An elapsed time model for strongly coupled inhibitory and excitatory neural networks

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Abstract

The elapsed time model has been widely studied in the context of mathematical neuroscience with many open questions left. The model consists of an age-structured equation that describes the dynamics of interacting neurons structured by the elapsed time since their last discharge. Our interest lies in highly connected networks leading to strong nonlinearities where perturbation methods do not apply. To deal with this problem, we choose a particular case which can be reduced to delay equations.

We prove a general convergence result to a stationary state in the inhibitory and the weakly excitatory cases. Moreover, we prove the existence of particular periodic solutions with jump discontinuities in the strongly excitatory case. Finally, we present some numerical simulations which ilustrate various behaviors, which are consistent with the theoretical results.

1 Introduction

Understanding the dynamics of neural processes is an interesting challenge from both mathematical and neuroscience viewpoint. Among the different models of neural assemblies, the elapsed time model has been widely studied by several authors. Long time convergence to steady state is studied in Pakdaman et al. [15, 17], Cañizo et al. [2], Mischler et al. [13]. Periodic solutions for strongly excitatory cases are built in Pakdaman et al. [16]. Modeling aspects can be found in Ly et al. [11], and Dumont et al. [6, 7], Salort et al. [21]. These aspects include the relation with other neural models, convergence to steady states, synchronization phenomena and the existence of periodic solutions. For the derivation from microscopic models, see Chevallier et al. [4] and Chevallier [3].

In the models we are interested in, neurons are subject to random discharges that interact with the rest of the network and the population of neurons is described by their elapsed time since last discharge. More

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precisely, the dynamics are governed by the following nonlinear age-structured equation

$$\begin{cases} \partial_t n + \partial_s n + p(s, N(t))n = 0 & t > 0, s > 0, \\ N(t) = n(t, s = 0) = \int_0^\infty p(s, N(t))n(t, s)\, ds & t > 0, \\ n(t = 0, s) = n_0(s) \geq 0 & s \geq 0, \end{cases} \quad (1)$$

where $n(t, \cdot)$ is the probability density of finding a neuron at time t, whose elapsed time since last discharge is $s \geq 0$. The function $N(t)$ represents the flux of discharging neurons at time t, which corresponds to the activity of the network in this particular case. The function p is the firing rate of neurons, which depends on the elapsed time s and the activity N. We say that the network is inhibitory if p is decreasing with respect to the activity and excitatory if p is increasing. Finally $n_0 \in L_s^1$ is the initial data.

The case of strong nonlinearities has been investigated in [16], when the neurons only interact via the variation of the refractory period. Here, we fix the refractory period and we assume that, after a fixed refractory state, the discharge rate of neurons follows an exponential law which parameter depends on the total activity via a smooth function φ. This leads to the following particular form the firing rate p:

$$p(s, u) = \varphi(u)\mathbb{1}_{\{s > \sigma\}}, \quad (2)$$

with $\sigma > 0$ the constant refractory period. We also assume that there exist two constants p_0, p_∞ such that

$$0 < p_0 \leq \varphi(\cdot) \leq p_\infty. \quad (3)$$

For this particular form of the discharge rate p, the network is inhibitory when $\varphi' \leq 0$ and excitatory when $\varphi' > 0$, in particular, is weakly excitatory if φ' is small. Moreover, the System (1) satisfies the mass conservation law, which reads

$$\int_0^\infty n(t, s)\, ds = \int_0^\infty n_0(s)\, ds = 1, \quad \forall t \geq 0, \quad (4)$$

and consequently we have the following bounds on N

$$0 \leq N(t) \leq p_\infty, \quad \forall t \geq 0.$$

This specific form of p allows us to investigate regimes with strong interactions as in [16], reducing the problem to a delay equation (see [5, 14, 20] for references). Other standard methods, as Doeblin's theory in [2], entropy method in [10, 15, 16, 17] or spectral methods in [13], provide results on exponential convergence to equilibrium but only for weak nonlinearities.

For a general firing rate p in System (1) it is conjectured that solutions converge to the unique steady state in the inhibitory case, whereas periodic solutions may arise in the excitatory case. This article is concerned to prove these conjectures for the specific form of the firing rate in (2).

The article is organized as follows. In section 2, we show that System (1) can be studied through a delay differential equation. Moreover from a given periodic activity $N(t)$ solving the delay equation, we can recover a solution of System (1) by using the arguments in [16]. In section 3, we prove convergence to equilibrium in the inhibitory case and the weakly excitatory case. In addition we prove a monotone convergence result in the excitatory case under certain conditions. Regarding periodic solutions, we prove in section 4 the existence of piece-wise constant σ-periodic and with more elaborate arguments we also prove the existence of 2σ-periodic solutions, which are piece-wise monotone. Finally, in section 5 we show numerical examples with several possible behaviors like multiplicity of solutions, convergence to equilibrium in different ways and periodic solution with jump discontinuities.

2 Reduction to a delay differential equation

For analysis purposes, we define the following function $\psi \colon [0, \infty) \to [0, \infty)$ as

$$\psi(u) := \frac{u}{\varphi(u)}, \qquad \text{therefore} \qquad \psi'(u) = \frac{\varphi(u) - u\varphi'(u)}{\varphi^2(u)}. \quad (5)$$

This function plays an important role in the study of System (1), because it can be reduced to a delay differential equation, as one can see in the following lemma:

Lemma 1. *We assume* (2) *and* (3). *For $t > \sigma$ the discharge flux $N(t)$ satisfies:*

$$\int_{t-\sigma}^{t} N(s)\,ds + \psi(N(t)) = 1. \tag{6}$$

Moreover, if $N(t)$ is smooth for $t > \sigma$, the following formula for $N'(t)$ holds:

$$N(t) - N(t-\sigma) + \psi'(N(t))N'(t) = 0. \tag{7}$$

In the same way, for $0 < t < \sigma$ the discharge flux satisfies

$$\int_{0}^{t} N(s)\,ds + \int_{0}^{\sigma-t} n_0(s)\,ds + \psi(N(t)) = 1, \tag{8}$$

and if $N(t)$ is smooth we have the following formula for $N'(t)$:

$$N(t) - n_0(\sigma - t) + \psi'(N(t))N'(t) = 0. \tag{9}$$

Proof. Using assumption (2), the equation for $N(t)$ is rewritten as

$$N(t) = \varphi(N(t)) \int_{\sigma}^{\infty} n(t,s)\,ds.$$

And using the mass-conservation property and the method of characteristics for $t > \sigma$, we obtain:

$$\int_{\sigma}^{\infty} n(t,s)\,ds = 1 - \int_{0}^{\sigma} N(t-s)\,ds.$$

Therefore, we get the first part of Lemma 1. The result for $0 < t < \sigma$ is proved in the same way. $\qquad\square$

The sign of ψ' plays a crucial role in the behavior of the system (see equation (7)). We will prove that complex dynamics can only occur when ψ' changes sign. This does not happen for the inhibitory case, because $\psi' > 0$ on $[0, p_\infty]$, and, in the excitatory case if $\psi' > 0$, on $[0, p_\infty]$. In this latter case, we say that the network is *weakly excitatory*. For instance, this holds if $0 < \varphi' \le p_0/p_\infty$. Otherwise, we say that the network is *strongly excitatory*, if ψ' changes sign (and $\varphi' > 0$).

In the following theorem we show how to recover solutions of the original renewal model from a given activity that is a solution of the integral equation (6).

