POST-PRESENTATION REPORT - STOCHASTIC NEUROSCIENCE SEMINAR

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Abstract. This report is based on the paper "Mean-field limit of interacting 2D nonlinear stochastic spiking neurons"[1] (Aymard, Campillo, Veltz; 2019). The main focus will be chapter 2 (A detailed stochastic model and its mean-field approximation) of the paper. Here we will derive and discuss appropriate statistical models for the considered system of neurons. Chapters 2.3 and 2.4 will be mostly emphasized, in where we develop the statistical model further by using a more sophisticated mean-field approach, and expressing the resulting equation in different ways.

1. Introduction. We will discuss a model, that considers a 2D system of interacting neurons. Also, we apply the idea of non-deterministically determined spikes. That is, rather than modelling spikes through threshold crossing of membrane potential, the spiking events are stochastically determined with the intensity increasing analogously with the membrane potential. Such a model will first be discussed. The use of stochastic spiking events is biologically relevant, and avoids certain problems occurring for deterministic models when trying to efficiently model the macroscopic behavior of a given system. Further we would like to apply mean-field theory to develop an approximation allowing us more mathematical tools to simulate the behaviour. A non-linear PDE will be derived, and this can be further expressed as coupled transport equation. In this report we will discuss how to arrive at these equations. Working with mean-field approximations of 2D systems is mathematically challenging, both theoretically and practically, and many associated problems have just recently been managed.

2. Model discussion.

2.1. Stochastic model. Let us consider a system of N identical neurons. Further we are defining the following

$$\begin{aligned} &v_i(t) \in \mathbb{R}\text{: membrane potential of neuron i at time t} \\ &w_i(t) \in \mathbb{R}\text{: adaptation current of neutron i at time t} \end{aligned}$$

Next we need to define the deterministic flow of both membrane potential and adaptation current, given by

$$\begin{aligned} \dot{v}_i(t) &= \tilde{\mathcal{V}}(v_i(t), w_i(t)), \text{ with } \tilde{\mathcal{V}}(v, w) := F(v) - w + I \\ \dot{w}_i(t) &= \mathcal{W}(v_i(t), w_i(t)), \text{ with } \mathcal{W}(v, w) := \frac{1}{\tau_w}(bv - w) \end{aligned} \tag{2.1}$$

for some paramenters τ_w and b, and I represents the input current. F is a nonlinearity, and there already exists a lot of theory and options for the choice of this. In the specific article which this report is based on, mostly exponential function have been utilized.

Then we also need to incorporate the stochastic spiking events. Each neuron i spikes at a given rate $\lambda(v_i) \geq 0$ and leads to the following jump transitions

$$\begin{aligned} &(v_i(t), w_i(t)) = (\bar{v}, w_i(t^-) + \bar{w}) \\ &(v_j(t), w_j(t)) = (v_j(t^-) + \frac{J}{N}, w_j(t^-)), \text{ for} j \neq i \end{aligned} \tag{2.2}$$

for some reset potential $\bar{v}$, jump in adaption current $\bar{w}$ and post-synaptic input $\frac{J}{N}$. These mechanics are stochastic, leading to an in general stochastic model.

2.2. Mean-field approximation. Now, we are ready to develop a mean-field approximation. The dynamics we just have described, can be expressed in the following way. Let $(v_i^N(t), w_i^N(t))_{1\leq i\leq N}$ denote the dynamics, then they may be rewritten as

$$
\begin{aligned}
v_i^N(t) &= v_{i,0}^N + \textstyle\int_0^t \tilde{\mathcal{V}}(v_i^N(s), w_i^N(s))ds \\
&\quad + \textstyle\int_0^t \int_0^\infty (\bar{v} - v_i^N(s^-))1_{\{z\leq\lambda(v_i^N(s^-))\}}\mathcal{N}^i(dz, ds) \\
&\quad + \tfrac{J}{N}\textstyle\sum_j \int_0^t \int_0^\infty 1_{\{z\leq\lambda(v_j^N(s^-))\}}\mathcal{N}^j(dz, ds) \\
w_i^N(t) &= w_{i,0}^N + \textstyle\int_0^t \mathcal{W}(v_i^N(s), w_i^N(s))ds \\
&\quad + \textstyle\int_0^t \int_0^\infty (\bar{w}1_{\{z\leq\lambda(v_i^N(s^-))\}}\mathcal{N}^i(dz, ds)
\end{aligned}
\tag{2.3}
$$

