A kinetic approach for large-scale interacting populations of noisy spiking neurons

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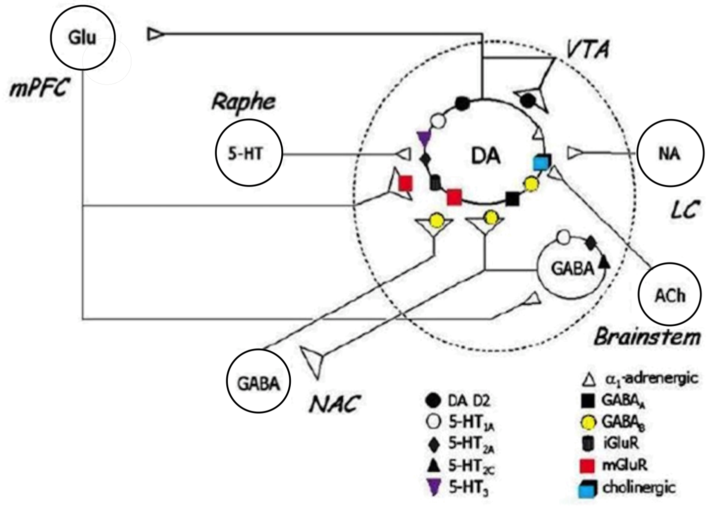


From: "The somatodendritic release of dopamine in the ventral tegmental area and its regulation by afferent transmitter systems",
A. Adell, F. Artigas, Neuroscience and Biobehavioral Reviews **28** (2004) 415-431.

1 Integro-partial differential equations for sets of connected neural population probability distributions

1.1 Dynamical system for a given population $\mathscr{P}_\gamma$, $\gamma = 1, 2, \ldots, P$

State variables of each cell $i = 1, 2, \ldots, K_\gamma$ in $\mathscr{P}_\gamma$:

V_i^γ : membrane potential $\widehat{R}_i^\gamma$: m-dimensional activation-inactivation ionic variables

ϕ_i^γ : variables describe the plasticity of the synaptic connections

Network dynamical system :

$$\begin{aligned}
\frac{dV_i^\gamma}{dt} &= I^\gamma(V_i^\gamma, \widehat{R}_i^\gamma) + I_{ext}^\gamma(t) + \frac{1}{K_\gamma}\sum_{j=1}^{K_\gamma} M^\gamma(V_i^\gamma, \widehat{R}_i^\gamma, \phi_i^\gamma, V_j^\gamma, \widehat{R}_j^\gamma, \phi_j^\gamma) + \eta_{i,t}^\gamma \\
\frac{d\widehat{R}_i^\gamma}{dt} &= \widehat{\Psi}^\gamma(V_i^\gamma, \widehat{R}_i^\gamma) \\
\frac{d\phi_i^\gamma}{dt} &= \Omega^\gamma(\phi_i^\gamma, V_i^\gamma, \widehat{R}_i^\gamma) \qquad i = 1, 2, \ldots, K_\gamma \qquad \gamma = 1, 2, \ldots, P
\end{aligned}$$

Final structure of the network dynamical system :

For $i = 1, 2, \ldots, K_\gamma$

$$\frac{dZ_i^\gamma}{dt} = \mathcal{F}^\gamma(Z_i^\gamma) + \frac{1}{K_\gamma}\sum_{j=1}^{K_\gamma} \mathcal{M}^\gamma(Z_i^\gamma, Z_j^\gamma) + \zeta_{i,t}^\gamma$$

where the vectors Z_i^γ, $\mathcal{F}^\gamma(Z_i^\gamma)$, $\zeta_{i,t}^\gamma$, $\mathcal{M}^\gamma(Z_i^\gamma, Z_j^\gamma)$ in $\mathbb{R}^{m+2}$ are given by

$$\begin{aligned}
Z_i^\gamma &= (V_i^\gamma, \widehat{R}_i^\gamma, \phi_i^\gamma) \\
\mathcal{F}^\gamma(Z_i^\gamma) &= (I^\gamma(V_i^\gamma, \widehat{R}_i^\gamma) + I_{ext}^\gamma(t),\ \widehat{\Psi}^\gamma(V_i^\gamma,\ \widehat{R}_i^\gamma), \Omega^\gamma(\phi_i^\gamma, V_i^\gamma, \widehat{R}_i^\gamma)) \\
\mathcal{M}^\gamma(Z_i^\gamma, Z_j^\gamma) &= (M^\gamma(V_i^\gamma, \widehat{R}_i^\gamma, \phi_i^\gamma, V_j^\gamma, \widehat{R}_j^\gamma, \phi_j^\gamma), \widehat{0}, 0) \\
\zeta_{i,t}^\gamma &= (\eta_{i,t}^\gamma, \widehat{0}, 0)
\end{aligned}$$

1.2 The mean field approach for coupled conductance-based neural populations

Spiking neurons are organized in a set of P connected populations.