Theorem 1 (Reconstructing a solution of (1) from a general activity). *Assume* (3). *Let $N \in L^\infty(0, \infty)$ a non-negative function and satisfying $\psi(N(t)) \in \mathcal{C}([\sigma, \infty)) \cap \mathcal{C}^1((0, \sigma))$ and the following conditions:*

1. *$\widetilde{n}(t) := N(\sigma - t) + \frac{d(\psi(N))}{dt}(\sigma - t) \ge 0 \quad for \quad 0 < t < \sigma$,*

2. *$\int_{t-\sigma}^{t} N(s)\,ds + \psi(N(t)) = 1 \quad for\ t \ge \sigma$, i.e., $\int_{0}^{\sigma} N(s)\,ds + \psi(N(\sigma)) = 1$ and N is solution of the integral equation (6).*

Then for any initial probability density n_0 satisfying $n_0(s) = \widetilde{n}(s)$ for $0 < s < \sigma$, the solution n of the linear problem

$$\begin{cases} \partial_t n + \partial_s n + p(s, N(t))n = 0 & t > 0,\ s > 0, \\ n(t, s=0) = N(t) & t > 0, \\ n(t=0, s) = n_0(s) & s > 0, \end{cases} \tag{10}$$

determines a solution of Equation (1) with $N(t)$ as activity.

From this theorem, we deduce that the behavior of $N(t)$ in Equation (1) is determined just by the initial data n_0 on $(0, \sigma)$ as long as it is a probability density.

Proof. In order to prove that the solution n of Equation (10) is actually a solution of Equation (1), we must verify the following conditions for all $t > 0$.

$$\psi(N(t)) = \int_\sigma^\infty n(t, s) \, ds \quad \text{and} \quad \int_0^\infty n(t, s) \, ds = 1. \tag{11}$$

Consider $M(t) := \int_0^\infty n(t, s) \, ds$ and observe that

$$
\begin{aligned}
M'(t) &= -\int_0^\infty \partial_s n(t, s) \, ds - \int_0^\infty p(s, N(t)) n(t, s) \, ds \\
&= N(t) - \varphi(N(t)) \int_\sigma^\infty n(t, s) \, ds \\
&= N(t) - \varphi(N(t)) M(t) + \varphi(N(t)) \int_0^\sigma n(t, s) \, ds.
\end{aligned}
\tag{12}
$$

For $0 < t < \sigma$ we deduce from conditions 1 and 2 that Equation (8) holds and by the method of characteristics we get that $M(t)$ satisfies that

$$
\begin{aligned}
M'(t) &= N(t) - \varphi(N(t)) M(t) + \varphi(N(t)) \left(\int_0^t n(t, s) \, ds + \int_t^\sigma n(t, s) \, ds \right) \\
&= N(t) - \varphi(N(t)) M(t) + \varphi(N(t)) \left(\int_0^t N(s) \, ds + \int_0^{\sigma - t} n_0(s) \, ds \right) \\
&= N(t) - \varphi(N(t)) M(t) + \varphi(N(t)) \left(1 - \psi(N(t)) \right) \\
&= \varphi(N(t))(1 - M(t)).
\end{aligned}
\tag{13}
$$

Similarly for $t > \sigma$ we deduce from condition 2 and the method of characteristics that for a.e. $t > \sigma$ the following equality holds

$$
\begin{aligned}
M'(t) &= N(t) - \varphi(N(t)) M(t) + \varphi(N(t)) \int_{t-\sigma}^t N(s) \, ds \\
&= \varphi(N(t)) \left(1 - M(t) \right).
\end{aligned}
\tag{14}
$$

Therefore we obtain that $M(t)$ satisfies the following differential equation for a.e. $t > 0$.

$$
\begin{cases}
M'(t) = \varphi(N(t))(1 - M(t)), \\
M(0) = 1.
\end{cases}
$$

This implies that $M(t) \equiv 1$ and we conclude (11) for all $t > 0$, which implies that n is a solution of (1) with $N(t)$ as activity. $\qquad \square$

In particular when the activity is periodic we can construct periodic solutions of (1), using only the Lipschitz continuity of $\psi(N(t))$ induced by (3) and (6).

Theorem 2 (Reconstruction of a solution from a periodic activity). *Assume* (3). *For $T > 0$, consider a non-negative T-periodic solution $N(t)$ of the integral equation (6) for all $t \in \mathbb{R}$. Then, there exists a unique T-periodic solution n of the linear Equation (10), which corresponds to a solution of the nonlinear System (1).*

Proof. By periodicity we can extend the solution of Equation (10) for all $t \in \mathbb{R}$ and from the method of characteristics we find a solution given by

$$n(t, s) = N(t - s) e^{-\int_0^s p(s', N(s' + t - s)) \, ds'},$$

thus we can consider as initial data

$$n(t = 0, s) = N(-s)e^{-\int_0^s p(s', N(s'-s))\, ds'},$$

which determines the unique T-periodic solution of (10). Therefore we can replicate the argument in the proof of Theorem 1 in the case $t > \sigma$ to conclude the result. □

3   Convergence to equilibrium

By using the delay equation (7), we prove that solutions of System (1) converge to a steady state in two cases. In the inhibitory and weakly excitatory case, the steady state is unique and we prove global convergence. In the strongly excitatory case, we prove a local convergence theorem with specific assumptions on ψ and for the smooth solution. For the function p defined in (2), these results extend the convergence beyond the standard case of weak interconnections.

We recall here that in both the inhibitory and the weakly excitatory cases ψ' satisfies:

$$\psi'(u) = \frac{\varphi(u) - u\varphi'(u)}{\varphi^2(u)} > 0, \quad \text{for } u \in [0, p_\infty], \tag{15}$$

while in the strongly excitatory case ψ' changes sign. We know from (5) and (6) that there exists a unique steady state determined by N^*, which is the unique solution of the equation

$$\sigma N^* + \psi(N^*) = 1, \text{ and therefore, } \quad n^* = N^* e^{-\int_0^s p(s', N^*)\, ds'}. \tag{16}$$

In the following theorem, we prove the convergence to the steady state, in the inhibitory and weakly excitatory cases.

Theorem 3 (Convergence to equilibrium in the inhibitory or weakly excitatory cases). *Assume that ψ' satisfies (15). Let n be the solution of (1). Then $n(t) \to n^*$ in L_s^1 and $N(t) \to N^*$ when $t \to \infty$, where (n^*, N^*) corresponds to the unique steady state of equation (1) given by (16).*

In order to achieve the result, we need the following two lemmas.

Lemma 2. *Assume that ψ satisfies (15). Then the activity $N(t)$ can not be strictly monotone over any interval of length larger than σ. In particular there exists a sequence of local maxima t_n (and resp. minima) such that $t_n \to \infty$.*

Proof. Assume the existence an interval $I \subset (0, \infty)$, with $|I| > \sigma$, such that $N(t)$ is increasing on I. Let $t_0 > \sigma$ such that $t_0, t_0 - \sigma \in I$, so we have that $N(t_0 - \sigma) < N(t_0)$. However we conclude from (7) that $N'(t_0) < 0$, which contradicts that $N(t)$ is increasing. Similarly, if we assume that N decreases on I we obtain a contradiction. Therefore, we conclude that $N(t)$ increases and decreases many infinitely times. □

Lemma 3. *If ψ satisfies (15), then*

$$\max_{t \in I_{k-1}} N(t) \geq \max_{t \in I_k} N(t), \quad \left(resp. \ \min_{t \in I_{k-1}} N(t) \leq \min_{t \in I_k} N(t) \right),$$

for $k \in \mathbb{N}$ and $I_k := [k\sigma, (k+1)\sigma]$.

Proof. We consider three cases to show that $\max_{t \in I_{k-1}} N(t) \geq \max_{t \in I_k} N(t)$:

1. If $\max\limits_{t \in I_k} N(t) = N(k\sigma)$ then the result is straightforward.

2. If $\max\limits_{t \in I_k} N(t) = N((k+1)\sigma)$ then $N'((k+1)\sigma) \geq 0$ and from formula (7) we get that $N(k\sigma) \geq N((k+1)\sigma)$ and the result is proved.

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3. If there exists $t_0 \in (k\sigma, (k+1)\sigma)$ such that $\max_{I_k} N = N(t_0)$ then $N'(t_0) = 0$ and by formula (7) we have $N(t_0) = N(t_0 - \sigma)$ and the result is proved.

