# Departament de Matemàtiques.

## A Decision-making Fokker-Planck model in Computational Neuroscience

José Antonio Carrillo · Stéphane Cordier · Simona Mancini

**Abstract** Minimal models for the explanation of decision-making in computational neuroscience are based on the analysis of the evolution for the average firing rates of two interacting neuron populations. While these models typically lead to multi-stable scenario for the basic derived dynamical systems, noise is an important feature of the model taking into account finite-size effects and robustness of the decisions. These stochastic dynamical systems can be analyzed by studying carefully their associated Fokker-Planck partial differential equation. In particular, we discuss the existence, positivity and uniqueness for the solution of the stationary equation, as well as for the time evolving problem. Moreover, we prove convergence of the solution to the stationary state representing the probability distribution of finding the neuron families in each of the decision states characterized by their average firing rates. Finally, we propose a numerical scheme allowing for simulations performed on the Fokker-Planck equation which are in agreement with those obtained recently by a moment method applied to the stochastic differential system. Our approach leads to a more detailed analytical and numerical study of this decision-making model in computational neuroscience.

**Keywords** Computational Neuroscience · Fokker-Planck Equation · General Relative Entropy

J.A. Carrillo

ICREA (Institució Catalana de Recerca i Estudis Avançats)

and Departament de Matemàtiques

Universitat Autònoma de Barcelona, E-08193 Bellaterra, Spain

Tel.: +34-93-5814548

E-mail: carrillo@mat.uab.es

S. Cordier, S. Mancini

Fédération Denis Poisson (FR 2964)

BP. 6759, Department of Mathematics (MAPMO UMR 6628)

University of Orléans and CNRS, F-45067 Orléans, France

### 1 Introduction

The derivation of biologically relevant models for the decision-making processes done by animals and humans to choose between alternative behaviors based on perceptual information is an important question in neurophysiology and psychology. It is quite common to observe bi-stability of the decisions taken in several psychological experiments widely used by neuroscientists. Archetypical examples of these multi-stable decision-making process are bistable visual perception, that is, two distinct possible interpretations of the same unchanged physical retinal image: Necker cube, Rubins face-vase, binocular rivalry and bistable apparent motion [6, 10, 16].

In order to explain these phenomena, biologically realistic noise driven neural circuits have been proposed in the literature [8] and even used to account qualitatively for some experimental data [19]. Minimal models proposed consist of two interacting families of neurons. Each family of neurons is characterized by their averaged firing rate, averaged number of spikes produced per time, measuring their activity level. These neuron families are more correlated to their own behavior than with others and this mechanism is mediated by inhibition from the rest of neurons and the sensory input. The external stimuli may produce an increasing activity of one of the neuron families leading to a decision state in which we have a high/low activity ratio of the firing rates. Decision-making in these models is then understood as the fluctuation-driven transition from a spontaneous state (similar firing rates of both families) to a decision state (high/low activity level ratio between the two families).

As already explained and discussed in different works [9,10,18], the theory of stochastic dynamical systems offers a useful framework for the investigation of the neural computation involved in these cognitive processes. Noise is an important ingredient in these models since such neural families are comprised of a large number of spiking neurons, and then the fluctuations arise naturally through noisy input and/or disorder in the collective behavior of the network. Moreover, this is used to introduce finite-size effect of the neuron families as discussed in [9,10].

The precise model considered in this work uses a Wilson-Cowan [20] type system for describing the evolution in time of the firing rates  $\nu_i$ , i = 1, 2, of two population of neurons:

$$\tau \frac{d\nu_i(t)}{dt} = -\nu_i(t) + \phi \left( \lambda_i + \sum_{j=1,2} w_{ij} \nu_j(t) \right) + \xi_i(t), \quad i = 1, 2,$$
 (1)

where  $\tau$  is the typical time relaxation and  $\xi_i(t)$ , i = 1, 2, represent a white noise of amplitude  $\beta$ , i.e., they correspond to independent brownian motions with variance  $\beta^2/2$ .

In (1) the function  $\phi(x)$  has a sigmoidal shape determining the response function of the neuron population to a mean excitation x given by  $x_i(t) =$ 

 $\lambda_i + \sum_j w_{ij} \nu_j$ , i = 1, 2 in each population:

$$\phi(x) = \frac{\nu_c}{1 + \exp(-\alpha(x/\nu_c - 1))},\tag{2}$$

where  $\lambda_i$  are the external stimuli applied to each neuron population and  $w_{ij}$  are the connection coefficients. The parameter  $\nu_c$  represents both the maximal activity rate of the population and the frequency input needed to drive the population to half of its maximal activity.

Following [17,13,9], we assume that neurons within a specific population are likely to correlate their activity, and to interact via strong recurrent excitation with a dimensionless weight  $w_+ > 1$  greater than a reference baseline value established to 1. Analogously, neurons in two different populations are likely to have anti-correlated activity expressed by a excitatory weight lower than baseline,  $w_- < 1$ . Furthermore, we assume that there is global feedback inhibition, as a result of which all neurons are mutually coupled to all other neurons in an inhibitory fashion; we will denote this inhibitory weight by  $w_I$ . As a result, the synaptic connection coefficients  $w_{ij}$ , representing the interaction between population i and j, are the elements of a  $2 \times 2$  symmetric matrix W given by

$$W = \begin{bmatrix} w_+ - w_I & w_- - w_I \\ w_- - w_I & w_+ - w_I \end{bmatrix},$$

The typical sypnaptic values considered in these works are such that  $w_{-} < w_{I} < w_{+}$  leading to cross-inhibition and self-excitation.

Applying standard methods of Ito calculus, see for instance [12], we can prove that the probability density  $p = p(t, \nu)$  of finding the neurons of both populations firing at averaged rates  $\nu = (\nu_1, \nu_2)$  at t > 0, satisfies a Fokker-Planck equation, alsow known as the forward Kolmogorov equation. Hence,  $p(t, \nu)$  must satisfy:

$$\partial_t p + \nabla \cdot ([-\nu + \Phi(\Lambda + W \cdot \nu)] p) - \frac{\beta^2}{2} \Delta p = 0$$
 (3)

where  $\nu \in \Omega = [0, \nu_m] \times [0, \nu_m]$ ,  $\Lambda = (\lambda_1, \lambda_2)$ ,  $\Phi(x_1, x_2) = (\phi(x_1), \phi(x_2))$ ,  $\nabla = (\partial_{\nu_1}, \partial_{\nu_2})$  and  $\Delta = \Delta_{\nu}$ . We choose to complete equation (3) by the following no-flux boundary conditions:

$$\left( \left[ -\nu + \Phi(\Lambda + W \cdot \nu) \right] p - \frac{\beta^2}{2} \nabla p \right) \cdot n = 0 \tag{4}$$

where n is the outward normal to the domain  $\Omega$ . Physically, these boundary conditions mean that neurons cannot spike with arbitrarily large firing rates and thus there is a typical maximal value of the averaged firing rate  $\nu_m$  and that the solution to (3) is a probability density function, i.e.,

$$\int_{\Omega} p(t,\nu) \, d\nu = 1. \tag{5}$$

In order to simplify notations, let us consider, from now on, the vector field  $F = (F_1, F_2)$ , representing the flux in the Fokker-Planck equation:

$$F = -\nu + \Phi(\Lambda + W \cdot \nu) = \begin{pmatrix} -\nu_1 + \phi(\lambda_1 + w_{11}\nu_1 + w_{12}\nu_2) \\ -\nu_2 + \phi(\lambda_2 + w_{21}\nu_1 + w_{22}\nu_2) \end{pmatrix}$$
(6)

then, equation (3) and boundary conditions (4) read:

$$\partial_t p + \nabla \cdot \left( F \, p - \frac{\beta^2}{2} \nabla p \right) = 0 \tag{7}$$

$$\left(F p - \frac{\beta^2}{2} \nabla p\right) \cdot n = 0$$
(8)

Let us first comment that the corresponding deterministic dynamical system to (1) in the absence of noise has a region of parameters exhibiting a multi-stable regime. The relevant fixed point solutions are the spontaneous state and the two states representing a decision, called decision states. For sufficiently strong inhibition  $w_I$  the two decision states are bistable with respect to one another. Let us point out that the deterministic dynamical system is not a gradient flow.

Let us also remark that equation (7) is linear in p, but we cannot have an explicit solution in exponential form to the associate steady state problem. Indeed, the drift vector F is not the gradient of a potential V as it can be easily checked. Hence, it is not possible to give an explicit expression, of the type  $\exp(-2V/\beta^2)$ , of the steady states of equation (7). Nevertheless, (see Sect. 2.3), we will show that the steady state solution has an exponential shape. This question is related to general problems of Fokker-Planck equations with non-gradients drifts [2,3] arising also in polymer fluid flow problems [4].