Dynamical system :

$$\frac{dZ_i^\gamma}{dt} = \mathcal{F}^\gamma(Z_i^\gamma) + \zeta_{i,t}^\gamma + \sum_{\alpha=1}^{P} \frac{1}{K_\alpha} \sum_{j=1}^{K_\alpha} \mathcal{M}^{\gamma\alpha}(Z_i^\gamma, Z_j^\alpha), \quad i = 1, 2, \dots, K_\gamma, \;\; \gamma = 1, 2, \dots, P$$

Joint probability distribution of stochastic variables :

$$p_t((Z_i^\alpha)_{i,\alpha}) = p_t((Z_i^1)_{i=1,2,\dots,K_1}, \dots, (Z_j^P)_{j=1,2,\cdots,K_P}), \quad \text{where } (Z_i^\alpha)_{i,\alpha} = (Z_i^\alpha)_{i=1,2,\dots,K_\alpha}^{\alpha=1,2,\dots,P}$$

Fokker Planck equation for this system :

$$\begin{aligned}\frac{\partial}{\partial t} p_t((Z_i^\alpha)_{i,\alpha}) = &- \sum_{\gamma=1}^{P} \sum_{i=1}^{K_\gamma} \frac{\partial}{\partial Z_i^\gamma} (\mathcal{F}^\gamma(Z_i^\gamma)\, p_t((Z_i^\alpha)_{i,\alpha})) \\ &- \sum_{\gamma=1}^{P} \sum_{i=1}^{K_\gamma} \frac{\partial}{\partial Z_i^\gamma} \left(\sum_{\alpha=1}^{P} \frac{1}{K_\alpha} \sum_{j=1}^{K_\alpha} \mathcal{M}^{\gamma\alpha}(Z_i^\gamma, Z_j^\alpha)\, p_t((Z_i^\alpha)_{i,\alpha}) \right) \\ &+ \frac{1}{2} \sum_{\gamma=1}^{P} \sum_{i=1}^{K_\gamma} (\beta_V^\gamma)^2 \frac{\partial^2}{\partial (V_i^\gamma)^2} p_t((Z_i^\alpha)_{i,\alpha})\end{aligned}$$

For each population $\mathscr{P}_\mu$, define set variables :

$$\widehat{n}^\mu(U) = \frac{1}{K_\mu}\sum_{i=1}^{K_\mu}\delta(Z_i^\mu - U)$$

$\delta(\cdot)$: Dirac distribution

Z_i^μ : solution of the dynamical system for the population $\mathscr{P}_\mu$

Z_i^μ and $U \in \mathbb{R}^{m+2}$

$U = (u, \hat{z}, s), u, s$:

u (resp. $\widehat{z}, s$), potential (resp. recovery, synaptic) meaning

Expectation value of $\widehat{n}^\mu(U)$ w.r.t p_t :

$$n^\mu(U,t) = \langle \widehat{n}^\mu(U) \rangle_{p_t}$$

$n^\mu(U,t)$: neural population probability distribution (PPD) for the population $\mathscr{P}_\mu$

Derivation of an equation for $n^\mu(U,t)$

Time derivative gives 3 terms :

$$\frac{\partial}{\partial t} n^\mu(U,t) = \gamma_1^\mu + \gamma_2^\mu + \gamma_3^\mu$$

$$\gamma_1^\mu = \int_\Omega \prod_{\delta=1}^{P}\prod_{l=1}^{K_\delta} dZ_l^\delta \sum_{\gamma=1}^{P}\sum_{i=1}^{K_\gamma} \{\mathcal{F}^\gamma(Z_i^\gamma) p_t((Z_i^\alpha)_{i,\alpha})\} \frac{\partial}{\partial Z_i^\gamma} \frac{1}{K_\mu} \sum_{j=1}^{K_\mu} \delta(Z_j^\mu - U)$$

one obtains : $$\gamma_1^\mu = \frac{-\partial}{\partial U}(\mathcal{F}^\mu(U) n^\mu(U,t))$$

$$\gamma_2^\mu = -\int_\Omega \prod_{\delta=1}^{P}\prod_{l=1}^{K_\delta} dZ_l^\delta \sum_{\gamma=1}^{P}\sum_{i=1}^{K_\gamma} \frac{\partial}{\partial Z_i^\gamma} \left\{ \sum_{\alpha=1}^{P} \frac{1}{K_\alpha} \sum_{l=1}^{K_\alpha} \mathcal{M}^{\gamma\alpha}(Z_i^\gamma, Z_l^\alpha) p_t((Z_i^\alpha)_{i,\alpha}) \right\} \frac{1}{K_\mu} \sum_{j=1}^{K_\mu} \delta(Z_j^\mu - U)$$

one obtains : $$\gamma_2^\mu = -\frac{\partial}{\partial U} \int_{R^{m+2}} dU' \sum_{\alpha=1}^{P} \mathcal{M}^{\mu\alpha}(U,U') \langle \widehat{n}^\mu(U) \widehat{n}^\alpha(U') \rangle_{p_t}.$$

the term γ_2^μ is exact (not really useful in applications).