with $\mathcal{N}^i$ are independent poisson random measures. Now the idea is to consider the interaction term, and assume propagation of chaos in the system, meaning that when the amount of particles is sufficiently large, the particles asymptotically behaves like independent particles with the same limit distribution. By the law of large numbers we can rewrite the interaction term as

$$
\begin{aligned}
\frac{J}{N}\sum_j \int_0^t \int_0^\infty 1_{\{z\leq\lambda(v_i^N(s^-))\}}\mathcal{N}^j(dz, ds) &= J\mathbb{E}\int_0^t \int_0^\infty 1_{\{z\leq\lambda(v_1^N(s^-))\}}\mathcal{N}^1(dz, ds) \\
&= J\int_0^t \mathbb{E}(\lambda(v(s)))
\end{aligned}
$$

, so the empirical distribution of the interacting particles is asymptotically converging to a deterministic distribution representing the distribution of a limit particle described by

$$
\begin{aligned}
v(t) &= v_0 + \textstyle\int_0^t \tilde{\mathcal{V}}(v(s), w(s))ds \\
&\quad + \textstyle\int_0^t \int_0^\infty (\bar{v} - v(s^-))1_{\{z\leq\lambda(v(s^-))\}}\mathcal{N}(dz, ds) \\
&\quad + J\textstyle\int_0^t \mathbb{E}(\lambda(v(s))) \\
w(t) &= w_0 + \textstyle\int_0^t \mathcal{W}(v(s), w(s))ds \\
&\quad + \textstyle\int_0^t \int_0^\infty (\bar{w}1_{\{z\leq\lambda(v(s^-))\}}\mathcal{N}(dz, ds)
\end{aligned}
\tag{2.4}
$$

in where the initial values (v_0, w_0) are chosen randomly according to some probability distribution μ_0. $\mathcal{N}$ is a again poisson random measure with intensity measure $dxdz$.

2.3. Non-linear PDE. Now, we would want to express our system given by (2.4) by a PDE, allowing us to apply numerical methods for solving PDEs to analyse the systems behaviour. The mean-field system (2.4) is a Piecewise-deterministic Markov Process (PDMP), and in order to derive a non-linear PDE for this system, we make use of the infiteimal generator of the process. This is a part I would like to emphazise more in this report, as its not explained too much in detail in the article. So let us start with some relevant mathematical definitions, before we can define a generator for a Markov Process. This part is based on [2].

Definition 2.1 (One-parameter family (OPF) of operators). *Let (E, ρ) be a metric space and let $\{X_t\}$ be an E-valued homogeneous Markov Process. Then define the OPF of operators P_f through*

$$P_t f(x) = \int f(y) P(t, x, dy) = \mathbb{E}[f(X_t] X_0 = x]$$

for all $f(x) \in C_b(E)$, where $C_b(E)$ is the set of all continuous and bounded functions on E. Assume that $P_f : C_b(E) \longrightarrow C_b(E)$. Then P_f forms a semigroup of operators on $C_b(E)$.

I will not discuss the theory of semigroups in further detail, as it is not too interesting or relevant in the context of this article. Properties of such groups, however, are used in the next steps without proof in order to reach the desired result.

Definition 2.2. *Define by $\mathcal{D}(\mathcal{L})$ the set of all $f \in C_b(E)$ such that the following limit exists*

$$\mathcal{L} f = \lim_{t \longrightarrow 0} \frac{P_f f - f}{t}$$

Definition 2.3 (Infinitesimal generator). *The operator $\mathcal{L} : \mathcal{D}(\mathcal{L}) \longrightarrow C_b(E)$ is called the infinitesimal generator of the operator semigroup P_t.*

Definition 2.4 (Generator of Markov Process). *The operator $\mathcal{L} : C_b(E) \longrightarrow C_b(E)$, defined in the previous definition, is called the generator of the Markov process $\{X_t\}$.*