In fact, in a bounded domain  $\Omega$  and under the assumption that the flux F is regular enough and incoming in the domain  $F \cdot n < 0$ , we will show the existence of an unique positive normalized steady state, or equilibrium profile, for the problem (7)-(8). This assumption on the drift F is verified in our particular computational neuroscience model for  $\nu_m$  large enough. In order to obtain this theorem we use classical functional analysis theorems via a variant of the Krein-Rutman theorem. This will be the first objective of Section 2. We will also prove existence, uniqueness and positivity of the probability density solution of the evolutionary Fokker-Planck equation, and also its convergence towards the unique normalized steady state of the Fokker-Planck equation. This result shows the global asymptotic stability of this unique stationary state leading to the final probability of the decision states in our neuroscience model.

Finally, Section 3 is devoted to the numerical study of the above model, to the discussion of the numerical results and their relation with those of [18, 9,10]. Let us remark that the Fokker-Planck approach has not been very well analyzed and used by computational neuroscientists due to its higher degree of sophistication. Moreover, the mathematical problem corresponding to (7)-(8) although linear, it has not been dealt with in detail due to their non classical

boundary conditions. This work shows that the direct treatment of the Fokker-Planck equation can be useful both at the analytical and the numerical level.

# 2 Existence, Uniqueness and Asymptotic Stability of the Stationary Solution

In this section we first study the existence, uniqueness and positivity of the solution of the associated stationary problem, see subsection 2.1, then we prove the existence and uniqueness of the solution for the Fokker-Planck model (7), see subsection 2.2. Finally, in subsection 2.3, we use the general relative entropy strategy [14,15] to show the decay of the relative entropy, and as a consequence, we can prove the convergence of this evolution toward the unique positive normalized solution of the stationary problem associated to (7)-(8).

Let us set the notation for this section. We will first assume we have a bounded domain  $\Omega \subset \mathbb{R}^2$  for which the divergence theorem and the standard trace theorems for Sobolev functions, for instance the embedding from  $H^2(\Omega)$  onto  $H^{3/2}(\partial\Omega)$ , are valid. Moreover, we need the strong maximum principle to apply, and thus, we will assume  $\Omega \in C^2$ . Obviously, this is not true for square like domains as in the computational neuroscience model at the origin of this work. However, it is true for smooth approximations of rectangular domains which avoid the corners in the domain of interest. As announced, we assume that the flux function satisfies

$$F \in C^1(\bar{\Omega}, \mathbb{R}^2) \text{ with } F \cdot n < 0 \text{ on } \partial\Omega,$$
 (9)

being n the outwards unit normal to  $\partial \Omega$ .

Let us, define the following linear operator  $\mathcal{A}$ , for every given  $u \in H^2(\Omega)$ :

$$\mathcal{A}u = -\frac{\beta^2}{2}\Delta u + \nabla \cdot (Fu).$$

Then, the Fokker-Planck problem (7)-(8) for the distribution function  $p(t,\nu)$  is just a particular case of the general Fokker-Planck equation for  $u(\nu,t)$  with non-gradient drift that reads:

$$\begin{cases} \frac{\partial u}{\partial t} + \mathcal{A}u = 0 & \text{in } \Omega \times (0, T) \\ \left( Fu - \frac{\beta^2}{2} \nabla u \right) \cdot n = 0 & \text{on } \partial \Omega \times (0, T) \end{cases}$$
(10)

and we endow the parabolic system (10) by the initial condition  $u(\cdot,0) = u_0(\cdot) \in L^2(\Omega)$ .

Concerning the stationary problem associated with (10), in subsection 2.1 we will consider the elliptic problem:

$$\begin{cases} \mathcal{A}u + \xi u = f & \text{in } \Omega \\ \left(Fu - \frac{\beta^2}{2}\nabla u\right) \cdot n = 0 & \text{on } \partial\Omega \,, \end{cases}$$
 (11)

with f a given function in  $L^2(\Omega)$  and  $\xi \in \mathbb{R}$  conveniently chosen, under the assumptions (9) and (5).

Finally, in subsection 2.3 we deal with problem (10), and its dual form:

$$\begin{cases} \frac{\partial v}{\partial t} = -F \cdot \nabla v + \frac{\beta^2}{2} \Delta v, & \text{in } \Omega \times (0, T) \\ \frac{\partial v}{\partial n} = 0, & \text{on } \partial \Omega \times (0, T) \end{cases}$$
 (12)

associated to the initial conditions:  $v_0(\cdot) = v(0, \cdot)$ .

### 2.1 Stationary problem

We consider here the stationary problem (11) and the bilinear form associated with A:

$$a(u,v) = \int_{\Omega} \frac{\beta^2}{2} \nabla u \cdot \nabla v \, d\nu - \int_{\Omega} u F \cdot \nabla v \, d\nu \,, \quad \forall \, u, v \in H^1(\Omega) \,. \tag{13}$$

It is easy to check that:

**Lemma 1** The bilinear form a(u, v) satisfies:

i. a(u,v) is continuous:

$$|a(u,v)| \le M||u||_{H^1}||v||_{H^1}, \quad \forall u, v \in H^1(\Omega),$$
 with  $M = \frac{\beta^2}{2} + ||F||_{\infty}.$ 

ii. a(u,v) is "coercive", that is, it verifies:

$$a(u,u)+\rho||u||_{L^2}^2\geq \theta||u||_{H^1}\quad\forall\,u\in H^1(\Omega)\,,$$
 with  $\rho=C+\theta$  with  $C=\frac{1}{\sqrt{2}\beta^2}$  and  $\theta=\beta^2/4$ .

**Proof.** i. We have, from (13):

$$|a(u,v)| \le \frac{\beta^2}{2} \int_{\Omega} |\nabla u| |\nabla v| \, d\nu + ||F||_{\infty} \int_{\Omega} |u| \, |\nabla v| \, d\nu \le$$
$$\le \left(\frac{\beta^2}{2} + ||F||_{\infty}\right) ||u||_{H^1} ||v||_{H^1},$$

where  $||F||_{\infty}$  corresponds to the maximum of |F| in  $\bar{\Omega}$ .

ii. We have, from (13):

$$\frac{\beta^2}{2} \int_{\Omega} |\nabla u|^2 d\nu \le a(u, u) + ||F||_{\infty} \int_{\Omega} |u| |\nabla u| d\nu.$$

Now, from the following inequality  $ab \le \varepsilon a^2 + b^2/4\varepsilon$ , with  $a, b, \varepsilon > 0$ , we get:

$$\int_{\varOmega} |\nabla u| |u| \, d\nu \le \varepsilon \int_{\varOmega} |\nabla u|^2 \, d\nu + \frac{1}{4\varepsilon} \int_{\varOmega} |u|^2 \, d\nu.$$

Then choosing  $\varepsilon$  so small that:  $\varepsilon ||F||_{\infty} \leq \beta^2/4$ , e.g.  $\varepsilon = \frac{\beta^2}{8||F||_{\infty}}$  we have:

$$\frac{\beta^2}{4} \int_{\Omega} |\nabla u|^2 d\nu \le a(u, u) + C \int_{\Omega} |u|^2 d\nu$$

with

$$C = \frac{1}{\sqrt{2}\beta^2}.$$

Finally, from this we obtain:

$$a(u,u) + \left(C + \frac{\beta^2}{4}\right) ||u||_{L^2}^2 \ge \frac{\beta^2}{4} ||u||_{H^1}^2$$

which ends the proof.

**Lemma 2** For each  $f \in L^2(\Omega)$ , problem (11) has an unique solution in  $H^2(\Omega)$  for  $\xi \geq \rho$ .

**Proof.** Applying Lemma 1 we have that  $a(u,v) + \xi \langle u,v \rangle_{L^2}$  is continuous and coercive, for  $\xi \geq \rho$ . Then, applying Lax-Milgram theorem, we have that, for each  $f \in L^2(\Omega)$ , there exists an unique  $u \in H^1(\Omega)$  such that,  $\forall v \in H^1(\Omega)$ :

$$\int_{\Omega} \left( \frac{\beta^2}{2} \nabla u \cdot \nabla v - uF \cdot \nabla v + \xi uv \right) d\nu = \int_{\Omega} f v \, d\nu. \tag{14}$$

By regularity, since  $f \in L^2(\Omega)$  then we have  $u \in H^2(\Omega)$  with traces for u and its derivatives on the boundary. Thus, integrating by parts (14), we get,  $\forall v \in H^1(\Omega)$ :

$$\int_{\Omega} \left( \nabla \cdot (Fu) - \frac{\beta^2}{2} \Delta u + \xi u - f \right) v \, d\nu + \int_{\partial \Omega} (Fu - \beta^2 \nabla u) \cdot n \, v \, d\sigma = 0. \tag{15}$$

If in (15), we choose  $v \in C_c^{\infty}(\Omega)$ , we get in distributional sense:

$$\int_{\Omega} \left( \nabla \cdot (Fu) - \frac{\beta^2}{2} \Delta u + \xi u - f \right) v \, d\nu = 0 \quad \forall v \in C_c^{\infty}(\Omega) \, .$$

Hence:

$$\nabla \cdot (Fu) - \frac{\beta^2}{2} \Delta u + \xi u - f = 0 \quad \text{in } L^2(\Omega).$$
 (16)

Moreover, replacing (16) in (15), we have:

$$\int_{\partial\Omega} \left( Fu - \frac{\beta^2}{2} \nabla u \right) \cdot n \, v \, d\sigma = 0, \forall v \in H^1(\Omega),$$

which implies:

$$\left(Fu - \frac{\beta^2}{2}\nabla u\right) \cdot n = 0 \quad \text{on } \partial\Omega\,,$$

that is, u satisfies the boundary conditions.