Analogously it is proved that $\min_{t \in I_{k-1}} N(t) \le \min_{t \in I_k} N(t)$. □

Now we can prove Theorem 3.

Proof. For $T > 0$ we define the sequence $N_n(t) = N(t+n)$ for $t \in [-T, T]$ and $n \in \mathbb{N}$ such that $n - T > \sigma$. From formula (7) we get that N' is uniformly bounded since $\psi'(u) > 0$, for $u \in [0, p_\infty]$. This allows to conclude that after extraction of a sub-sequence, $N_n(t)$ converges uniformly in $[-T, T]$ to some function $N_\infty(t)$ defined on $\mathbb{R}$. Moreover $N_\infty(t)$ satisfies for all $t \in \mathbb{R}$ the equation (6) so in particular $N_\infty \in \mathcal{C}_b^1(\mathbb{R})$, and from Lemma 3, we deduce that for all $k \in \mathbb{Z}$

$$\max_{t \in I_k} N_\infty(t) = \limsup_{t \to \infty} N(t), \quad \left(\text{resp. } \min_{t \in I_k} N_\infty(t) = \liminf_{t \to \infty} N(t) \right),$$

and in particular $N^+ := \max_{t \in \mathbb{R}} N_\infty(t) = \max_{t \in I_k} N_\infty(t)$ (resp. $N^- := \min_{t \in \mathbb{R}} N_\infty(t) = \min_{t \in I_k} N_\infty(t)$).

Next, we prove that $N_\infty(t)$ is a constant function. Choose $t^-, t^+ \in \mathbb{R}$, with $t^- < t^+$, such that $N(t^+) = N^+$, $N(t^-) = N^-$ and $|t^+ - t^-| \le \sigma$. Since $N'(t^\pm) = 0$, from equation (7) we get $N(t^\pm) = N(t^\pm - \sigma)$ and thus by iteration we get

$$N(t^\pm) = N(t^\pm - j\sigma), \quad \forall j \in \mathbb{N}.$$

Consider now $k \in \mathbb{N}$. By evaluating formula (6) for $t = t^\pm - j\sigma$ for $j = 1, \ldots, k$ and taking the sum over j, the following equality holds

$$\int_{t^+ - k\sigma}^{t^+} N_\infty(s) + k\psi(N^+) \, ds = \int_{t^- - k\sigma}^{t^-} N_\infty(s) \, ds + k\psi(N^-),$$

and we conclude

$$\psi(N^+) - \psi(N^-) = \frac{1}{k} \left(\int_{t^-}^{t^+} N_\infty(s) \, ds - \int_{t^- - k\sigma}^{t^+ - k\sigma} N_\infty(s) \, ds \right).$$

Hence by taking $k \to \infty$ we conclude $\psi(N^+) = \psi(N^-)$ and this implies $N^+ = N^-$, since ψ is strictly increasing. Therefore N_∞ is a constant function.

Since N_∞ satisfies formula (6), we conclude by uniqueness of the solution of equation (16) that $N_\infty = N^*$. In particular we conclude that $N(t) \to N^*$ when $t \to \infty$ and the convergence of $n(t)$ is obtained via the method of characteristics and Lebesgue's theorem. □

In strongly excitatory networks, ψ' changes sign, therefore the above theorem does not apply. And also there is no steady state uniqueness. In this case, we prove the following local convergence theorem.

Theorem 4 (Monotone convergence in the strongly excitatory case). *Let $N^* > 0$ be a solution of (16) (i.e. a steady-state activity of (1)), and consider $N \in \mathcal{C}[0, \sigma]$ satisfying the following conditions:*

1. $N(t) < N(\sigma) < N^*$ *for all $t \in (0, \sigma)$ (resp. $N(t) > N(\sigma) > N^*$).*

2. $\int_0^\sigma N(s) \, ds + \psi(N(\sigma)) = 1.$

3. $\psi'(u) < 0$ *for $u \in [N_-, N^*]$ with $N_- = \min\limits_{t \in [0,\sigma]} N(t)$ (resp. for $u \in [N^*, N_+]$ with $N_+ = \max\limits_{t \in [0,\sigma]} N(t)$).*

Then there exists a strictly increasing (resp. decreasing) solution $N(t)$ of (6), which extends the given $N \in \mathcal{C}[0, \sigma]$. Moreover if N^* is the unique steady state activity lying on $[N(\sigma), N^*]$ (resp. on $[N^*, N(\sigma)]$), then $N(t) \to N^*$ when $t \to \infty$.

We point out that to be a solution of the time elapsed model (1), we need to find a compatible initial data $n_0(s)$. Theorem 1 can help in that direction.

Proof. We start with the proof of the case $N(t)$ increasing. Consider $\widetilde{\psi} \colon \mathbb{R} \to \mathbb{R}$ a smooth Lipschitz function such that for some constant $\alpha > 0$ we have $\widetilde{\psi}'(u) < -\alpha$ and

$$\widetilde{\psi} \equiv \psi \quad \text{on} \quad [N_-, N^*].$$

Thus the following delay differential equation

$$\begin{cases} \frac{d}{dt}\widetilde{\psi}(u(t)) = u(t-\sigma) - u(t) & t > \sigma, \\ u(t) \equiv N(t) & t \in [0, \sigma], \end{cases} \tag{17}$$

has a unique global $u \in \mathcal{C}^1[\sigma^+, \infty) \cap \mathcal{C}[0, \infty)$ by applying Cauchy-Lipschitz theorem. We call this global solution as $N(t)$ as well. From equation (17) we observe that

$$\int_{t-\sigma}^{t} N(s)\, ds + \widetilde{\psi}(N(t))$$

is constant and from condition 2 we have that

$$\int_{t-\sigma}^{t} N(s)\, ds + \widetilde{\psi}(N(t)) = 1. \tag{18}$$

Next we prove that $N(t) < N^*$ for all $t > \sigma$. Suppose that there exists $t^* > \sigma$ such that $N(t^*) = N^*$ and $N(t) < N^*$ for $t < t^*$. Thus from equation (18) we observe that

$$1 = \int_{t^*-\sigma}^{t^*} N(s)\, ds + \psi(N^*) < \sigma N^* + \psi(N^*),$$

which contradicts equation (16) and hence $N(t) < N^*$ for all $t > \sigma$.

Now we prove that $N'(t) > 0$ for all $t > \sigma$. From equation (17) we have that $N'(\sigma^+) > 0$ and from continuity there exists $\varepsilon > 0$ such that $N'(t) > 0$ for $t \in (\sigma, \sigma + \varepsilon)$. Suppose that there exists a first local maximum $t_* > \sigma$, so that $N'(t_*) = 0$ and from equation (17) we get $N(t_* - \sigma) = N(t_*) > N(\sigma)$. If $t_* < 2\sigma$ then we contradict condition 1 and if $t_* \geq 2\sigma$ we contradict the monotony of $N(t)$ on $[\sigma, t_*]$. Therefore $N'(t) > 0$ for all $t > \sigma$.

From monotony and boundedness of N, we conclude in particular that N is a solution of equation (6) for $t > \sigma$. Moreover, if N^* is the unique steady state on the interval $[N(\sigma), N^*]$, then it is straightforward that $N(t) \to N^*$ when $t \to \infty$. The proof of $N(t)$ decreasing is analogous. $\qquad\square$

Figure 1 shows an example of this theorem.