These definitions of generators helps us analyzing the stochastic process with Kolmogorov equations, as is done in the article. Let us further express the OPF of operators in terms of the generator

$$P_t = \exp(\mathcal{L} t)$$

which is allowed due to properties of the semigroup operator. We now consider a function $\mu(x, t) := (P_t f)(x) = \mathbb{E}[f(X_t) X_0 = x]$. By standard differentiation of this, we obtain

$$\frac{\partial u}{\partial t} = \frac{d}{dt}(e^{\mathcal{L} t} f) = \mathcal{L} u \tag{2.5}$$

with boundary conditions $u(x, 0) = P_0 f(x) = f(x)$. So $u(x, t)$ solves the given boundary value problem (2.5), known as the Backward Kolmogorov equation.

We can also define the adjoint operator P_t^*, given such that

$$\int_{\mathbb{R}} P_t f(x) d\mu(x) = \int_{\mathbb{R}} f(x) d(P_t^* \mu)(x)$$

and with similar argumentation, writing $P_t^* = \exp(\mathcal{L}^* t)$ and $\mu_t := P_t^* \mu$, with μ being the initial distribution, yields

$$\frac{\partial u_t}{\partial t} = \mathcal{L}^* u_t \tag{2.6}$$

with $\mu_0 = \mu$. This is called the Forward Kolmogorov equation.

So, why is this great? Well, if we know the generator of a Markov process $\mathcal{L}$, by solving these Kolmogorov equations we can calculate the statistics of the process. This is exactly what is done in the article, the Kolmogorov equations are describing the evolution of the distribution of the limit particles given in (2.4). If we have the initial distribution and the generator, we can calculate the transition probability density by solving the Forward Kolmogorov equation. Refering to the article[1], the generator in weak form of our process is given by

$$\mathcal{L}_{\mu(t)}\varphi(v,w) = \mathcal{L}^t_{\mu(t)}\varphi(v,w) + \mathcal{L}^j_{\mu(t)}\varphi(v,w) \tag{2.7}$$

where $\mathcal{L}^t_{\mu(t)}\varphi(v,w)$ and $\mathcal{L}^j_{\mu(t)}\varphi(v,w)$ are denoting the generators for the "ODE" part and the jump part, respectively. They are given by

$$\mathcal{L}^t_{\mu(t)}\varphi(v,w) := \mathcal{V}_\mu(v,w)\frac{\partial\varphi(v,w)}{\partial v} + \mathcal{W}_\mu(v,w)\frac{\partial\varphi(v,w)}{\partial v}$$

$$\mathcal{L}^j_{\mu(t)}\varphi(v,w) := \lambda(v)(\varphi(\bar{v},\bar{w}+w) - \varphi(v,w))$$

with

$$\mathcal{V}_\mu(v,w) = \tilde{\mathcal{V}}(v,w) + J\int\int_{\mathbb{R}^2}\lambda(v')\mu(dv',dw')$$

And the inverse operator is given by

$$\langle\mathcal{L}^*_\mu u,\varphi\rangle = \langle\mu,\mathcal{L}_\mu\varphi\rangle$$

, for details i refer to the article[1]. In the end we arrive at an expression for the evolution of the distribution, given by the strong Forward Kolmogorov equation, and expressed with the adjoint of the process generator, as we also discussed earlier. Namely

$$\frac{\partial}{\partial t}\mu(t) = \mathcal{L}^*_{\mu(t)}u(t) = \left(\mathcal{L}^{t*}_{\mu(t)} + \mathcal{L}^{j*}_{\mu(t)}\right)\mu(t) \tag{2.8}$$

which in the end reads, when substituting in the adjoint operator

$$\begin{aligned}&\tfrac{\partial}{\partial t}\mu(t,v,w) + \tfrac{\partial}{\partial v}(\mu(t,v,w)\mathcal{V}_{\mu(t)}(v,w)) + \tfrac{\partial}{\partial w}(\mu(t,v,w)\mathcal{W}(v,w))\\ &= -\lambda(v)\mu(t,v,w) + \delta_{\bar{v}}(v)\textstyle\int_{\mathbb{R}}\lambda(\tilde{v})\mu(t,\tilde{v},w-\bar{w})d\tilde{v}\end{aligned} \tag{2.9}$$

This equation is solved numerically to study the behaviour of the mean-field system. The equation is also sometimes called the Differential Chapman-Kolmogorov Equation, and can be intuitivaly understood in the following way. The second and the third term describes the deterministic drift of membrane potential and adaptation current in the system. The fourth term describes the loss of mass in the distribution for where the neurons are spiking, and the fifth and final term describes the gain of mass in the distribution at the reset potential, right after spiking events.