Let us now define the linear operator:

$$T_{\xi}: L^{2}(\Omega) \to L^{2}(\Omega), \qquad T_{\xi}f = u, \quad \forall f \in L^{2}(\Omega) \text{ and } \forall \xi \geq \rho$$

with u the unique solution of (11). In particular, we can prove that:

**Lemma 3** The operator  $T_{\xi}: H^2(\Omega) \to H^2(\Omega)$  is a compact operator for all  $\xi \geq \rho$ .

**Proof.** We have that there exists  $u = T_{\xi}f$  solution of (11), for any  $f \in H^2(\Omega)$ . By regularity, we have  $u \in H^4(\Omega)$  and from the estimate  $||u||_{H^4(\Omega)} \le C||f||_{H^2(\Omega)}$ , we get that  $T_{\xi}$  maps  $H^2(\Omega)$  onto itself. Moreover, the compactness of the imbedding,  $H^4(\Omega) \hookrightarrow H^2(\Omega)$  implies that  $T_{\xi}$  is a compact operator.  $\square$ 

Consider now the cone K:

$$K = H^2_+(\Omega) = \{ u \in H^2(\Omega) \, | \, u(\nu) \ge 0 \text{ a.e } \nu \in \Omega \},$$

we remark that it has non-empty interior, see [1, Page 360] and it corresponds to everywhere positive functions in  $\Omega$ . To prove the existence of solution to our problem, we shall use the following theorem derived from the Krein-Rutman theorem:

**Theorem 1 (Krein-Rutman)** Let X be a Banach space,  $K \subset X$  a solid cone (i.e the cone has non-empty interior  $K^0$ ),  $T: X \to X$  a compact linear operator which is strongly positive, i.e,  $Tf \in K^0$  if  $f \in K \setminus \{0\}$ . Then, r(T) > 0, and r(T) is a simple eigenvalue with an eigenvector  $v \in K^0$ ; there is no other eigenvalue with positive eigenvector.

**Lemma 4** The operator  $T_{\xi}$  is strongly positive in  $H^2_+(\Omega)$  under the assumption  $\xi \ge \max(\rho, \|(\nabla \cdot F)^-\|_{L^{\infty}(\Omega)})$ .

**Proof.** We first start by defining the operator L as follows:

$$Lu = Au + \xi u$$
,

then,  $Lu = f \ge 0$  if  $u = T_{\xi}f$ . Under the assumptions on  $\xi$ , we have that the operator has a zero order term given by  $\xi + \nabla \cdot F \ge 0$  on  $\Omega$ . Thus, we can apply the weak maximum principle to L, see [11, page 329] deducing that

$$\min_{\nu \in \bar{\Omega}} u = -\max_{\nu \in \partial \Omega} u^{-}.$$

Now, assume that the minimum of u in  $\Omega$  is negative, then it is achieved at a  $\nu_0 \in \partial \Omega$  such that  $u(\nu_0) < 0$ . Using (9) we get

$$\frac{\beta^2}{2} \frac{\partial u}{\partial n}(\nu_0) = u(\nu_0) F \cdot n > 0,$$

contradicting the fact that  $\nu_0$  is a minimum at the boundary. Thus, we have proved  $u \geq 0$  and that  $T_{\xi}$  maps nonnegative functions into itself:  $T_{\xi}: H^2_+(\Omega) \to H^2_+(\Omega)$ .

Suppose now  $f \in K \setminus \{0\}$  and  $u = T_{\xi}f$ . Moreover, if there exists  $\nu_0 \in \Omega$ , such that  $u(\nu_0) = 0$ , then

$$\min_{Q} u = u(\nu_0) = 0,$$

because  $u(\nu) \geq 0$ ,  $\forall \nu \in \Omega$ . Therefore, by the strong maximum principle, we have u = C constant and thus, u = 0. This is a contradiction because  $f \neq 0$ . Then, we have

$$u(\nu) > 0$$
,  $\forall \nu \in \Omega$ .

Consider now  $\nu_0 \in \partial \Omega$ , we will prove that  $u(\nu_0) > 0$ . If  $u(\nu_0) = 0$ , then it is a strict minimum of u at the boundary, and thus

$$\frac{\partial u}{\partial n}(\nu_0) < 0.$$

by Hopf's lemma [11, page 330]. Using (9), we have

$$\frac{\beta^2}{2} \frac{\partial u}{\partial n}(\nu_0) = u(\nu_0) F \cdot n = 0,$$

which is in contradiction. Thus,  $u(\nu) > 0$ ,  $\forall \nu \in \bar{\Omega}$ , i.e.  $u \in K^0$ .

We can now prove the main theorem:

**Theorem 2** Under assumptions (9), there exists an unique probability density function  $u_{\infty} \in H^4(\Omega)$ ,  $u_{\infty}(\nu) > 0$  in  $\bar{\Omega}$  satisfying:

$$\begin{cases} \mathcal{A}u = 0 & \text{in } \Omega \\ \left(Fu - \frac{\beta^2}{2}\nabla u\right) \cdot n = 0 & \text{on } \partial\Omega \end{cases}$$
 (17)

### **Proof.** (a) Existence and positivity

Using Lemma 3 and 4, we have that  $T_{\xi}$  satisfies the hypothesis in Theorem 1 for  $\xi$  large enough. Therefore,  $r(T_{\xi}) > 0$  and there exists a positive eigenvector v such that  $T_{\xi}v = r(T_{\xi})v$ , i.e.,

$$\mathcal{A}(r(T_{\xi})v) + \xi r(T_{\xi})v = v.$$

Let  $u = r(T_{\xi})v$ , then u satisfies the boundary conditions in (11) and,

$$Au + \xi u = \lambda u$$
 with  $\lambda = \frac{1}{r(T_{\xi})}$ .

equivalent to,

$$\mathcal{A}u = (\lambda - \xi)u. \tag{18}$$

Multiplying by  $\varphi \in H^1(\Omega)$  on both sides of (18) and integrating by parts, we obtain:

$$\int_{\Omega} \frac{\beta^2}{2} \nabla u \cdot \nabla \varphi \, d\nu - \int_{\Omega} u F \cdot \nabla \varphi \, d\nu = (\lambda - \xi) \int_{\Omega} u \varphi \, d\nu.$$

Then, choosing  $\varphi = 1$ , we get:

$$(\lambda - \xi) \int_{\Omega} u \, d\nu = 0.$$

But u > 0, because  $u = r(T_{\xi})v > 0$ , thus  $\xi = \lambda = \frac{1}{r(T_{\xi})}$ . Therefore, the existence and positivity of a stationary state, i.e., Au = 0 are obtained, since we can choose any multiple of u, we take the one satisfying the normalisation condition (5).

### (b) Uniqueness

Let  $u_1 > 0$  satisfies (17). By standard regularity theory,  $u_1 \in H^2(\Omega)$  and then  $u_1 \in K$ . Hence, we have:

$$\mathcal{A}u_1 + \xi u_1 = \frac{1}{r(T_{\xi})}u_1$$

by recalling that  $\xi = \frac{1}{r(T_{\xi})}$ . This implies  $\mathcal{A}(r(T_{\xi})u_1) + \xi r(T_{\xi})u_1 = u_1$ . On the other hand, by definition of  $T_{\xi}$ , we also have  $\mathcal{A}(T_{\xi}u_1) + \xi T_{\xi}u_1 = u_1$ . Therefore,  $T_{\xi}u_1 = r(T_{\xi})u_1$ .

Recalling that  $r(T_{\xi})$  is a simple eigenvalue, we obtain  $u_1 = cu$ . By means of the normalisation hypothesis (5), we finally prove the uniqueness of the solution. By Hopf's Lemma proceeding as in the last part of Lemma 4, we deduce the strict positivity of  $u_{\infty}$ .