Mean field estimate : $$\langle \widehat{n}^\mu(U) \widehat{n}^\alpha(U') \rangle_{p_t} \approx \langle \widehat{n}^\mu(U) \rangle_{p_t} \langle \widehat{n}^\alpha(U') \rangle_{p_t}.$$

Fluctuations of $\widehat{n}^\mu(U)$ (resp. $\widehat{n}^\alpha(U')$) :

small for K_μ (resp. K_α) large and are $O(\frac{1}{\sqrt{K_\mu}})$ (resp. $O(\frac{1}{\sqrt{K_\alpha}})$).

$$\gamma_2^\mu = -\frac{\partial}{\partial U} \int_{R^{m+2}} dU' \sum_{\alpha=1}^{P} \mathcal{M}^{\mu\alpha}(U,U') n^\mu(U,t) n^\alpha(U',t).$$

$$\gamma_3^\mu = \frac{1}{2}\int_\Omega \prod_{\delta=1}^{P}\prod_{l=1}^{K_\delta} dZ_l^\delta \sum_{\gamma=1}^{P}\sum_{i=1}^{K_\gamma}(\beta_V^\gamma)^2 p_t((Z_i^\alpha)_{i,\alpha})\frac{1}{K_\mu}\frac{\partial^2}{\partial(V_i^\gamma)^2}\sum_{j=1}^{K_\mu}\delta(Z_j^\mu - U)$$

one obtains : $$\gamma_3^\mu = \frac{(\beta_V^\mu)^2}{2}\frac{\partial^2}{\partial u^2}n^\mu(U,t)$$

Finally, the (PPD) : $n^\mu(U,t)$ **satisfies the following system of (nonlinear)** IPDE :

$$\begin{aligned}\frac{\partial}{\partial t}n^\mu(U,t) = &-\frac{\partial}{\partial U}(\mathcal{F}^\mu(U)n^\mu(U,t))\\ &-\frac{\partial}{\partial U}\int_{R^{m+2}} dU' \sum_{\alpha=1}^{P}\mathcal{M}^{\mu\alpha}(U,U')n^\mu(U,t)n^\alpha(U',t)\\ &+\frac{1}{2}(\beta_V^\mu)^2\frac{\partial^2}{\partial u^2}n^\mu(U,t) \quad \mu = 1,2,\ldots,P\end{aligned}$$

$$U = (u,\widehat{z},s),\ u,s\in\mathbb{R},\ \widehat{z}\in\mathbb{R}^m$$

2 Application to coupled large-scale Fitzhugh-Nagumo networks

Dynamical system is given by (for all $i = 1, 2, \dots, K_\gamma, \gamma = 1, 2, \dots, P$)

$$\begin{aligned}
\frac{dV_i^\gamma}{dt} &= F^\gamma(V_i^\gamma, X_i^\gamma) + I_{ext}^\gamma(t) + \eta_{i,t}^\gamma + \sum_{\alpha=1}^{P} \frac{1}{K_\alpha} \sum_{j=1}^{K_\alpha} M^{\gamma\alpha}(V_i^\gamma, X_i^\gamma, \phi_i^\gamma, V_j^\alpha, X_j^\alpha, \phi_j^\alpha) \\
\frac{dX_i^\gamma}{dt} &= G^\gamma(V_i^\gamma, X_i^\gamma) \\
\frac{d\phi_i^\gamma}{dt} &= \Omega^\gamma(\phi_i^\gamma, V_i^\gamma, X_i^\gamma)
\end{aligned}$$

where

$$\begin{aligned}
F^\gamma(V, X) &= -k^\gamma V(V - a^\gamma)(V - 1) - X \\
G^\gamma(V, X) &= b^\gamma(V - m^\gamma X).
\end{aligned}$$

For each i^{th} cell in $\mathscr{P}_\gamma$

V_i^γ : membrane potential

X_i^γ : one dimensional recovery variable

ϕ_i^γ : one dimensional synaptic variables

Parameters $k^\gamma, a^\gamma, b^\gamma, m^\gamma$ govern the dynamics of the FN neural model in the population $\mathscr{P}_\gamma$

The mean field equations are

$$
\begin{aligned}
\frac{\partial}{\partial t} n^\mu(V,X,\phi,t) = &- \frac{\partial}{\partial V}((F^\mu(V,X) + I^\mu_{ext}(t))n^\mu(V,X,\phi,t)) \\
&- \frac{\partial}{\partial X}(G^\mu(V,X)n^\mu(V,X,\phi,t)) - \frac{\partial}{\partial \phi}(\Omega^\mu(\phi,V,X)n^\mu(V,X,\phi,t)) \\
&- \frac{\partial}{\partial V}\int_{R^3} dV'dX'd\phi' \sum_{\alpha=1}^{P} M^{\mu\alpha}(V,X,\phi,V',X',\phi')n^\mu(V,X,\phi,t)n^\alpha(V',X',\phi',t) \\
&+ \frac{1}{2}(\beta^\mu_V)^2 \frac{\partial^2}{\partial V^2} n^\mu(V,X,\phi,t)
\end{aligned}
$$

$\mu = 1, 2, \ldots, P.$

2.1 Statistical measures from the stochastic and integro-partial differential systems

Main goal : comparison of the (numerical) solutions of

♣ SCDE: **(thousands) of stochastic coupled differential equations,**

♠ ICPDE: **(P) integro coupled partial differential equations.**

Both systems numerically implemented over the same domain $\Omega \times \Lambda \times \Phi$

$$\Omega = [V_{min}, V_{max}] \text{ (resp. } \Lambda = [X_{min}, X_{max}],\ \Phi = [\phi_{min}, \phi_{max}]) :$$

Bounded domains of variation of potential (resp. recovery, synaptic coupling variables)

Identical initial conditions have been chosen in both cases :

ICPDE: normalized Gaussian function $n(V, X, \phi, t = 0)$:
mean and standard deviation parameters $(V_0, \sigma_V), (X_0, \sigma_X), (\phi_0, \sigma_\phi)$.