4 Periodic solutions for strongly excitatory networks

From equation (6) we can also construct various periodic solutions for the activity $N(t)$, which generate periodic solutions of the System (1) by means of Theorem 2. However, we observe from the integral equation (6) that a σ-periodic solution satisfies that $\int_{t-\sigma}^{t} N(s)ds$ is constant and thus $\psi(N(t))$ is also constant. Hence, except when ψ is locally constant, the only continuous σ-periodic solutions are constant (steady states). When ψ' changes sign, we build several types of solutions including piece-wise constant discontinuous σ-periodic solutions and piece-wise smooth discontinuous 2σ-periodic solutions.
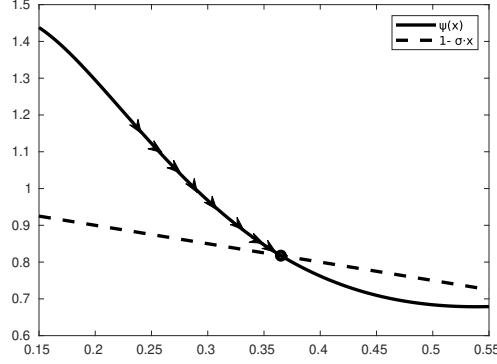
Figure 1: An example of an increasing solution converging to equilibrium. The solution remains in the region where ψ is strictly decreasing.

4.1 Piece-wise constant periodic solutions

Our first goal is to build σ periodic solutions with jump discontinuities which keep constant the value of $\psi(N(t))$. As a consequence of Theorem 2, this is possible when ψ' changes sign and some structure condition is met on ψ.

Theorem 5 (Existence of piece-wise constant σ-periodic activities). *Assume that ψ' changes sign. Let $N_1 \neq N_2$ be numbers in $(0, p_\infty]$ such that $\psi(N_1) = \psi(N_2)$. Consider the function defined by*

$$N(t) = \begin{cases} N_1 & when \quad t \in [0, \alpha), \\ N_2 & when \quad t \in [\alpha, \sigma), \end{cases} \tag{19}$$

and assume there is an $\alpha \in (0, \sigma)$ such that

$$\alpha N_1 + (\sigma - \alpha)N_2 + \psi(N_1) = 1. \tag{20}$$

Then the periodic extension of $N(t)$ determines a σ-periodic solution of System (1).

Remark 1. *Notice that, if such an α exists, there is a steady state between N_1 and N_2, because if $N_1 < N_2$ then $\sigma N_1 + \psi(N_1) < 1 < \sigma N_2 + \psi(N_2)$. Therefore there exists N^* such that $\sigma N^* + \psi(N^*) = 1$. If $N_2 < N_1$ we proceed in the same way exchanging N_1 and N_2*

Remark 2. *The same construction can be done for a piece-wise constant $N(t)$ with more than one jump, as long as it verifies the equation (6) and ψ remains constant for the values taken by $N(t)$.*

As an example where condition (20) is verified, consider $\sigma = 1$ and $\varphi(N) = \left(1 + e^{-9N+3.5}\right)^{-1}$ so that

$$\psi(N) = N(1 + e^{-9N+3.5}).$$

As we see in Figure 2, ψ' changes sign and there are three solutions of the equation $\psi(u) = 0.9$. Take N_1 as the minimal solution and N_2 as the maximal one, so that there exists $\alpha := \frac{N_2 - 0.1}{N_2 - N_1} \in (0, 1)$ such that

$$\alpha N_1 + (1 - \alpha)N_2 = 0.1,$$

since $N_1 < 0.1 < N_2$. Therefore condition (20) holds and $N(t)$ defined in (19) determines a periodic solution of (1) by means of Theorem 2.

We can also get continuous periodic solutions for a specific type of firing rates as we state it in the following proposition.
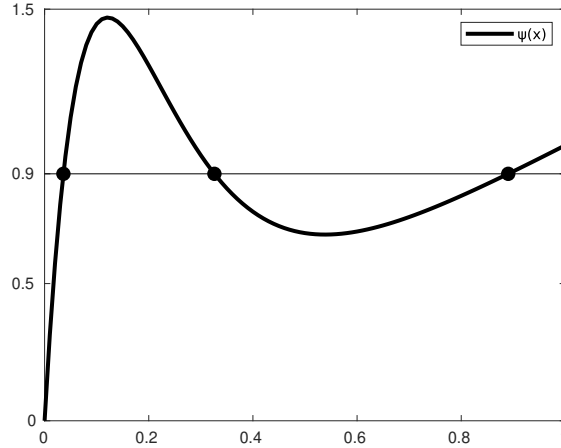
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Figure 2: Graphic of $\psi(u) = u(1 + e^{-9u+3.5})$.

Proposition 1. *Let φ be a smooth function such that $\varphi(u) = Cu$ on some interval $[a, b] \subseteq [0, p_\infty]$ with $C > 1$. Assume moreover that $\sigma > 0$ satisfies the inequality*

$$a\sigma < 1 - \frac{1}{C} < b\sigma. \tag{21}$$

Let u be a bounded σ periodic function such that $\int_0^\sigma u(s)\,ds = 0$. Then there exists $\alpha > 0$ such that

$$N(t) := \frac{1}{\sigma}\left(1 - \frac{1}{C}\right) + \alpha u(t)$$

is a solution of (6).

Proof. Let u be a bounded σ periodic function such that $\int_0^\sigma u(s)\,ds = 0$. For $\alpha > 0$ small enough, $N(t)$ defined in Proposition 1 is such that $N(\mathbb{R}) \subset [a, b]$, and so, N satisfies (6) because $\psi(N(\cdot)) = \frac{1}{C}$. □

4.2 Piece-wise monotone 2σ-periodic solutions

With more elaborate arguments inspired in the works of Hadeler et al. in [9] on periodic solutions of differential delay equations, we can also build 2σ-periodic solutions of System (1), which are piece-wise monotone. In order to achieve the result, we study the delay differential equation given by

$$\frac{d}{dt}\psi(N(t)) = N(t - \sigma) - N(t). \tag{22}$$

Theorem 6 (Existence of piece-wise monotone 2σ-periodic solutions). *Assume that ψ is smooth with ψ' changing sign. Consider $\underline{N} > 0$ such that it is a local minimum of ψ and there exists $\varepsilon > 0$ such that ψ is strictly convex on $(\underline{N} - \varepsilon, \underline{N} + \varepsilon)$. Then for $\sigma > 0$ small enough there exists a 2σ periodic solution $N(t)$ of (22) with $\psi(N) \in W^{1,\infty}(\mathbb{R})$, such that $N(t)$ is strictly decreasing on $(0, 2\sigma)$ with a discontinuity at σ.*

If in addition $\psi(\underline{N}) < 1$ and $\psi(\underline{N} \pm \varepsilon) > 1$, then there exists a solution n of equation (1) such that the activity $N(t)$ solves (6).

Proof. Since ψ is strictly convex around the local minimum $\underline{N}$, consider $\bar{N}^-$, $\bar{N}^+$ be two positive constants such that

$$\psi(\bar{N}^-) = \psi(\bar{N}^+), \quad \bar{N}^- < \underline{N} < \bar{N}^+$$

with ψ strictly decreasing on $[\bar{N}^-, \underline{N}]$ and strictly increasing on $[\underline{N}, \bar{N}^+]$. We construct a periodic solution $N(t)$ of (22) satisfying the following conditions:

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1. $\begin{cases} \underline{N} < N(t) < \bar{N}^+, \ N'(t) < 0 & \text{for } t \in (0,\sigma), \\ \bar{N}^- < N(t) < \underline{N}, \ N'(t) < 0 & \text{for } t \in (\sigma, 2\sigma). \end{cases}$

2. $N(0^+) = \bar{N}^+, \ N(2\sigma^-) = \bar{N}^-.$

3. $\psi(N(\sigma^-)) = \psi(N(\sigma^+)).$

The first step is to build a periodic solution solving equation (22) on $(0,\sigma)$ and $(\sigma, 2\sigma)$, which satisfies conditions 1 and 2. Let C be the closed subset of the Banach space $\mathcal{C}[0,\sigma]$ defined by

$$C := \left\{ N(t) \in \mathcal{C}[0,\sigma]\colon N(0) = \bar{N}^+, \ N(t) \text{ non-increasing}, \ \psi(N(t)) \geq \psi(\bar{N}^+) - (\bar{N}^+ - \bar{N}^-)\sigma \text{ for } t \in [0,\sigma] \right\}.$$

Observe that for σ small enough we assure that $\psi(N(t)) > \psi(\underline{N})$ for all $t \in [0,\sigma]$. Our strategy is to build a solution on $[0,2\sigma]$ such that its restriction to $[0,\sigma]$ is a fixed point of an operator in C.