### 2.2 Time evolution problem

Let us first consider the bilinear form associated to A:

$$a(t, u, v) = \int_{\Omega} \frac{\beta^2}{2} \nabla u \cdot \nabla v \, d\nu - \int_{\Omega} u F \cdot \nabla v \, d\nu \,, \quad \forall u, v \in H^1(\Omega) \,, \tag{19}$$

It is easy to check that:

- i. Let  $T \in \mathbb{R}_+^*$ , then the mapping  $t \mapsto a(t, u, v)$  is measurable on [0, T], for fixed  $u, v \in H^1(\Omega)$  since it is constant in time.
- ii. The bilinear form a(t, u, v) is continuous:

$$|a(t, u, v)| \le M||u||_{H^1}||v||_{H^1}, \quad \forall t \in [0, T], \ u, v \in H^1(\Omega),$$

and coercive

$$a(t, u, u) + \rho ||u||_{L^2}^2 \ge \theta ||u||_{H^1} \quad \forall t \in [0, T], \ u \in H^1(\Omega)$$

with M > 0,  $\theta$  and  $\rho$  given in Lemma 1.

We say that u is a weak solution of (10) if  $u \in L^2(0,T;H^1(\Omega))$  and satisfies:

$$\frac{d}{dt} \int_{\Omega} uv \, d\nu + a(t, u, v) = \int_{\Omega} fv \, d\nu. \tag{20}$$

**Theorem 3** Problem (10) has an unique strong solution.

**Proof.** The existence of an unique weak solution to (10) is proved applying [21, Theorem 27.3]. Moreover, the weak solution u belongs to  $L^2(0, T; H^2(\Omega))$ , see [21, Theorem 27.5]. Now, integrating by parts (20), with f = 0, we get:

$$\int_{\Omega} \left( \frac{\partial u}{\partial t} - \frac{\beta^2}{2} \Delta u + \nabla \cdot (Fu) \right) v \, d\nu + \int_{\partial \Omega} \left( Fu - \frac{\beta^2}{2} \nabla u \right) \cdot n \, v \, d\sigma = 0 \,, \quad (21)$$

for all  $v \in H^1(\Omega)$ . Choosing  $v \in C_c^{\infty}(\Omega)$ , we obtain, in the distributional sense:

$$\frac{\partial u}{\partial t} - \frac{\beta^2}{2} \Delta u + \nabla \cdot (Fu) = 0, \tag{22}$$

which is equivalent to  $\partial_t u + \mathcal{A}u = 0$ . Finally, replacing (22) in (21), we have:

$$\int_{\partial\Omega} \left( Fu - \frac{\beta^2}{2} \nabla u \right) \cdot n \, v \, d\sigma = 0 \qquad \forall \, v \in H^1(\Omega),$$

yielding to:  $\left(Fu - \frac{\beta^2}{2}\nabla u\right) \cdot n = 0$  on  $\partial\Omega$ . Hence the weak solution u is in fact a strong solution.

Concerning the positivity of the solution of (10), we remark that since the flux F has negative divergence, the maximum principle does not hold in our case. Nevertheless, it is possible to prove the positivity for the solution using the relative entropy decay, as shown in the next section. Concerning the dual problem (12), it is a standard evolution problem with Neumann boundary conditions for which classical references apply, see [11].

### 2.3 Convergence to steady state

In order to show the positivity of the solution of problem (10) and the convergence to the stationary solution,  $u_{\infty}$  of problem (17), we need to prove the decay of the relative entropy, see [15]. We will hence consider problems (10) and (12). We first prove the following conservation result:

**Lemma 5** Given any strong solution of (10) with normalized initial data, then the solution satisfies mass conservation, that is:

$$\int_{\Omega} u(t,\nu) d\nu = \int_{\Omega} u_0(\nu) d\nu = 1.$$
(23)

**Proof.** Let us consider the product of u and v, respectively solutions to (10) and (12). Integrating over the phase space  $\Omega$  the derivative in time of uv, and using (10) and (12), we get:

$$\frac{d}{dt} \int_{\Omega} uv \, d\nu = -\int_{\Omega} \left( -Fu + \frac{\beta^2}{2} \nabla u \right) \cdot \nabla v \, d\nu + \int_{\Omega} u \frac{\partial v}{\partial t} \, d\nu =$$

$$= \int_{\Omega} uF \cdot \nabla v \, d\nu - \frac{\beta^2}{2} \int_{\Omega} u \Delta v \, d\nu + \int_{\Omega} u \frac{\partial v}{\partial t} \, d\nu = 0.$$

Hence,

$$\int_{\Omega} uv \, d\nu = \int_{\Omega} u_0 v_0 \, d\nu$$

and the result follows by considering that constant functions are solutions of (12).

Given any convex function  $H = H(\omega)$ , where  $\omega = u_2/u_1$  and  $u_1$  and  $u_2$  are strong solutions of (10) with  $u_1 > 0$  in  $\bar{\Omega}$ , we have the following:

**Lemma 6** For any  $u_1$  and  $u_2$  strong solutions of (10), and v strong solution of (12) with  $u_1, v > 0$  in  $\bar{\Omega}$ , then:

$$\frac{d}{dt} \left[ v u_1 H \left( \omega \right) \right] = \frac{\beta^2}{2} \left( \nabla \cdot \left[ v^2 \nabla \left( \frac{u_1}{v} H \left( \omega \right) \right) \right] - v u_1 H'' \left( \omega \right) \left| \nabla \left( \omega \right) \right|^2 \right) - \nabla \cdot \left[ F v u_1 H \left( \omega \right) \right] \tag{24}$$

**Proof.** Let us develop the left hand side of (24), using (10) and (12):

$$\frac{d}{dt} \left[ vu_1 H \left( \omega \right) \right] = -\nabla \cdot \left[ Fu_1 v H \left( \omega \right) \right] + u_1 F \cdot \nabla \left( v H \left( \omega \right) \right) 
- u_1 H \left( \omega \right) F \cdot \nabla v + \frac{u_2}{u_1} v H' \left( \omega \right) \nabla \cdot \left( u_1 F \right) 
- v H' \left( \omega \right) \nabla \cdot \left( u_2 F \right) - \frac{\beta^2}{2} u_1 H \left( \omega \right) \Delta v 
+ \frac{\beta^2}{2} \left[ v H \left( \omega \right) - \frac{u_2}{u_1} v H' \left( \omega \right) \right] \Delta u_1 + \frac{\beta^2}{2} v H' \left( \omega \right) \Delta u_2 .$$

We separate now the computation in two parts: the one concerning first order derivatives (I) and the one concerning second order derivatives (II). We start by computing (I). Leaving the first term unchanged and developing the following ones, we get:

$$(I) = -\nabla \cdot [Fu_1vH(\omega)] + u_1H(\omega)F \cdot \nabla v$$

$$+ vH'(\omega)F \cdot \left(\nabla u_2 - \frac{u_2}{u_1}\nabla u_1\right) - u_1H(\omega)F \cdot \nabla v$$

$$+ \frac{u_2}{u_1}vH'(\omega)\nabla u_1 \cdot F + vH'(\omega)u_2\nabla \cdot F$$

$$- vH'(\omega)\nabla u_2 \cdot F - vH'(\omega)u_2\nabla \cdot F = -\nabla \cdot [Fu_1vH(\omega)].$$

Concerning the second part (II), we start developing  $\nabla \cdot \left[v^2 \nabla \left(\frac{u_1}{v} H(\omega)\right)\right]$ , and find that:

$$\nabla \cdot \left[ v^{2} \nabla \left( \frac{u_{1}}{v} H\left( \omega \right) \right) \right] = -u_{1} H\left( \omega \right) \Delta v + \left[ v H\left( \omega \right) - \frac{u_{2}}{u_{1}} v H'\left( \omega \right) \right] \Delta u_{1}$$

$$+ v H'\left( \omega \right) \Delta u_{2} - \nabla v H'\left( \omega \right) \left( \nabla u_{2} - \frac{u_{2}}{u_{1}} \nabla u_{1} \right)$$

$$+ H'\left( \omega \right) \nabla u_{2} \cdot \nabla v + v H''\left( \omega \right) \nabla u_{2} \cdot \nabla \left( \omega \right)$$

$$- \frac{u_{2}}{u_{1}} H'\left( \omega \right) \nabla u_{1} \cdot \nabla v - \frac{u_{2}}{u_{1}} v H''\left( \omega \right) \nabla u_{1} \cdot \nabla \left( \omega \right).$$

Multiplying by  $\frac{\beta^2}{2}$ , recalling part (II) of our development and that  $u_1 \nabla (\omega) = \nabla u_2 - \frac{u_2}{u_1} \nabla u_1$ , we then get:

$$\frac{\beta^{2}}{2}\nabla\cdot\left[v^{2}\nabla\left(\frac{u_{1}}{v}H\left(\omega\right)\right)\right]=\left(II\right)+\frac{\beta^{2}}{2}vu_{1}\left|\nabla\left(\omega\right)\right|^{2}H''\left(\omega\right),$$

which completes the proof in the case H is smooth.