In chapter 3.4-3.5 of the book "Handbook of Stochastic Methods"[3] this equation is derived generally for different types of processes by considering the evolution of the expectation of a function $f(z)$. First we define and require that for all $\epsilon > 0$

$$i)\ \frac{\lim_{\Delta t\to 0}\int f(x)[p(x,t+\Delta t\mid y,t')}{\Delta t} := W(x\mid z,t)$$

$$ii)\ \lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|x-z|<\epsilon}(x_i-z_i)p(x,t+\Delta t\mid z,t):=A_i(z,t)+O(\epsilon)$$

$$iii)\ \lim_{\Delta t\to 0}\frac{1}{\Delta t}\int_{|x-z|<\epsilon}(x_i-z_i)(x_j-z_j)p(x,t+\Delta t\mid z,t):=B_{ij}(z,t)+O(\epsilon)$$

Then by the definition of the differentiation, and assuming that $f(z)$ is twice differentiable

$$\frac{\partial}{\partial t}\int f(x)p(x,t\mid y,t')dx=\frac{\lim_{\Delta t\to 0}\int f(x)[p(x,t+\Delta t\mid y,t')-p(x,t\mid y,t')]}{\Delta t}dx \tag{2.10}$$

, now further the idea is to split the domain in two parts, $\mid x-z\mid\geq\epsilon$ and $\mid x-z\mid<\epsilon$. Then $f(z)$ is expressed as a Taylor series of second order, and inserted in (2.10). The integral is split over these sub-domains separately, and after solving the integral and adding appropriate boundary conditions as done in [3], we arrive at a similar differential equation as we deduced before, just in general form, namely

$$\begin{aligned}\frac{\partial}{\partial t}p(z,t\mid y,t')=-\sum_i\frac{\partial}{\partial z_i}[A_i(z,t)p(z,t\mid y,t')]+\frac{1}{2}\sum_{i,j}\frac{\partial^2}{\partial z_i\partial z_j}[B_{ij}(z,t)p(z,t\mid y,t')]\\+\int[W(z\mid x,t)p(z,t\mid y,t')-W(x\mid z,t)p(z,t\mid y,t')]dx\end{aligned} \tag{2.11}$$

with the first term expressing deterministic drift, with coefficient $A_i(z,t)$. The second term describing diffusion, with coefficient $B_{ij}(z,t)$. And the final term describing a jumping process, driven by some transition probabilities W. To compare with our process, described by equation (2.9), our process is driven by a deterministic drift in two dimensions, as well as stochastic spiking events.

2.4. Transport equations. Finally we will also discuss a further development of the non-linear PDE given by (2.9). In the previous derivation, we split the domain in two regions, and we will exploit a somewhat similar idea now. By splitting the domain in two, we can express the mean-field dynamics equivalently with coupled transport equations. A transport equation in general is somehow explaining the flow in or out of a given space, or the flow across the boundary. So, a natural choice in our case, is choosing the interface at the reset potential, that is

$$\Gamma:=(\bar{v},w):w\in\mathbb{R}$$

, leading to the following two sub-domains

$$\Omega_1:=\{(v,w)\in\mathbb{R}^2,v<\bar{v}\},\qquad\Omega_2:=\{(v,w)\in\mathbb{R}^2,v>\bar{v}\}$$