Now for $N \in C$ we define $M(t)$ as the solution of the backward problem

$$\begin{cases} \frac{d}{dt}\psi(M(t)) = N(t-\sigma) - M(t), & t \in (\sigma, 2\sigma). \\ M(2\sigma) = \bar{N}^-. \end{cases} \tag{23}$$

For σ small enough, this equation is well-posed in the classical sense on $[\sigma, 2\sigma]$. Moreover we have $\psi'(M(t)) < 0$, $M'(t) < 0$ and $\frac{d}{dt}\psi(M(t))$ verifies

$$\frac{d}{dt}\psi(M(t)) \leq \bar{N}^+ - \bar{N}^-, \quad \forall t \in (\sigma, 2\sigma).$$

By integrating this inequality, between t and 2σ, we get $\psi(M(t)) \geq \psi(\bar{N}^+) - (\bar{N}^+ - \bar{N}^-)\sigma > \psi(\underline{N})$, and since $M(2\sigma) = \bar{N}^-$ we have $\bar{N}^- < M(t) < \underline{N}$ for $t \in (\sigma, 2\sigma)$. Similarly, we define $L(t)$ as the solution of problem

$$\begin{cases} \frac{d}{dt}\psi(L(t)) = M(t-\sigma) - L(t), & t \in (2\sigma, 3\sigma). \\ L(2\sigma) = \bar{N}^+, \end{cases} \tag{24}$$

so that for σ small enough it is well-posed in the classical sense on $[2\sigma, 3\sigma]$. Moreover we have $\psi'(L(t)) > 0$, $L'(t) < 0$, and $\psi(L(t)) \geq \psi(\bar{N}^+) - (\bar{N}^+ - \bar{N}^-)\sigma > \psi(\underline{N})$, which implies that $\underline{N} < L(t) < \bar{N}^+$ for $t \in (2\sigma, 3\sigma)$, since $L(2\sigma) = \bar{N}^+$.

Therefore we define the continuous map $T\colon C \to C$ given by $T[N](t) = L(t - 2\sigma)$ and we look for a fixed point of the operator T in order to find a 2σ-periodic function $N(t)$ with $\psi(N(0^+)) = \psi(N(2\sigma^-))$, satisfying equation (22) on $(0,\sigma)$ and $(\sigma, 2\sigma)$ with jump discontinuities such that $\psi(N(t))$ is continuous.

Now we proceed to prove that T is a contraction for σ small enough. Consider $N_1, N_2 \in C$ with their respective M_1, M_2 and L_1, L_2. For the difference between M_1 and M_2 we have for $t \in [\sigma, 2\sigma]$

$$|M_2(t) - M_1(t)| \leq A_\sigma |\psi(M_2(t)) - \psi(M_1(t))|$$
$$\leq A_\sigma \left| \int_t^{2\sigma} \frac{d}{dt}\left(\psi(M_1(t')) - \psi(M_2(t'))\right) dt' \right|$$
$$\leq \sigma A_\sigma \|N_2 - N_1\|_\infty + \sigma A_\sigma \|M_1 - M_2\|_\infty,$$

with $A_\sigma := \max\left\{ \left|(\psi^{-1})'(u)\right| : \psi(\bar{N}^+) - (\bar{N}^+ - \bar{N}^-)\sigma \leq u \leq \psi(N^+) \right\}$ and ψ^{-1} is the local inverse around $\bar{N}^-$. Since $\sigma A_\sigma \to 0$ when $\sigma \to 0$, we deduce the following estimate for σ small enough

$$\|M_2 - M_1\|_\infty \leq \frac{\sigma A_\sigma}{1 - \sigma A_\sigma} \|N_2 - N_1\|_\infty. \tag{25}$$

Analogously for the difference between L_1 and L_2 we get

$$\|L_2 - L_1\|_\infty \leq \frac{\sigma B_\sigma}{1 - \sigma B_\sigma} \|M_2 - M_1\|_\infty, \tag{26}$$

with $B_\sigma := \max\left\{\left|\left(\psi^{-1}\right)'(u)\right| : \psi(\bar{N}^+) - (\bar{N}^+ - \bar{N}^-)\sigma \leq u \leq \psi(N^+)\right\}$ and ψ^{-1} is now considered as the local inverse around $\bar{N}^+$. Therefore we conclude from estimates (25) and (26) that T a contraction and we get a unique 2σ-periodic function $N(t)$ satisfying the conditions 1 and 2 and solving (22) on $(0, \sigma)$ and $(\sigma, 2\sigma)$.

The next step is to prove that the constructed solution $N(t)$ verifies the condition 3. From equation (22) we deduce that

$$Q(t) := \int_{t-\sigma}^{t} N(s)\, ds + \psi(N(t))$$

is piece-wise constant and we get the following equalities

$$
\begin{aligned}
\psi(N(\sigma^-)) - \psi(N(0^+)) &= \int_{\sigma}^{2\sigma} N(s)\, ds - \int_{0}^{\sigma} N(s)\, ds, \\
\psi(N(2\sigma^-)) - \psi(N(\sigma^+)) &= \int_{0}^{\sigma} N(s)\, ds - \int_{\sigma}^{2\sigma} N(s)\, ds.
\end{aligned}
\tag{27}
$$

Since $\psi(N(0^+)) = \psi(\bar{N}^+) = \psi(\bar{N}^-) = \psi(N(2\sigma^-))$, we conclude that $\psi(N(\sigma^-)) = \psi(N(\sigma^+))$. Moreover, we conclude that $\psi(N(t))$ is absolutely continuous and thus $Q(t)$ is constant and given by

$$Q(t) \equiv Q[\bar{N}^+] := \psi(\bar{N}^+) + \int_{\sigma}^{2\sigma} N(s)\, ds.$$

This proves the first part of theorem.

Assume now the additional hypothesis $\psi(\underline{N}) < 1$ and $\psi(\underline{N} \pm \varepsilon) > 1$, thus there exist two pairs $(\bar{N}_1^-, \bar{N}_1^+)$, $(\bar{N}_2^-, \bar{N}_2^+)$ of positive numbers such that for σ small enough, the following conditions hold

- $\psi(\bar{N}_1^-) = \psi(\bar{N}_1^+)$ and $\psi(\bar{N}_2^-) = \psi(\bar{N}_2^+)$.

- $\bar{N}_1^- < \bar{N}_2^- < \underline{N} < \bar{N}_2^+ < \bar{N}_1^+$.

- $\psi(\bar{N}_1^+) > 1 - \sigma \bar{N}_1^-$ and $\psi(\bar{N}_2^-) < 1 - \sigma \bar{N}_2^+$.