Let us now define the relative entropy operator:

$$\mathcal{H}_{v}(u_{2}|u_{1}) = \int_{\Omega} v u_{1} H(\omega) \ d\nu \tag{25}$$

and the decay operator:

$$\mathcal{D}_{v}(u_{2}|u_{1}) = \int_{\Omega} v u_{1} H''(\omega) \left| \nabla \left( \frac{u_{2}}{u_{1}} \right) \right|^{2} d\nu.$$
 (26)

Then we have the following:

**Theorem 4** For any  $u_1$  and  $u_2$  strong solutions of (10), and v strong solution of (12) with  $u_1, v > 0$  in  $\bar{\Omega}$ , if H is a smooth convex function then, the relative entropy is decreasing in time and

$$\frac{d}{dt}\mathcal{H}_v(u_2|u_1) = -\frac{\beta^2}{2}\mathcal{D}_v(u_2|u_1) \le 0.$$
(27)

**Proof.** Integrating (24) over the domain  $\Omega$ , we get:

$$\frac{d}{dt} \int_{\Omega} v u_1 H(\omega) d\nu = -\frac{\beta^2}{2} \int_{\Omega} v u_1 H''(\omega) |\nabla(\omega)|^2 d\nu - \int_{\partial\Omega} (F \cdot n) v u_1 H(\omega) d\sigma + \frac{\beta^2}{2} \int_{\partial\Omega} v^2 \nabla\left(\frac{u_1}{v} H(\omega)\right) \cdot n d\sigma.$$

We just have to show that the integration on the boundaries are equal to zero. Developing the last term, we get:

$$\begin{split} \int_{\partial\Omega} (F \cdot n) v u_1 H\left(\omega\right) \, d\sigma + \frac{\beta^2}{2} \int_{\partial\Omega} v^2 \nabla \left(\frac{u_1}{v} H\left(\omega\right)\right) \cdot n \, d\sigma \; = \\ \int_{\partial\Omega} (F \cdot n) v u_1 H\left(\omega\right) + \frac{\beta^2}{2} \frac{\partial u_1}{\partial n} v H\left(\omega\right) \, d\sigma \\ + \int_{\partial\Omega} \frac{\beta^2}{2} u_1 \frac{\partial v}{\partial n} H\left(\omega\right) + \frac{\beta^2}{2} v H'\left(\omega\right) u_1 \frac{\partial\omega}{\partial n} \, d\sigma. \end{split}$$

Then, applying boundary conditions in (10) and (12), we have:

$$(F \cdot n)vu_1H(\omega) - \frac{\beta^2}{2} \frac{\partial u_1}{\partial n}vH(\omega) = 0,$$
$$\frac{\beta^2}{2} u_1 \frac{\partial v}{\partial n}vH(\omega) = 0.$$

Finally, recalling that  $\omega = u_2/u_1$ , that from (10) we have

$$F \cdot n = \frac{\beta^2}{2} \frac{1}{u_1} \frac{\partial u_1}{\partial n},$$

and applying (12), we obtain:

$$\int_{\partial\Omega} \frac{\beta^2}{2} v H'(\omega) u_1 \frac{\partial\omega}{\partial n} d\sigma = \int_{\partial\Omega} \frac{\beta^2}{2} \left( v H'(\omega) \frac{\partial u_2}{\partial n} - v H'(\omega) \frac{\partial u_1}{\partial n} \frac{u_2}{u_1} \right) d\sigma =$$

$$\int_{\partial\Omega} \frac{\beta^2}{2} v H'(\omega) \frac{\partial u_2}{\partial n} - v H'(\omega) (F \cdot n) u_2 d\sigma = 0,$$

and the theorem is proved.

We can now prove the positivity of the solution of the evolution problem for the linear Fokker-Planck equation (10).

**Theorem 5** If  $u_0$  is nonnegative, then the solution u of problem (10) is nonnegative.

**Proof.** Consider the operators (25) and (26), and let  $u_1$  be the stationary solution  $u_{\infty}$  of problem (11), and v a positive constant, say v=1. We recall that,  $u_{\infty} > 0$  in  $\bar{\Omega}$  and that constants are solution to (12). Moreover, let  $H(\omega) = \omega^-$ , the negative part of  $\omega$ ,  $\omega^- = max(-\omega, 0)$ . Then  $H(\omega)$  is a positive and convex function than can be approximated easily by smooth convex positive functions  $H_{\delta}(\omega)$ . Thus, we can obtain

$$\frac{d}{dt} \int_{\Omega} u_{\infty} H_{\delta} \left( \frac{u_2}{u_{\infty}} \right) d\nu \le 0.$$

and by approximation  $\delta \to 0$ , we deduce

$$h(t) := \int_{\Omega} u_{\infty} H\left(\frac{u_2(t,\nu)}{u_{\infty}}\right) d\nu \le \int_{\Omega} u_{\infty} H\left(\frac{u_2(0,\nu)}{u_{\infty}}\right) d\nu, \qquad (28)$$

for all  $t \geq 0$ . Here,  $u_2$  is any solution of (10) endowed by the positive initial condition  $u_2(t=0,\nu_1,\nu_2)=u_0(\nu_1,\nu_2)\geq 0$ . Hence, the function  $h(t)\geq 0$  is decreasing in time, because of (28), and at the initial time t=0, h(0)=0. Therefore, h(t)=0 for all  $t\geq 0$ , and, as  $u_{\infty}$  is positive,  $u_2$  must be nonnegative.

The consequences of the existence of this family of Liapunov functionals given in Theorem 4 for (10) have already been explored for several equations in [14,15] where they have been called general relative entropy (GRE) inequalities. The same conclusions apply here.

Corollary 1 Given F satisfying (9) and any solution u with normalized initial data  $u_0$  to (10), then the following properties hold:

*i)* Contraction principle:

$$\int_{\Omega} |u(t,\nu)| \, d\nu \le \int_{\Omega} |u_0(\nu)| \, d\nu. \tag{29}$$

ii)  $L^p$  bounds, 1 :

$$\int_{\Omega} u_{\infty}(\nu) \left| \frac{u(t,\nu)}{u_{\infty}(\nu)} \right|^{p} d\nu \le \int_{\Omega} u_{\infty}(\nu) \left| \frac{u_{0}(\nu)}{u_{\infty}(\nu)} \right|^{p} d\nu. \tag{30}$$

iii) Pointwise estimates:

$$\inf_{\nu \in \Omega} \frac{u_0(\nu)}{u_{\infty}(\nu)} \le \frac{u(t,\nu)}{u_{\infty}(\nu)} \le \sup_{\nu \in \Omega} \frac{u_0(\nu)}{u_{\infty}(\nu)}. \tag{31}$$

This corollary is a consequence of the GRE inequality in Theorem 4 with H(s) = |s|,  $H(s) = |s|^p$ , and  $H(s) = (s - k)_+^2$  respectively by approximation from smooth convex functions. Moreover, the GRE inequality gives the convergence of the solution u(t) to the stationary state  $u_{\infty}$ .

Corollary 2 (Long time asymptotics) Given F satisfying (9) and any solution u with normalized initial data  $u_0$  to (10), then

$$\lim_{t \to \infty} \int_{\Omega} |u(t, \nu) - u_{\infty}(\nu)|^2 d\nu = 0.$$
 (32)

**Proof.** Using the general entropy inequality with  $H(s) = s^2/2$  and v = 1, we get from Theorem 4 that

$$\int_{\Omega} \frac{u(T,\nu)^2}{u_{\infty}(\nu)} d\nu + 2 \int_{0}^{T} \int_{\Omega} u_{\infty}(\nu) \left| \nabla \left( \frac{u(t,\nu)}{u_{\infty}(\nu)} \right) \right|^2 d\nu dt \le \int_{\Omega} \frac{u_0(\nu)^2}{u_{\infty}(\nu)} d\nu , \quad (33)$$

for all T > 0. From (33), we deduce that

$$\int_0^\infty \int_{\Omega} u_\infty(\nu) \left| \nabla \left( \frac{u(t,\nu)}{u_\infty(\nu)} \right) \right|^2 \, d\nu \, dt < \infty \,,$$

and thus, there exits  $\{t_n\} \nearrow \infty$  such that for any fixed T > 0

$$\int_{t_n}^{t_n+T} \int_{\Omega} u_{\infty}(\nu) \left| \nabla \left( \frac{u(t,\nu)}{u_{\infty}(\nu)} \right) \right|^2 d\nu dt \to 0 \quad \text{as } n \to \infty.$$