Let $F_{\mu(t)}=(\mathcal{V}_{\mu(t)},\mathcal{W})$, and now we go back to the forward Kolmogorov equation and consider the term

$$\langle\mu(t),\nabla\varphi\cdot F_{\mu(t)}\rangle=\int\int_{\mathbb{R}^2}\nabla\varphi\dot{(}\mu(t)F_{\mu(t)})$$

and then we consider this by separating according to the already defined domains

$$\langle\mu(t),\nabla\varphi\cdot F_{\mu(t)}\rangle=\int\int_{\Omega_1}\nabla\varphi\cdot(\mu(t)F_\mu(t))+\int\int_{\Omega_2}\nabla\varphi\cdot(\mu(t)F_{\mu(t)})$$

$$
\begin{aligned}
&= -\int\int_{\Omega_1} \varphi div(\mu(t)F_{\mu(t)}) + \int_{\mathbb{R}} \varphi(\bar{v},w)\mu(t,\bar{v}^-,w)F_{\mu(t)}(\bar{v},w)\cdot\begin{pmatrix}1\\0\end{pmatrix}dw \\
&\quad -\int\int_{\Omega_2} \varphi div(\mu(t)F_{\mu(t)}) + \int_{\mathbb{R}} \varphi(\bar{v},w)\mu(t,\bar{v}^+,w)F_{\mu(t)}(\bar{v},w)\cdot\begin{pmatrix}-1\\0\end{pmatrix}dw \\
&= -\int\int_{\mathbb{R}^2}(\mu(t)F_{\mu(t)}) - \int_{\mathbb{R}} \varphi(\bar{v},w)\tilde{\mu}(t,\cdot,w)\mathcal{V}_{\mu(t)}(\bar{v},w)dw
\end{aligned}
$$

where $\tilde{\mu}(t,\cdot,w) := \mu(t,\bar{v}^+,w) - \mu(t,\bar{v}^-,w)$ is the jump of the distribution over the interface Γ. By the use of test functions φ with support on the whole domain, we obtain the PDE

$$\partial_t\mu(t) + \partial_v(\mu(t)\mathcal{V}_{\mu(t)}) + \partial_w(\mu(t)\mathcal{W}) = -\lambda\mu(t) \tag{2.12}$$

with $\mu(t=0) = \mu_0$ on $\Omega_1 \cup \Omega_2$, and with the interface condition

$$\mathcal{V}_{\mu(t)}(\bar{v},w)\tilde{\mu}(t,\cdot,w) = \int_{\mathbb{R}} \lambda(v')\sigma_{\bar{w}}\mu(t,v',w)dv' \tag{2.13}$$

$\forall w \in \mathbb{R}$. So equation (2.12) is our transport PDE equation, with the interface condition (2.13). Looking at (2.12), it is very similar to our non-linear PDE (2.9) from section 2.3. However, the last term in (2.9), which describes the gain of distribution mass at the reset, is now included in the interface condition. So a possible interpretation of the condition (2.13), is that it takes care that the flow of membrane potential over our interface, which is the reset potential, equals the gain of probability mass here, which sounds intuitive. Hence these PDEs, derived in section 2.3 and 2.4 respectively, are equivalent, but the transport equation allows for even more possible numerical tools to simulate the dynamics and study the behaviour of the system.

3. Summary. We have discussed a non-linear stochastic 2D model describing the behaviour of a system of interacting neurons. First we defined the model, with deterministic flow of membrane potential and adaptation current combined with jump transitions at stochastically determined spiking events. Using mean-field theory, we could reduce this system to basically a one neuron problem, in that all neurons behave identically asymptotically, and this limit particle is described by a deterministic distribution in the limit. In order to simulate these dynamics more easily, we wish to develop a non-linear PDE describing the evolution of the distribution. This was done by introducing the idea of generators of stochastic processes, and in combination with the initial distribution, the evolution could be interpreted by the Kolmogorov equations. The resulting PDE was also compared to a more general differential Chapman-Kolmogorov equation. In the end, we quickly discussed the possibility of rewriting the PDE as a transport PDE. This resulted in a pretty similar looking equation, but with a interface condition over the reset, allowing us other methods to numerically study the behaviour.

4. References.

REFERENCES

[1] R. V. Benjamin Aymard, Fabien Campillo, "Mean-field limit of interacting 2d nonlinear stochastic spiking neurons," 2019.
[2] G. Pavliotis, "Applied stochastic processes," 2009.
[3] C. Gardiner, *Handbooks of Stochastic Methods*. Springer-Verlag, 1996.