SCDE: all cells initial data $(V_i^\gamma(t = 0), X_i^\gamma(t = 0), \phi_i^\gamma(t = 0)), i = 1, 2, \dots, K_\gamma, \gamma = 1, 2, \dots, P$, selected through the use of $i.i.d.$ Gaussian random variables with the same moments as the ones used for the solution of ICPDE.

From a probabilistic point of view, how can one extract information on dynamical variables V, X, ϕ, for any cell in the full system, at any time ?

Define a neural population *potential* distribution

ICPDE

marginal distribution $$\rho^\mu(V,t) = \int_{R^2} n^\mu(V,X,\phi,t)\,dX d\phi$$

Continuous firing measure $$\varphi_{\rho^\mu}(t) = \int_\theta^{+\infty} \rho^\mu(V',t)dV'$$

SCDE counting process about the presence (at a given time t, for any cell i in $\mathscr{P}_\mu$) of the potential $V_i^\mu(t)$ in a given subinterval $[a_j, b_j] = \text{bin}_j$.
The $\text{bin}_{j,j=1,\dots,N}$ build a partition of Ω, all with same length: $|\text{bin}_j| = \lambda = \frac{V_{max}-V_{min}}{N}$

Discrete distribution $\xi^\mu(t)$ given by

$$\xi^\mu(t) = \{\, p_j^\mu(t),\quad j=1,2,\dots,N\,\} = \left\{ \left(\frac{\mathcal{N}(V_i^\mu(t) \in [a_j,b_j])}{K_\mu * N_{trials}},\ 1 < i < K_\mu \right),\ j=1,2,\dots,N \right\}$$

$\mathcal{N}$ is the number of occurrences for all trials. N_{trials} is total number of trials.

Discrete firing measure: $$\varphi_{\xi^\mu}(t) = \sum_{j > (\theta - V_{min})/\lambda} p_j^\mu(t).$$

2.2 Comparison of the two types of probability distributions

continuous one : $\rho^{\mu}(V,t)$

discrete one : $\xi^{\mu}(t)$

as well as

averages, variances, covariances and firing measures derived from these two distributions.

2.3 Numerical results for a single population

2.3.1 Excitatory synapses, uniform connectivity

all to all connectivity

$\phi_i, i = 1, 2, \ldots, K$: constant values.

Use sigmoidal functions for the detection of presynaptic events (simple form)

$$\sigma_\Theta^E(V) = (1 + e^{-\beta(V - V_\Theta^E)})^{-1}$$

Synaptic input current $I_{syn,i}(t)$ for each cell i :

$$I_{syn,i}(t) = \frac{1}{K} J^E (V_S^E - V_i) \sum_{j=1}^{K} \sigma_\Theta^E(V_j)$$

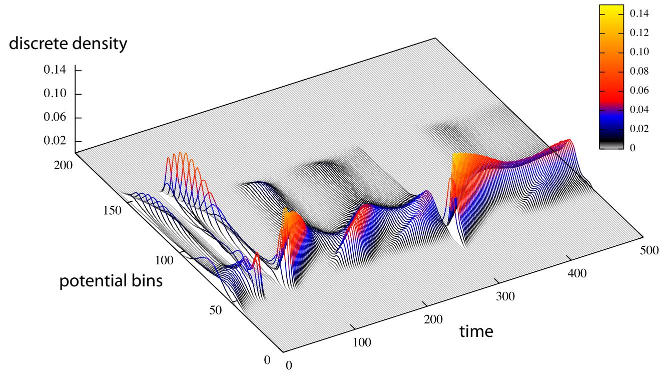
$J^E, V_S^E, \beta, V_\Theta^E$: parameters

Stochastic system (SCDE) :

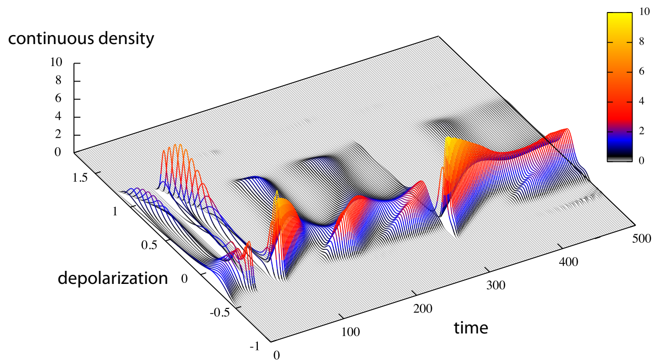
$$\begin{aligned}\frac{dV_i}{dt} &= F(V_i, X_i) + I_{ext}(t) + \eta_{i,t} + I_{syn,i}(t)\\ \frac{dX_i}{dt} &= G(V_i, X_i) \qquad\qquad i = 1, 2, \ldots, K\end{aligned}$$

Integro-partial differential equation (IPDE) for PPD $n(V, X, t)$:

$$\begin{aligned}\frac{\partial}{\partial t}\, n(V, X, t) = & \frac{-\partial}{\partial V}\left\{(F(V, X) + I_{ext}(t))\, n(V, X, t)\right\}\\ & - \frac{\partial}{\partial X}\left\{G(V, X)\, n(V, X, t)\right\}\\ & - J^E \frac{\partial}{\partial V}\left\{(V_S^E - V)\, n(V, X, t)\right\} \int_{R^2} dV' dX' \sigma_\Theta^E(V')\, n(V', X', t)\\ & + \frac{\beta_V^2}{2} \frac{\partial^2}{\partial V^2}\, n(V, X, t).\end{aligned}$$