By applying Theorem 2 we can construct two periodic solutions of the System (1) with respective masses $Q[\bar{N}_1^+]$ and $Q[\bar{N}_2^+]$, so we need to find a constant $N_0^+ > 0$ such that $Q[N_0^+] = 1$. Observe we have the following inequalities

$$
\begin{aligned}
Q[\bar{N}_1^+] &> \psi(\bar{N}_1^+) + \sigma \bar{N}_1^- > 1 \\
Q[\bar{N}_2^+] &< \psi(\bar{N}_2^+) + \sigma \bar{N}_2^+ < 1.
\end{aligned}
\tag{28}
$$

Since $Q[\cdot]$ is continuous with respect to the variable $\bar{N}^+$, we conclude by applying the intermediate value theorem the existence of $N_0^- \in (\bar{N}_1^-, \bar{N}_2^-)$ and $N_0^+ \in (\bar{N}_2^+, \bar{N}_1^+)$ such that $Q[N_0^+] = 1$. Therefore the corresponding periodic solution $N(t)$ of the delay equation (22) satisfies the equation (6) and the conditions 1, 2 and 3. $\qquad\square$

Remark 3. *We can also construct 2σ-periodic solutions $N(t)$ of (22) around a local maximum of ψ, which are piece-wise strictly increasing and preserve the value of ψ at jump discontinuities.*

5 Numerical simulations

In order to illustrate the theoretical results of the previous sections, we present numerical results for different networks with multiple steady states, with different types of convergence to equilibrium, and with periodic solutions with jump discontinuities. The numerical illustrations we present below are obtained by solving the equation (1) with a classical first-order upwind scheme.
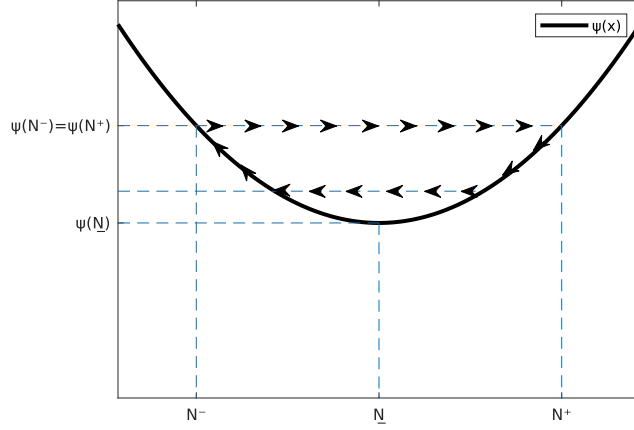
Figure 3: An example of ψ with a local minimum at $\underline{N}$. The trajectory in arrows over the graph of ψ indicates the variations of periodic solution $N(t)$ and the horizontal arrows indicate a jump discontinuity, which preserves the value of $\psi(N)$ at these jumps.

5.1 Example 1: Convergence to different steady states

Our first example is a numerical simulation with multiple steady states. For this example we choose

$$\varphi(N) = \frac{1}{1 + e^{-9N+3.5}}, \quad \sigma = \frac{1}{2}. \tag{29}$$
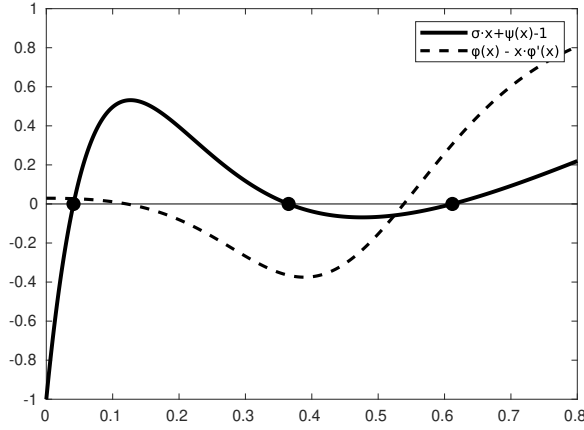
Figure 4: Graphical representation of the three equilibria and the sign of ψ', for examples 1 and 2. Two of them are in the region where $\psi' > 0$ and the other one is the region where $\psi' < 0$.

In this case ψ' changes sign twice since $\varphi(u) - u\varphi'(u)$ does and from equation (16) we get three steady states given by $N_*^1 \approx 0.0410$, $N_*^2 \approx 0.3650$ and $N_*^3 \approx 0.6118$, as we observe in Figure 4.

When we take $n_0(s) = \frac{1}{2}e^{-(s-1)+}$ as the initial data, we have three different solutions for $N(0)$ determined by the equation

$$N(0) = \varphi(N(0)) \int_\sigma^\infty n_0(s)\, ds, \tag{30}$$

that are given by $N_0^1 \approx 0.0281$, $N_0^2 \approx 0.4089$, $N_0^3 \approx 0.7114$. These values determine three different branches of solutions, which numerically converge to their respective steady states. In Figure 5a we observe that
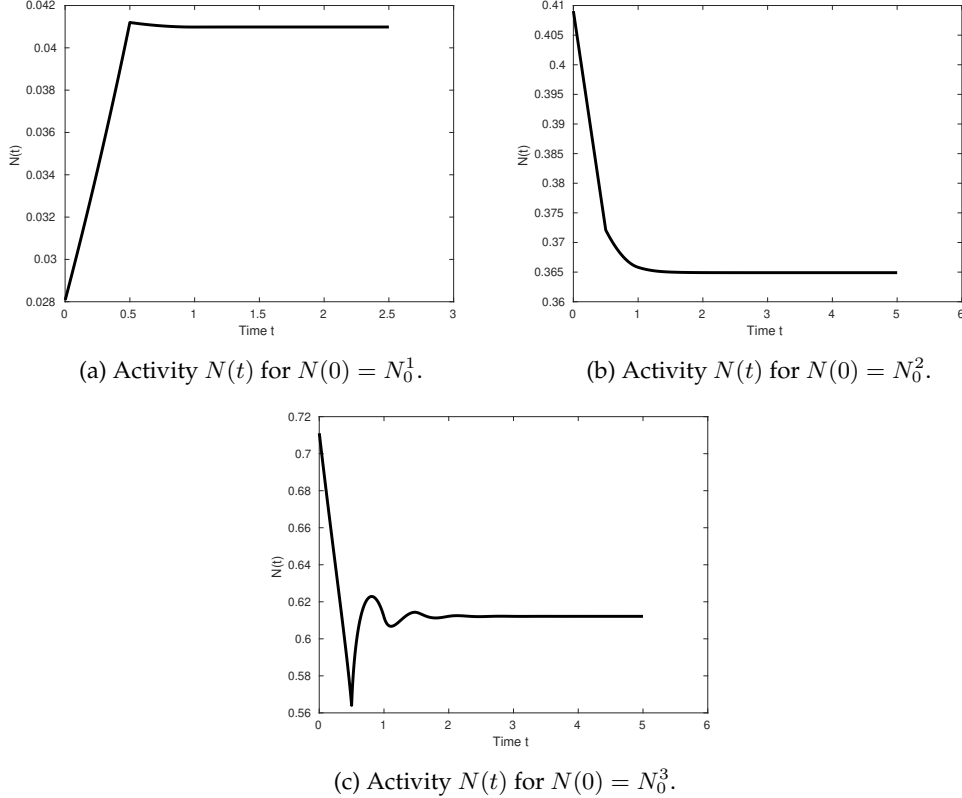
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(a) Activity $N(t)$ for $N(0) = N_0^1$.

(b) Activity $N(t)$ for $N(0) = N_0^2$.

(c) Activity $N(t)$ for $N(0) = N_0^3$.

Figure 5: **Example 1.** Activities of different solutions with $n_0(s) = \frac{1}{2}e^{-(s-1)+}$ for different values of $N(0)$.

$N(t)$ is increasing in $[0, \sigma]$ and then approaches to the value N_*^1, which corresponds to a convergence to equilibrium according to Theorem 3. Moreover we observe in Figure 5b that $N(t)$ converges monotonically to N_*^2, which satisfies $\psi'(N_*^2) < 0$. This is compatible with Theorem 4 in the case when $\psi'(N(t))$ remains negative for all $t \geq 0$. Finally in Figure 5c we observe that $N(t)$ converges to N_*^3 in the same way stated in Theorem 3 with $\psi'(N_*^3) > 0$.

5.2 Example 2: Possible jump discontinuities

Under the same φ defined in (29), consider now as initial data $n_0(s) = e^{-(s-0.5)}\mathbb{1}_{\{s>0.5\}}$. In this case we also get three possible solutions for $N(0)$ in Equation (30), which are given by $N_0^1 \approx 0.0423$, $N_0^2 \approx 0.2887$, $N_0^3 \approx 0.9958$.