Now, developing the square, we deduce

$$\int_{\Omega} u_{\infty} \left| \nabla \left( \frac{u(t)}{u_{\infty}} \right) \right|^{2} d\nu = \int_{\Omega} \left( \frac{|\nabla u(t)|^{2}}{u_{\infty}} - 2 \frac{\nabla u(t) \cdot \nabla u_{\infty}}{u_{\infty}^{2}} u(t) + \frac{|\nabla u_{\infty}|^{2}}{u_{\infty}^{3}} u(t)^{2} \right) d\nu 
= \int_{\Omega} \left( \frac{|\nabla u(t)|^{2}}{u_{\infty}} + \frac{|\nabla u_{\infty}|^{2}}{u_{\infty}^{3}} u(t)^{2} \right) d\nu 
+ \int_{\Omega} u(t)^{2} \nabla \cdot \left( \frac{\nabla u_{\infty}}{u_{\infty}^{2}} \right) d\nu - \int_{\partial\Omega} \frac{u(t)^{2}}{u_{\infty}^{2}} \frac{\partial u_{\infty}}{\partial n} d\sigma$$
(34)

where an integration by parts has been done in the last term. Taking into account that the stationary solution  $u_{\infty} \in H^4(\Omega)$  and that is strictly positive, from Theorem 2, we get that  $u_{\infty}$  and their derivatives up to second order are in  $C(\bar{\Omega})$  with  $u_{\infty}$  bounded away from zero. From this fact together with the boundary condition

$$\frac{\beta^2}{2} \frac{\partial u_{\infty}}{\partial n} = u_{\infty}(F \cdot n),$$

and the  $L^2$  estimates in (30), we conclude that there exists a constant depending only on F,  $u_0$  and  $u_\infty$  such that the terms

$$\int_{\partial\Omega} \frac{u(t)^2}{u_{\infty}^2} \frac{\partial u_{\infty}}{\partial n} d\sigma, \qquad \int_{\Omega} u(t)^2 \nabla \cdot \left(\frac{\nabla u_{\infty}}{u_{\infty}^2}\right) d\nu,$$

and

$$\int_{\Omega} \frac{|\nabla u_{\infty}|^2}{u_{\infty}^3} u(t)^2 d\nu$$

are uniformly bounded in  $t \geq 0$ . This implies immediately that

$$\int_{t_n}^{t_n+T} \int_{\Omega} \frac{|\nabla u(t)|^2}{u_{\infty}} \, d\nu \, dt$$

is uniformly bounded in n. Therefore, defining the sequence  $u_n(t,\nu) := u(t+t_n,\nu)$  for all  $t \in [0,T]$  and  $\nu \in \Omega$ , we deduce that  $u_n \in L^2(0,T;H^1(\Omega))$  uniformly bounded in n since  $u_{\infty}$  is bounded away from zero. Using this fact and the  $L^2$ -bounds in (30), we can come back to the equation satisfied by u(t)

and check that  $\frac{\partial u_n}{\partial t} \in L^2(0,T;H^{-1}(\Omega))$  uniformly in n. The standard Aubin-Lions's compactness lemma implies the existence of a subsequence, denoted with the same index, such that  $u_n \to u_*$  strongly in  $L^2(0,T;L^2(\Omega))$  and weakly in  $L^2(0,T;H^1(\Omega))$ .

From (34), we can easily deduce that

$$0 \le \int_0^T \int_{\Omega} u_{\infty}(\nu) \left| \nabla \left( \frac{u_*(t,\nu)}{u_{\infty}(\nu)} \right) \right|^2 d\nu dt$$

$$\le \liminf_{n \to \infty} \int_0^T \int_{\Omega} u_{\infty}(\nu) \left| \nabla \left( \frac{u_n(t,\nu)}{u_{\infty}(\nu)} \right) \right|^2 d\nu dt \to 0 \quad \text{as } n \to \infty,$$

and thus,  $u_*/u_{\infty}$  is constant. Due to the normalisation condition in (23), then  $u_* = u_{\infty}$ . Since the limit is the same for all subsequences, we deduce the desired claim.

Remark 1 (Splitting and Rate of Convergence) We finally remark that, even if the flux F is not in a gradient form, following [2,3,4], once we have the existence, uniqueness and positivity for the solution  $u_{\infty}$  to the stationary problem associated to (7), we may split the flux F into a gradient part plus a non gradient one. In fact, let A be defined by  $A = -\log u_{\infty}$ , so that  $e^{-A} = u_{\infty}$  is the solution of the stationary problem associated to (7). Then we have:

$$\nabla \cdot \left( Fe^{-A} + \frac{\beta^2}{2} \nabla A e^{-A} \right) = 0,$$

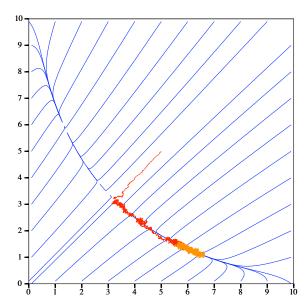
or equivalently

$$\nabla \cdot \left( \left( F + \frac{\beta^2}{2} \nabla A \right) e^{-A} \right) = 0,$$

Defining  $G = (F + \frac{\beta^2}{2} \nabla A)$ , we have split F as  $F = -\frac{\beta^2}{2} \nabla A + G$ . In particular, we note that G is such that  $\nabla \cdot (Ge^{-A}) = 0$ , but we do not have yet an explicit form for G. Once this splitting is done, a variation of entropy-entropy dissipation arguments as in [5, Subsection 2.4] in bounded domains with the no-flux boundary conditions should lead to an exponential rate of convergence under the assumption that the hessian matrix of A,  $D^2A$ , is positive definite with an explicit rate given by the minimum eigenvalue of  $D^2A$ . However, we do not know under which assumptions we can show that the hessian matrix of the potential A is positive definite or equivalently that  $u_{\infty}$  is log-concave. It is worthy to mention that the Krein-Rutman theorem used shows that all other eigenvalues of problem (11) are negative but no general conditions on the explicit form of F to measure the spectral gap are known to our knowledge.

### 3 Numerical method and results

In this section, we will consider a particular relevant case of the neuroscience model discussed in the introduction, exactly corresponding to the discussion



**Fig. 1** Dynamics, in the unbiased case, of the dynamical system (1) in the deterministic case (straight lines) and the stochastic case (un-straight line). Straight lines highlight an approximation of the slow-manifold to which belongs the equilibrium point of the system. The un-straight line becomes clearer when the time spent in a point becomes bigger: the particle starts his dynamic in the point (5,5), moves almost straight foward towards the slow-manifold, and then oscillates towards the stable point.

in [9]. We will consider the following values of the synaptic connection parameters:  $w_+ = 2.35$ ,  $w_I = 1.9$  and  $w_- = 1 - r(w_+ - 1)/(1 - r)$ , r = 0.3; which corresponds to self-excitation and cross-inhibition between the two neuron families. The sigmoidal response function is determined from  $\alpha = 4$  and  $\nu_c = 20Hz$  with external stimuli corresponding to two cases:  $\lambda_1 = 15Hz$  and  $\lambda_2 = \lambda_1 + \Delta \lambda$ , with  $\Delta \lambda = 0$  for the unbiased case or  $\Delta \lambda = 0.1$  for the biased one. The relaxation time for the system is chosen to  $\tau = 10^{-2}s$ .

It can be shown, by means of direct simulations of the stochastic differential system (1), that there is a slow-fast behaviour of the solutions towards equilibrium. More precisely, it is possible to show that, see [9], system (1) is characterised by two stable and one unstable equilibrium points; for example, in the unbiased case, if  $\Delta\lambda = 0$ , the stable decision states are in  $S_1 = (1.32, 5.97)$  and its symmetric  $S_3 = (5.97, 1.32)$ , and the unstable spontaneous state is in  $S_2 = (3.19, 3.19)$ , whereas in the biased case  $\Delta\lambda = 0.1$  the stable decision states are in  $S_1 = (1.09, 6.59)$  and  $S_3 = (5.57, 1.53)$  and the unstable spontaneous state is in  $S_2 = (3.49, 3.08)$ . For instance, in figure 1, we highlight, in the unbiased case, the fast convergence of one realisation of (1) towards the slow-manifold to which the equilibrium points belongs, and its very slow convergence towards one of the two stable points. The discussion of this behaviour is beyond the goal of this paper, and a possible way to use this slow-fast feature of the SDE system (1) will be investigated elsewhere.

We will now propose a numerical scheme to approximate the solution of the Fokker-Planck equation (7). Let us first comment that a direct approximation

by simple finite differences has an important drawback in terms of computing time. The main issue being this slow-fast feature of the system, producing then a kind of metastable solution that takes a long time to evolve to the final equilibrium solution concentrating its probability around the decision states.

In order to discretise and perform numerical simulation of equation (7), we apply an explicit finite volume method on the bounded domain  $\Omega = [0, \nu_m] \times [0, \nu_m]$ . We recall that for  $\nu_m$  large enough  $F \cdot n < 0$ , hence verifying assumption (9), and so we choose  $\nu_m = 10$  in our numerical simulations. In order to simplify notations below, we have set  $\tau = 1$ , but in the figures the time scale has been adjusted to take into account the relaxation time  $\tau$  and being comparable to results in [9] discussed below.