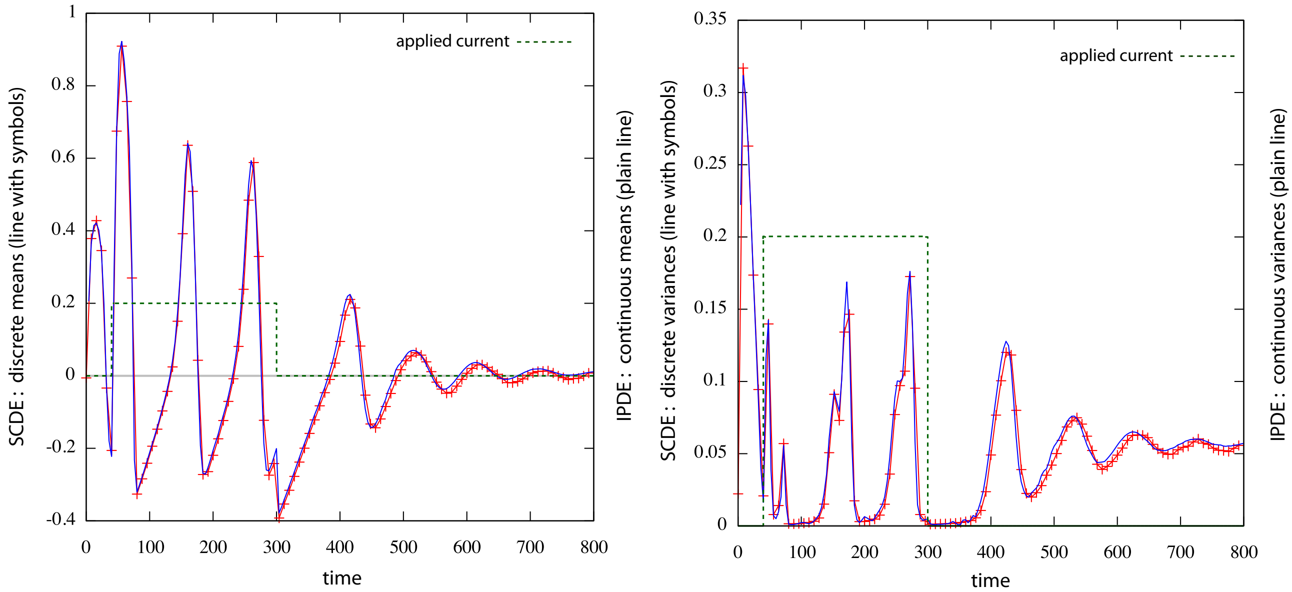


(a) Evolution of the normalized discrete probability density $\xi(t)$, solution of the stochastic dynamical system.



(b) Evolution of the normalized continuous probability density $\rho(V, t)$, solution of the MVFP equation.

Figure 1 – Time behavior of probability densities.



(a) Mean values of potential obtained from SCDE and IPDE.

(b) Variance of potential obtained from SCDE and IPDE.

Figure 2 – Excitatory synapses, uniform connectivity.

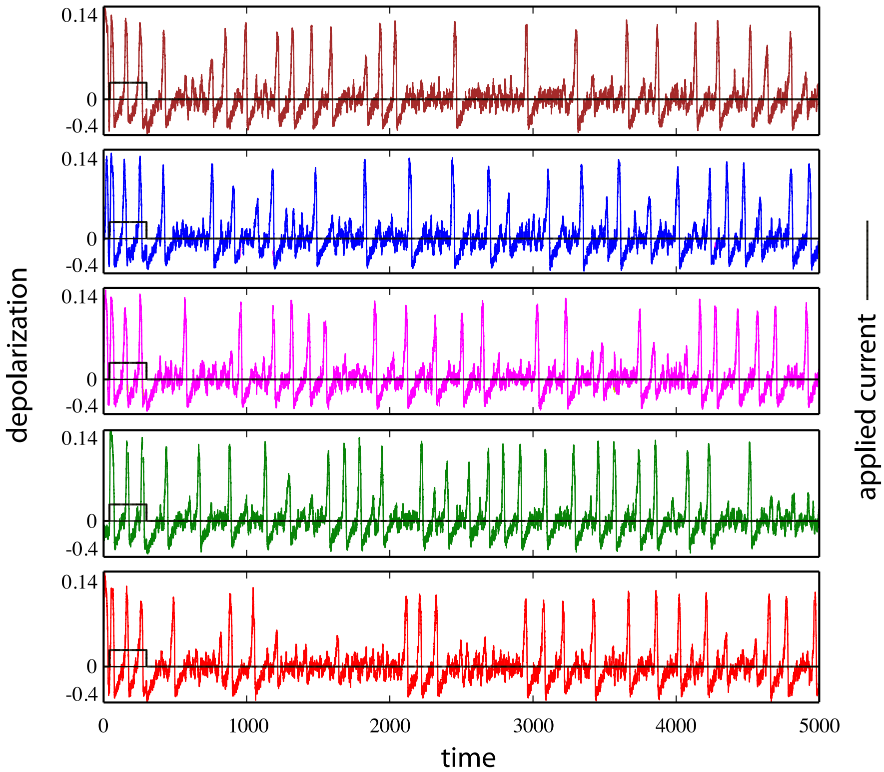


Figure 3 – Excitatory synapses, uniform connectivity.
Depolarizations versus time for 5 randomly selected cells (SCDE).