In Figure 6a we observe that $N(t)$ is decreasing in $[0, \sigma]$ and then approaches to the value N_*^1, which corresponds again to a convergence to equilibrium according to Theorem 3. In Figure 6b we observe that $N(t)$ converges monotonically to N_*^2, which satisfies $\psi'(N_*^2) < 0$. In this case the solution is increasing and it corresponds to the behaviour stated in Theorem 4. Moreover in Figure 6c we observe that $N(t)$ has a jump discontinuity at some $t_0 \in (0, \sigma)$ that causes the solution to change to the branch of N_0^1 and then $N(t)$ converges to N_*^1 afterwards. At the jump time, the solution preserves the value of ψ as we show in Figure 6d. The horizontal arrows represent the change of $N(t)$ along the graph of ψ at this discontinuity.

5.3 Example 3: Periodic solutions

To describe periodic solutions we simulate two different examples.

(a) Activity $N(t)$ for $N(0) = N_0^1$.

(b) Activity $N(t)$ for $N(0) = N_0^2$.

(c) Activity $N(t)$ for $N(0) = N_0^3$.

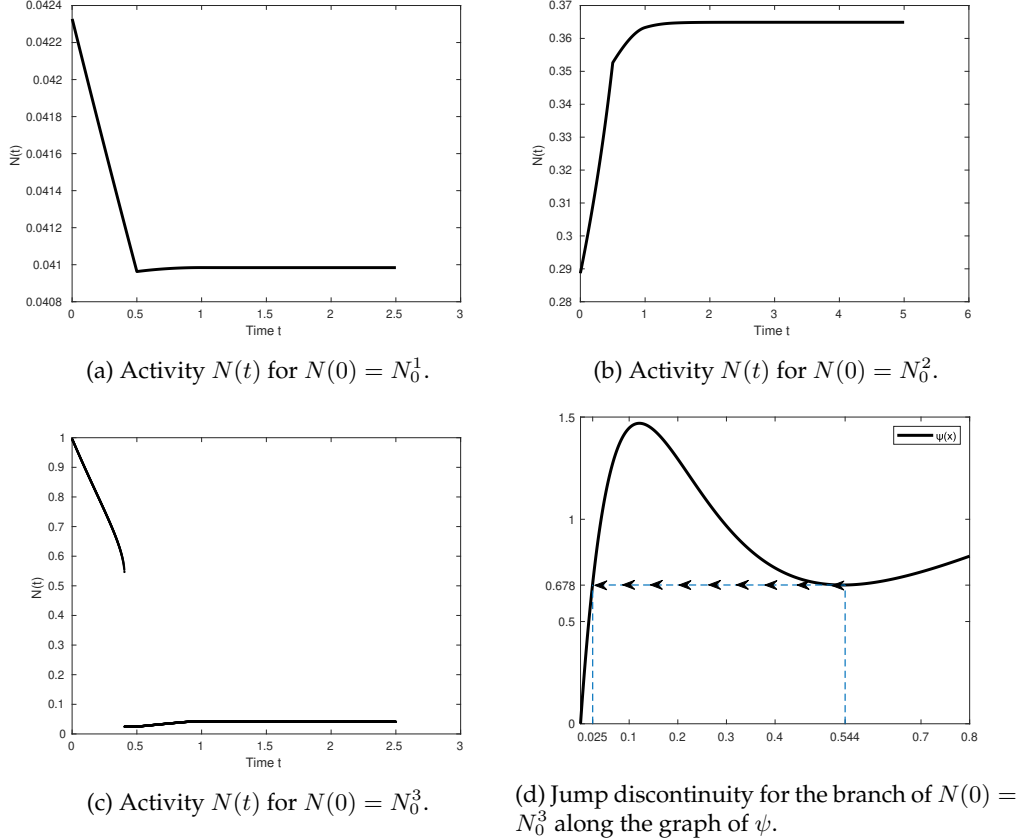(d) Jump discontinuity for the branch of $N(0) = N_0^3$ along the graph of ψ.

Figure 6: **Example 2.** Activities of different solutions with $n_0(s) = e^{-(s-0.5)}\mathbb{1}_{\{s>0.5\}}$ for different values of $N(0)$.

Example 3.1. We consider the firing rat determined by

$$\varphi(N) = \max\{\min(1.6\,N, 1), 0.25\}, \quad \sigma = 1.$$

From equation (16), there exists a unique steady state with $N_* = 0.375$ and $\psi'(N_*) = 0$. Moreover, we observe in Figure 7 that the solution with initial data $n_0(s) = e^{-s}$ converges to a σ-periodic solution of (6), which is piece-wise constant whose values oscillate between $N_1 = \frac{0.25}{1.6}$ and $N_2 = \frac{1}{1.6}$. This periodic profile is an example of the type of solutions presented in Theorem 5.

Example 3.2. Next, we consider the firing rate determined by

$$\varphi(N) = \frac{10N^2}{N^2 + 1} + 0.5, \quad \sigma = 1,$$

From equation (16) there exists a unique steady state with $N_* \approx 0.8186$ and $\psi'(N_*) < 0$. For the initial data $n_0(s) = e^{-(s-1)}\mathbb{1}_{\{s>1\}}$, we observe in Figure 8a that the solution is asymptotic to a periodic pattern with jump discontinuities. The period is larger than 1 since $\psi(N(t))$ is not converging to a constant as we see in Figure 8b.

5.4 Example 4: A non monotone firing rate

Since dynamics in Equation (1) depend heavily on the function ψ, theoretical results are valid not only in the strictly excitatory or inhibitory case. This allows to include non monotone examples of functions φ, which represents a more realistic assumption in the model.
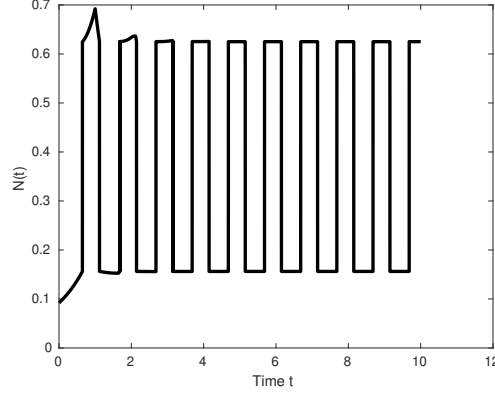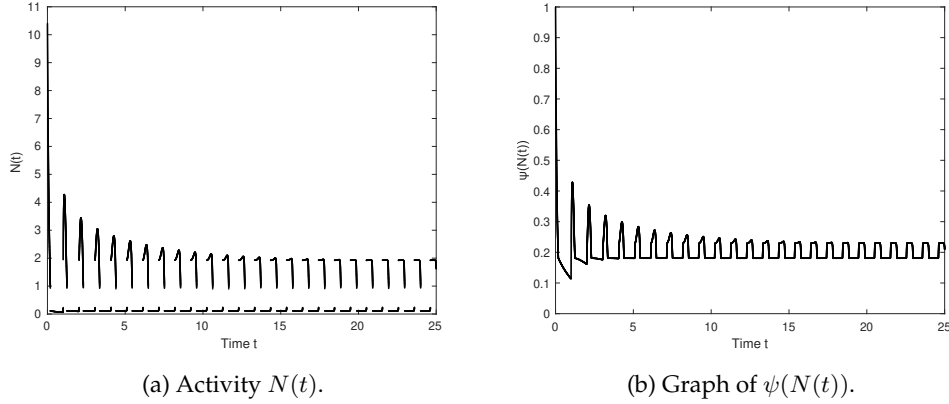
Figure 7: **Example 3.1.** Activity $N(t)$ for $n_0(s) = e^{-s}$.

(a) Activity $N(t)$.

(b) Graph of $\psi(N(t))$.

Figure 8: **Example 3.2.** Behavior for $n_0(s) = e^{-(s-1)}\mathbb{1}_{\{s>1\}}$.