Let  $i = 0...M_1 - 1$  and  $j = 0...M_2 - 1$ , and consider the discrete variables:

$$n_i = \nu_1(i) = \left(i + \frac{1}{2}\right) \Delta \nu_1,$$
  
$$n_j = \nu_2(j) = \left(j + \frac{1}{2}\right) \Delta \nu_2,$$

where  $\Delta\nu_1$  and  $\Delta\nu_2$  are the mesh size along the  $\nu_1$  and  $\nu_2$  direction respectively:

$$\Delta \nu_i = \frac{\nu_m}{M_i}.$$

Thus, the discrete variables  $n_i$  are defined at the centre of the squared cells. Moreover, let  $\Delta t$  be the time discretisation step, so that  $p^k(i,j)$  represents the distribution function  $p(k\Delta t, n_i, n_j)$ . We note that  $p^k(i,j)$  are the unknown values of the discretised distribution function inside the meshes, whereas  $p^k(i-\frac{1}{2},j-\frac{1}{2})$  are the interpolated values at their interfaces. The discretised Fokker-Planck equation is then given by:

$$p^{k+1}(i,j) = p^k(i,j) + \Delta t \mathcal{F}^k(i,j), \tag{35}$$

where:

$$\mathcal{F}^{k}(i,j) = \frac{1}{\Delta\nu_{1}} \left( F^{k} \left( i + \frac{1}{2}, j \right) - F^{k} \left( i - \frac{1}{2}, j \right) \right) + \frac{1}{\Delta\nu_{2}} \left( G^{k} \left( i, j + \frac{1}{2} \right) - G^{k} \left( i, j - \frac{1}{2} \right) \right),$$

with  $F^k(i+\frac{1}{2},j)$  and  $G^k(i,j+\frac{1}{2})$  the fluxes at the interfaces respectively defined by :

$$F^{k}\left(i+\frac{1}{2},j\right) = \left(-n_{i+1/2} + \phi(\lambda_{1} + w_{11}n_{i+1/2} + w_{12}n_{j})\right)p^{k}\left(i+\frac{1}{2},j\right)$$
$$-\frac{\beta^{2}}{2\Delta\nu_{1}}\left(p^{k}(i+1,j) - p^{k}(i,j)\right),$$
$$G^{k}\left(i,j+\frac{1}{2}\right) = \left(-n_{j+1/2} + \phi(\lambda_{2} + w_{21}n_{i} + w_{22}n_{j+1/2})\right)p^{k}\left(i,j+\frac{1}{2}\right)$$
$$-\frac{\beta^{2}}{2\Delta\nu_{2}}\left(p^{k}(i,j+1) - p^{k}(i,j)\right).$$

We choose the most simple interpolation at the interfaces:

$$p^{k}\left(i+\frac{1}{2},j\right) = \frac{p^{k}(i+1,j) + p^{k}(i,j)}{2},$$

and

$$p^{k}\left(i, j + \frac{1}{2}\right) = \frac{p^{k}(i, j + 1) + p^{k}(i, j)}{2}.$$

Remark 2 Concerning the CFL condition and in order to diminish the computational time, we compute an adaptative time step  $\Delta t$  at every iteration. We require, for example, that:

$$\frac{p^k(i,j)}{2} \le p^{k+1}(i,j) \le \frac{3p^k(i,j)}{2}.$$

These conditions lead to the following time step bound:

$$\Delta t |\mathcal{F}^k(i,j)| \leq \frac{p^k(i,j)}{2}.$$

Finally we define at each iteration the following  $\Delta t$ , for i, j such that  $p^k(i, j) \neq 0$  and  $\mathcal{F}^k(i, j) \neq 0$ :

$$\Delta t = \min_{i,j} \frac{p^k(i,j)}{2|\mathcal{F}^k(i,j)|}.$$

This adaptive time step condition gains a factor 100 in the time computations, with respect to the classical one, but it depends on the number of discretisation points. For instance, in our simulations we need at least  $M_1 = M_2 = 200$ , in order to capture the growth of the double picked distribution.

Finally, we choose to stop our computation when the difference between two successive distribution profiles is smaller than  $10^{-10}$ , and we say in this case that we have reached the equilibrium.

Using the above discretisation we compute various quantities as the marginals  $N_1(t, \nu_1)$  and  $N_2(t, \nu_2)$  of the distribution function p:

$$N_1(t,\nu_1) = \int_0^{\nu_m} p(\nu_1,\nu_2,t) d\nu_2,$$

$$N_2(t,\nu_2) = \int_0^{\nu_m} p(\nu_1,\nu_2,t) d\nu_1,$$

representing the behaviour of each neuron population. We compute as well, the first,  $\mu_1(t)$ ,  $\mu_2(t)$ , and second  $\gamma_{11}(t)$ ,  $\gamma_{12}(t)$ ,  $\gamma_{22}(t)$  moments associated to the distribution function p. They are respectively given by:

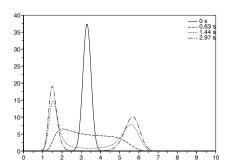
$$\mu_i(t) = \int \int_{\Omega} \nu_i p(\nu_1, \nu_2, t) d\nu_1 d\nu_2, \quad i = 1, 2,$$

$$\gamma_{ij}(t) = \int \int_{\Omega} \nu_i \nu_j p(\nu_1, \nu_2, t) d\nu_1 d\nu_2, \quad i, j = 1, 2.$$

Moreover, we will compute the probabilities  $\rho_i(t)$  for a couple of firing rates  $(\nu_1, \nu_2)$  to belong to some domains  $\Omega_i$ :

$$\rho_i(t) = \int \int_{\Omega_i} p(\nu_1, \nu_2, t) d\nu_1 d\nu_2.$$

In particular, the domains  $\Omega_i$  will be three boxes centered at the three equilibrium points:  $\Omega_1 = [0, 2] \times [5, 10]$  and  $\Omega_3 = [5, 10] \times [0, 2]$  for the two stable points  $S_1$  and  $S_3$ ,  $\Omega_2 = [2, 5] \times [2, 5]$  for the unstable one,  $S_2$ .



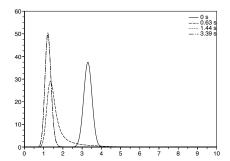
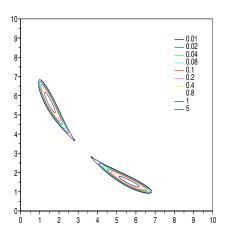


Fig. 2 Time evolution for the marginals  $N_1(t, \nu_1)$ . Left: unbiased case. Right: biased case.

We present now some numerical results, obtained starting from an initial condition given by a Gaussian centered at (3,3), near the unstable position  $S_2$ , as in [9]. We considered here both the unbiased  $(\Delta \lambda = 0)$  and the biased  $(\Delta \lambda = 0.1)$  case, both with a standard deviation  $\beta = 0.1$ .



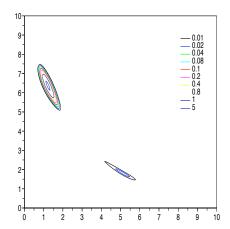


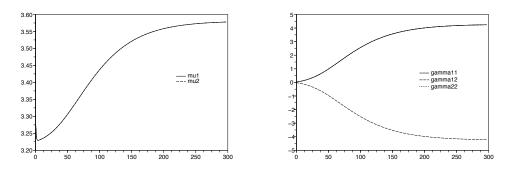
Fig. 3 Contour level for the equilibrium solution. Left: unbiased case. Right: biased case.

In figure 2 we represent the evolution in time of the marginal  $N_1(t)$ . In the unbiased case (left), it is clearly shown the convergence of the density probability function towards an equilibrium with a double pick distribution. In the biased case (right), the distribution function at equilibrium is mostly

concentrated around one of the two stable points. Moreover, we remark the slow-fast behaviour of the distribution time evolution: fast diffusion, and slow growth of the two picks.

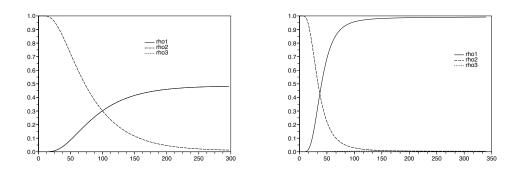
In figure 3 we give in the unbiased case (left) and the biased case (right), the contour levels of the density  $p(\nu_1, \nu_2)$  at equilibrium. We note that there are two points of mass concentration around  $S_1$  and  $S_3$  which are the stable equilibrium points of system (1). We remark that, in the unbiased case the probability density is symmetrically distributed along the slow-manifold, whereas in the biased case there is no more symmetry, but still a little proportion of the population is concentrated around one of the stable points,  $S_1$ .