2.3.2 Excitatory synapses, time dependent non uniform connectivity

Network dynamical system for non uniform, time dependent couplings between cells

$$\frac{dV_i}{dt} = F(V_i, X_i) + I_{ext}(t) + \eta_{i,t} + I_{syn,i}(t)$$
$$\frac{dX_i}{dt} = G(V_i, X_i)$$
$$\frac{d\phi_i}{dt} = \Omega(\phi_i, X_i)$$

Connection term M of Hebbian type:

$$M(V_i, X_i, \phi_i, V_j, X_j, \phi_j) = (V_S^E - V_i)\, J^E \varGamma(\phi_i\,, \phi_j\,)\, \sigma_\Theta^E(V_j)$$

with

$$\varGamma(\phi_i, \phi_j) = \phi_i\, \phi_j$$
$$\varOmega(\phi_i, X_i) = -\alpha\, \phi_i + \beta\, \sigma_\phi(X_i)$$

σ_ϕ : sigmoidal function, $\sigma_\phi(X) = (1 + e^{-\nu(X - X_S)})^{-1}$

V_S^E , J^E, α, β, ν, X_S : parameters

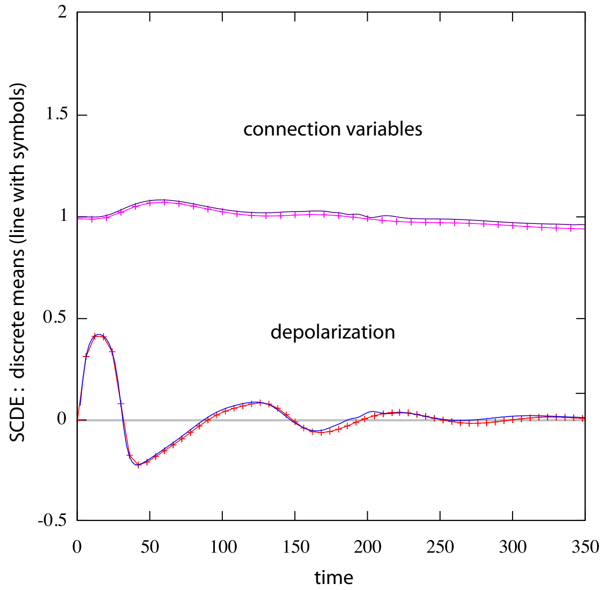
♣ Goal : Detect high **joint** ionic activity at the pre and post synaptic levels.

Mean field equation for this kind of neural network system.

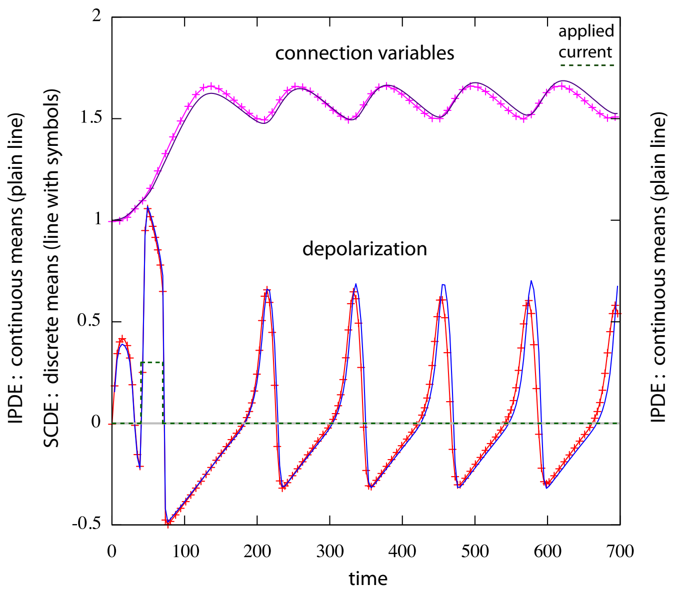
Probability distribution $n(V, X, \phi, t)$

of depolarization, recovery and connection variables $(V, X, \phi) \in \mathbb{R}^3$ at time t.

$$
\begin{aligned}
\frac{\partial}{\partial t} n(V, X, \phi, t) = &- \frac{\partial}{\partial V} \left\{ (F(V, X) + I_{ext}(t))\, n(V, X, \phi, t) \right\} \\
&- \frac{\partial}{\partial X} \left\{ G(V, X)\, n(V, X, \phi, t) \right\} \\
&- J^E \frac{\partial}{\partial V} \left\{ (V_S^E - V)\; n(V, X, \phi, t) \right\} \int_{R^3} dV' dX' d\phi' \sigma_\Theta^E(V')\, \Gamma(\phi, \phi')\, n(V', X', \phi', t) \\
&- \frac{\partial}{\partial \phi} \left\{ \Omega(\phi, X)\, n(V, X, \phi, t) \right\} + \frac{\beta_V^2}{2} \frac{\partial^2}{\partial V^2} n(V, X, \phi, t)
\end{aligned}
$$

