All optical neuromimetic devices”, started in January 2016, co-supervised by Romain Veltz and Stéphane Barland (INLN).

PhD in progress: Pascal Helson, “Study of plasticity laws with stochastic processes”, started in September 2016, co-supervised by Romain Veltz and Etienne Tanré (Inria TOSCA).

PhD in progress: Quentin Cormier, “Biological spiking neural networks", started in September 2017, co-managed (“co-encadré”) by Romain Veltz and Etienne Tanré (Inria TOSCA).

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Major publications by the team in recent years

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