In figure 4 we show, only for the unbiased case, the evolution in time of the moments of order one,  $\mu_1$  and  $\mu_2$  (on the left), and two,  $\gamma_{11}$ ,  $\gamma_{12}$  and  $\gamma_{22}$  (on the right). Let us comment that this computation recovers in a exact manner the



**Fig. 4** Moments  $\mu_1, \mu_2, \gamma_{11}, \gamma_{12}, \gamma_{22}$  with respect to time, in the unbiased case.

approximation on the evolution of moments done in [9]. The moment method has been used in the computational neuroscience community [18,9,10] in order to approximate the collective averaged quantities of the stochastic differential system (1) by solving deterministic systems. These moment methods need

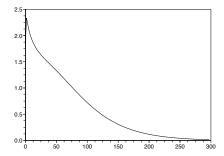


**Fig. 5** Evolution in time of the densities  $\rho_i(t)$ . Left: unbiased case. Right: biased case.

a closure assumption to give closed systems of equations and therefore, they have inherent errors in their approximation. Nevertheless, in this particular

case they lead to good qualitative approximations comparing our results to the ones in [9] whose detailed numerical study is currently under way.

In figure 5 we show the evolution in time of three probabilities,  $\rho_i$  for i = 1, 2, 3, of finding the firing rates in three different domains  $\Omega_1 = [0, 2] \times [5, 10]$ ,  $\Omega_2 = [2, 5] \times [2, 5]$   $\Omega_3 = [5, 10] \times [0, 2]$  and respectively in the unbiased (left) and biased (right) cases. We note that each domain contains one of the three equilibrium points and thus we can refer to  $\rho_1$  and  $\rho_3$  as the probabilities of each decision states and to  $\rho_2$  as the probability of the spontaneous state. We have set the initial condition we consider implies  $\rho_1(0) = \rho_3(0) \simeq 0$  and  $\rho_2(0) \simeq 1$ . Moreover, in the unbiased case, the symmetry of the problem leads to  $\rho_1(t) = \rho_3(t)$  for every  $t \geq 0$ , i.e., the two decision states are taken with equal probability. Whereas, in the biased case,  $\rho_3$  remains very small and one decision state is obtained with large probability.



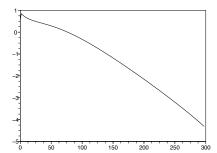


Fig. 6 Convergence toward the stationary solution, in the unbiased case. Right: in logarithmic scale

In figure 6 we show the convergence of the solution of the Fokker-Planck equation to its stationary state in  $L^2$  norm. On the left we present the convergence with respect to time and on the right the same result, but in logarithmic scale. We remark that, a linear regression done on the second half of the curve has a slope of -0.19 with a standard deviation of 0.031, and a linear regression done on the last quarter of the curve has a slope of -0.08 with a standard deviation of 0.004. We conclude then that, after a small transition period, the convergence of the solution towards its stationary state has an exponential behavior.

Finally, we perform a different numerical test, intended to be a first step in the study of the escaping time problem (or first passage problem). We consider only the unbiased case, because we know that for a time large enough the probability function p must be distributed in equal parts on both the domains  $\Omega_1$  and  $\Omega_3$ , no matter what would be the initial condition. We let the diffusion coefficient  $\beta$  to vary in the set (0.2, ..., 1), see table 1, and choose as initial data a Gaussian distribution concentrated near the stable point  $S_1$ , hence in the domain  $\Omega_1$ . We then stop the numerical simulation when half of the mass has arrived in the  $\Omega_3$  domain, that is when  $\rho_1(T) < 2\rho_3(T)$ . We shall call escaping time, the smallest time T at which the above condition is verified. In table 1, we give the values of the escaping time T (expressed in seconds) for

different values of the diffusion coefficient  $\beta$ . As one may expect, the bigger the diffusion coefficient is the smaller would be the escaping time T. Moreover,

 Table 1 Escaping Time.

β	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
${ m T}$	12.91	3.33	1.70	1.12	0.80	0.60	0.49	0.37	0.30

a linear regression on the logarithm of these values shows that the expectation of the escaping time T has an exponential behaviour (the standard deviation being  $\sigma = 0.14$  and the slope -2.2), as it is shown also in figure 7 where we plot in logarithmic scale the values for the escaping time T with respect to the diffusion coefficient  $\beta$ . It is well known, see for example [12], for one dimensional problems, that the expectation of a first passage problem is given by the Kramers law,  $\mathbb{E}(t) = \exp\left(H/\beta^2\right)$ , where H represents the potential gap and  $\beta$  the diffusion coefficient. This kind of behavior has been proved also on some particular multi-dimensional problems. Nevertheless, to our knowledge, there is no proof that for general multi-dimensional problem the expectation of the escaping time has an exponential behaviour.

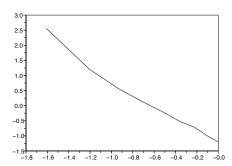


Fig. 7 Escaping time T with respect to the diffusion coefficient  $\beta$  in log scale.

Acknowledgements JAC acknowledges partial support from DGI-MICINN (Spain) project MTM2008-06349-C03-03 and 2009-SGR-345 from AGAUR-Generalitat de Catalunya. SC and SM acknowledge support by the ANR project MANDy, Mathematical Analysis of Neuronal Dynamics, ANR-09-BLAN-0008-01. The authors would like to thanks G. Deco and N. Berglund for their many inspiring discussions and the CRM (Centre de Recerca Matemática) in Barcelona where part of this work was done during the thematic program in Mathematical Biology.

### References

1. Amann H (1976) Fixed Point Equations and Nonlinear Eigenvalue Problems in Ordered Banach Spaces. SIAM Review, 18(4):620-709.

- Arnold A, Carlen E (2000) A generalized Bakry-Emery condition for non-symmetric diffusions. EQUADIFF 99 Proceedings of the Internat. Conference on Differential Equations, Berlin 1999, B. Fiedler, K. Groger, J. Sprekels (Eds.); World Scientific, SIngapore/New Jersey/ Hong Kong: 732-734.
- 3. Arnold A, Carlen E, Ju Q (2008) Large-time behavior of non-symmetric Fokker-Planck type equations. Communications on Stochastic Analysis, 2(1):153-175.
- 4. Arnold A, Carrillo J A, Manzini C (2009) Refined Long-time Asymptotics for Some Polymeric Fluid flow Models. to appear in Comm. Math. Sci.
- Arnold A, Markowich P, Toscani G, Unterreiter A (2001) On convex Sobolev inequalities and the rate of convergence to equilibrium for Fokker-Plack type equations. Comm. PDE, 26:43-100.
- 6. Attneave F (1971) Multistability in perception. Sci. Am., 225:6371.
- 7. Berglund N, Gentz B (2005) Noise-Induced Phenomena in Slow-Fast Dynamical Systems. A Sample-Paths Approach. Springer, Probability and its Applications
- 8. Brody C, Romo R, Kepecs A (2003) Basic mechanisms for graded persistent activity: discrete attractors. continuous attractors, and dynamic representations. Curr. Opin. Neurobiol., 13:204211.
- 9. Deco G, Martí D (2007) Deterministic Analysis of Stochastic Bifurcations in Multi-stable Neurodynamical Systems. Biol Cybern 96(5):487-496.
- 10. Deco G, Scarano L, Soto-Faraco S (2007) Webers Law in Decision Making: Integrating Behavioral Data in Humans with a Neurophysiological Model. The Journal of Neuroscience, 27(42):1119211200.
- 11. Evans LC (1998) Partial Differential Equations, AMS.
- 12. Gardiner CW (1985) Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences. Springer-Verlag.
- 13. La Camera G, Rauch A, Luescher H, Senn W, Fusi S (2004) Minimal models of adapted neuronal response to In Vivo-Like input currents. Neural Computation, 16(10):2101-2124.
- 14. Michel P, Mischler S, Perthame B (2004) General entropy equations for structured population models and scattering. C.R. Acad. Sc. Paris, Ser. I 338(9):697-702.
- 15. Michel P, Mischler S, Perthame B (2005) General relative entropy inequality: an illustration on growth models. J.Math.Pures Appl., 84(9):1235-1260.
- 16. Moreno-Bote R, Rinzel J, Rubin N (2007) Noise-Induced Alternations in an Attractor Network Model of Perceptual Bistability. J. Neurophysiol., 98:1125-1139.
- 17. Renart A, Brunel N, Wang X (2003) Computational Neuroscience: A Comprehensive Approach. Chapman and Hall, Boca Raton.
- 18. Rodriguez R, Tuckwell HC (1996) Statistical properties of stochastic nonlinear dynamical models of single neurons and neural networks. Phys. Rev. E, 54:55855590.
- 19. Romo R, Salinas E (2003) Flutter discrimination: neural codes, perception, memory and decision making. Nat. Rev. Neurosci., 4:203218.
- 20. Wilson HR, Cowan JD (1972) Excitatory and inhibitory interactions in localized populations of model neurons. Biophy. J., Vol. 12(1):1-24.
- 21. Wolka J (1987) Partial Differential Equations. Cambridge University Press.