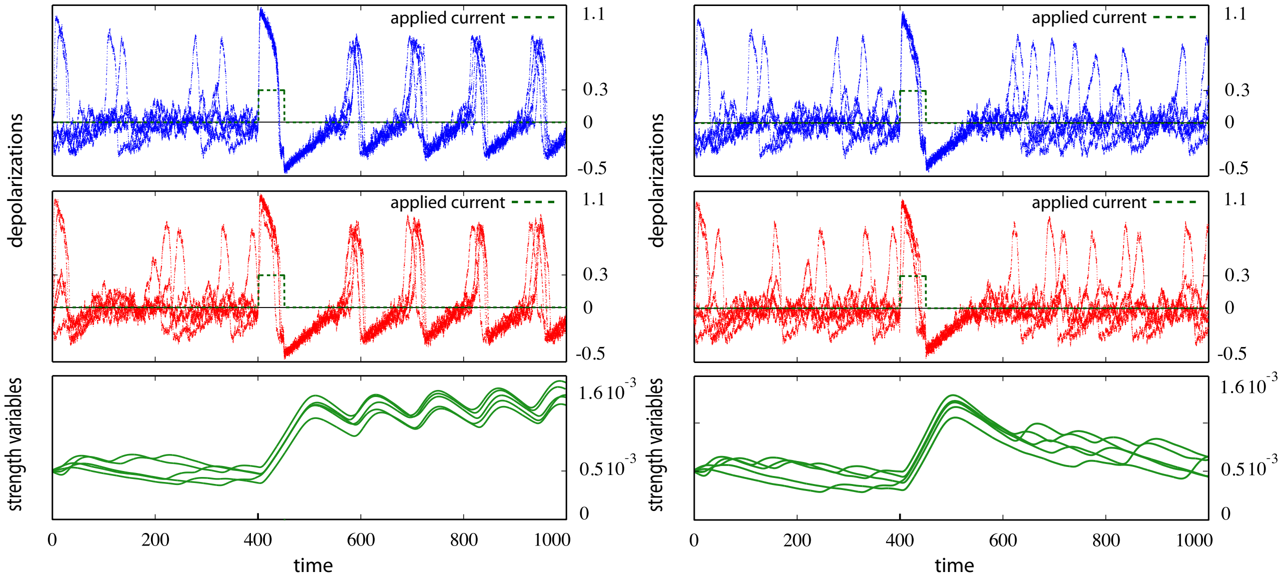


(a) Excitatory synapses. Mean values of potential and connection variables obtained from IPDE and SCDE. No applied current.



(b) Excitatory synapses. Mean values of potential and connection variables obtained from IPDE and SCDE. A step current is applied: rhythm generation.

Figure 4 – Non uniform, time dependent connectivity.



(a) Excitatory synapses. Superimposed time development over a sample of 5 trials, of potential and strength variables of 2 arbitrarily chosen cells.

(b) Inhibitory synapses. Superimposed time development over a sample of 5 trials, of potential and strength variables of 2 arbitrarily chosen cells.

Figure 5 – Non uniform, time dependent connectivity.

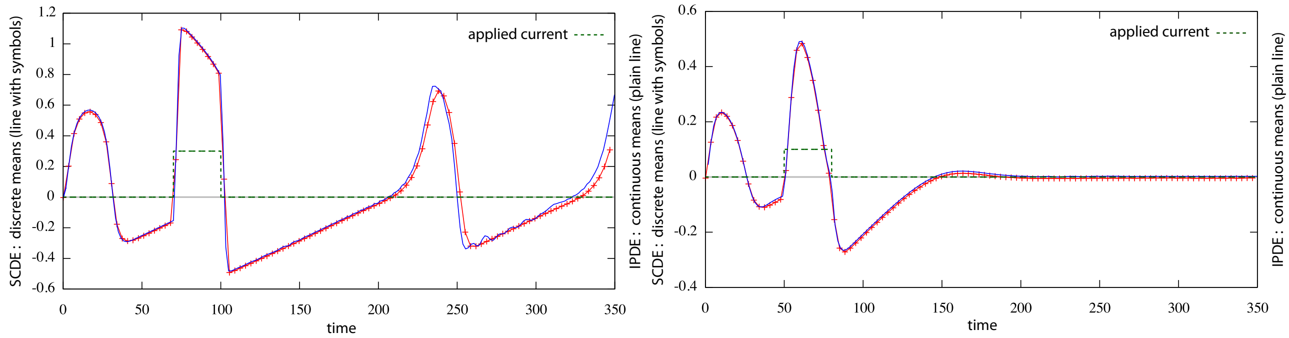
2.4 Two large-scale excitatory and inhibitory connected populations

Two networks $\mathscr{P}_E$ and $\mathscr{P}_I$ of neural populations with different parameters k^α, a^α, b^α, m^α, $\alpha = E, I$.

Coupled system of equations for the probability distributions
for the excitatory and the inhibitory populations $n^E(V,X,t)$ and $n^I(V,X,t)$

$$\begin{aligned}
\frac{\partial}{\partial t} n^E(V,X,t) = &- \frac{\partial}{\partial V}\left\{(F^E(V,X) + I^E_{ext}(t))n^E(V,X,t)\right\} \\
&- \frac{\partial}{\partial X}\left\{G^E(V,X)n^E(V,X,t)\right\} \\
&- J^E \frac{\partial}{\partial V}\left\{(V^E_S - V)n^E(V,X,t)\right\}\int_{R^2} dV' dX' \sigma^E_\Theta(V')n^E(V',X',t) \\
&- J^{EI} \frac{\partial}{\partial V}\left\{(V^{EI}_S - V)n^E(V,X,t)\right\}\int_{R^2} dV' dX' \sigma^{EI}_\Theta(V')n^I(V',X',t) \\
&+ \frac{1}{2}(\beta^E_V)^2 \frac{\partial^2}{\partial V^2} n^E(V,X,t)
\end{aligned}$$

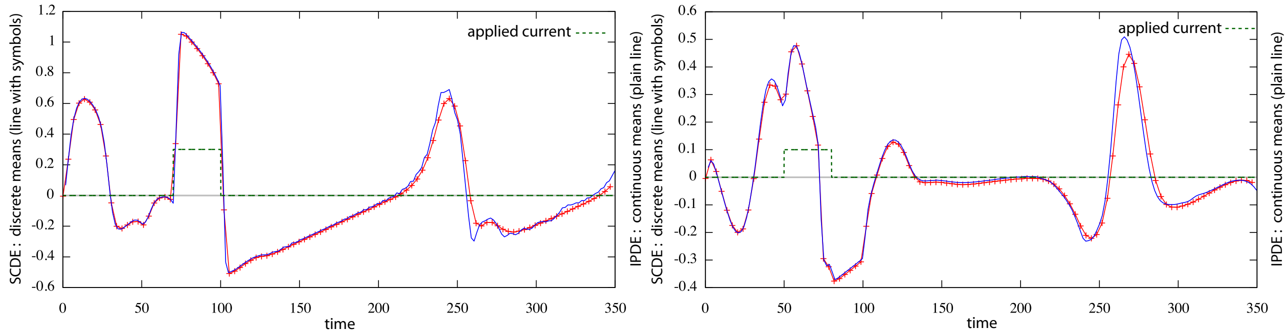
For $n^I(V,X,t)$: make an exchange between the indices I and E.



(a) Mean values of potential for $\mathscr{P}_E$.

(b) Mean values of potential for $\mathscr{P}_I$.

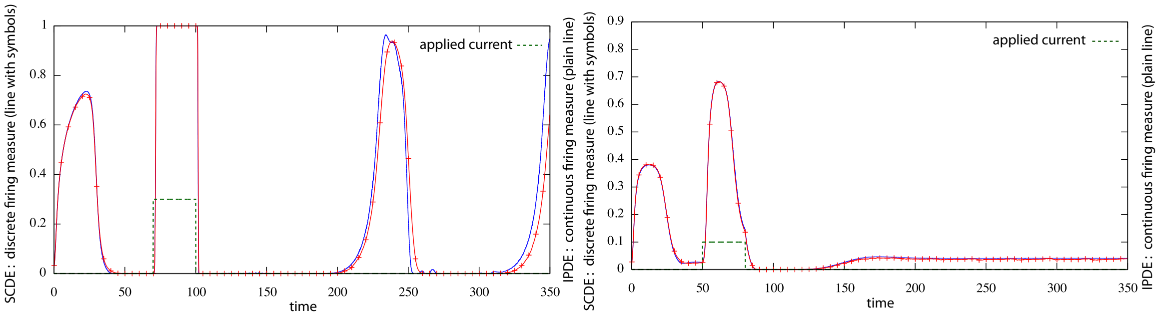
Figure 6 – No coupling between $\mathscr{P}_E$ and $\mathscr{P}_I$



(a) Mean values of potential for $\mathscr{P}_E$.

(b) Mean values of potential for $\mathscr{P}_I$.

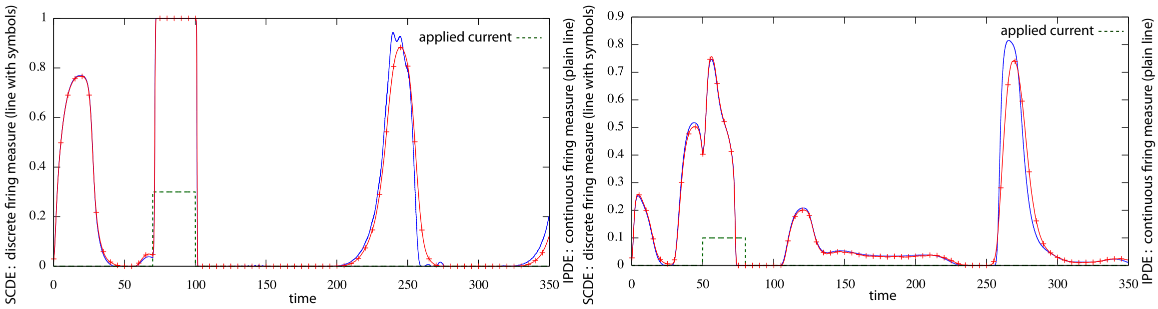
Figure 7 – Coupling between $\mathscr{P}_E$ and $\mathscr{P}_I$



(a) Firing measures for $\mathscr{P}_E$.

(b) Firing measures for $\mathscr{P}_I$

Figure 8 – No coupling between $\mathscr{P}_E$ and $\mathscr{P}_I$



(a) Firing measures for $\mathscr{P}_E$.

(b) Firing measures for $\mathscr{P}_I$

Figure 9 – Coupling between $\mathscr{P}_E$ and $\mathscr{P}_I$

3 Conclusion

♣ Mean field equations have been derived for a set of probability distributions governing the dynamical behavior of a set of noisy populations of neurons: **McKean-Vlasov-Fokker-Planck** equations (MVFP).

Numerical integration of these equations has been made in some cases of connected neural networks and showed that statistical measurements obtained in this scheme are in good agreement with those obtained by direct simulations of (finite size) stochastic neural dynamical systems.