For this example we choose the firing rate determined by

$$\varphi(N) = 8e^{-(N-0.1)^2} + 8e^{-(N-3)^2}, \quad \sigma = \frac{1}{5}.$$

Unlike of previous examples, the function φ is non monotone as we see in Figure 9.

In this case ψ' changes sign and there exists three steady states with $N_*^1 \approx 1.4423$, $N_*^2 \approx 2.0695$, $N_*^3 \approx 3.0711$, as we note in Figure 10.

When we take as initial data $n_0(s) = \frac{2}{3}(1 + \cos(s))e^{-s}$ we get three possible solutions for $N(0)$ in Equation (30), which are given by $N_0^1 \approx 1.4976$, $N_0^2 \approx 1.8163$, $N_0^3 \approx 3.7037$. These values determine three different branches of solutions.

In Figure 11a we observe that $N(t)$ decreasing on $[0, \sigma]$ and the solution converges to the steady stated determined by N_*^1, which corresponds to the behaviour stated in Theorem 3. In Figure 11b we see that $N(t)$ converges monotonically to N_*^2, which $\psi'(N_*^2) < 0$. In this case the solution is increasing and it corresponds to the behaviour stated in Theorem 4. Furthermore in Figure 11c we observe that $N(t)$ has a jump discontinuity at some $t_0 \in (0, \sigma)$ that causes the solution to change to the branch of N_0^1 and then $N(t)$ converges to N_*^1 afterwards. At this jump time, the solution preserves the value of ψ as we show in Figure 11d. The horizontal arrows represent the change of $N(t)$ along the graph of ψ at this discontinuity. We observe essentially the same behaviors of Example 2.
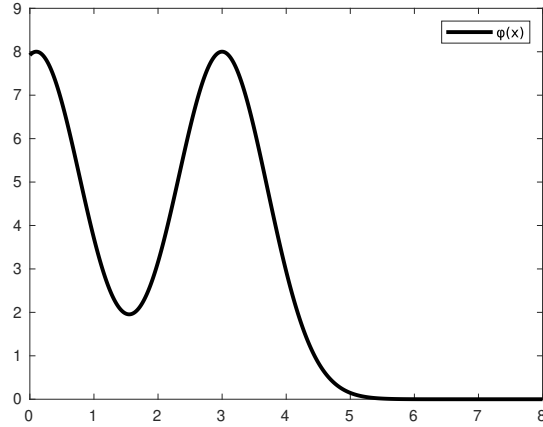
15

Figure 9: Graphical representation of φ, which changes two times from a excitatory regime to an inhibitory one.
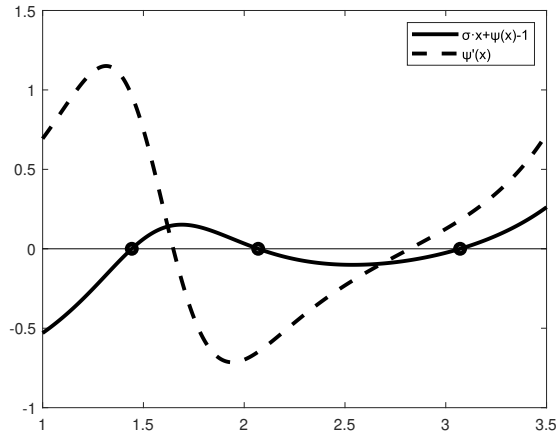

Figure 10: Graphical representation of the three equilibria and the sign of ψ', for example 4. Two of them are in the region where $\psi' > 0$ and the other one is the region where $\psi' < 0$.

6   Perspectives

In the present analysis of System (1) with the firing rate p modulated by amplitude as given by (2), we have exhibited some possible qualitative behaviours of solutions. Steady-state convergence always occurs in the inhibitory and the weakly excitatory networks. And this can also occur for strongly excitatory connections, in particular situations. Periodic solutions can be built for strongly excitatory connections. Our method is based on the derivation of a nonlinear delay equation for the network activity. Moreover, numerical simulations are consistent with the theoretical results obtained about the convergence to equilibrium and the existence of jump discontinuities. This study provides possible behaviors which might arise for a more general firing rate. From this particular example of firing rate, we can think that the model induces an implicit delay, which is consistent with the interpretation of the discharge dynamics in the elapsed time model.

Regarding convergence to equilibrium, we conjecture that the convergence rate in Theorem 3 for the inhibitory and weakly excitatory case is exponential, as it occurs in [16] for a variant of the firing rate p, which is also given by an indicator function. Moreover, we expect the convergence in Theorem 4 for monotone solutions in the strongly excitatory case to be exponential as well.

(a) Activity $N(t)$ for $N(0) = N_0^1$.

(b) Activity $N(t)$ for $N(0) = N_0^2$.

(c) Activity $N(t)$ for $N(0) = N_0^3$.

(d) Jump discontinuity for the branch of $N(0) = N_0^3$ along the graph of ψ.
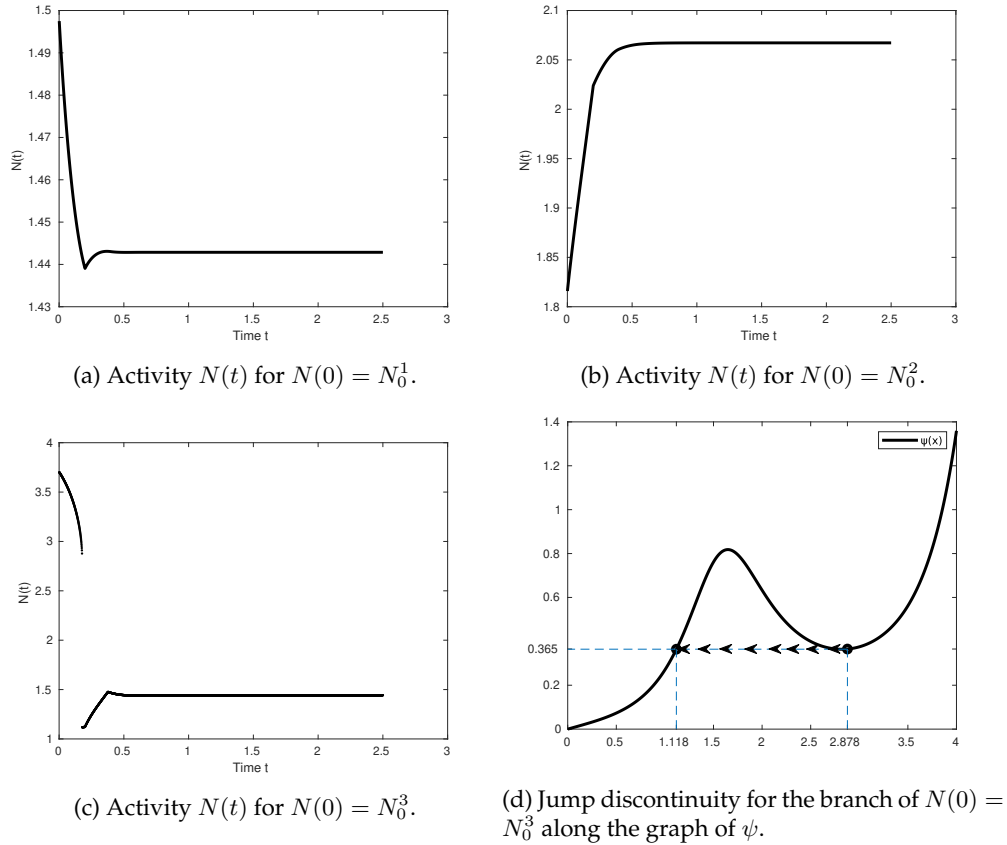
Figure 11: **Example 4.** Activities of solutions with $n_0(s) = \frac{2}{3}(1 + \cos(s))e^{-s}$ for different values of $N(0)$.

Concerning the existence of periodic solutions, it remains open to prove the existence of periodic continuous solutions when p is not locally a linear function and also to find periodic solutions with a period other than a multiple of σ. With respect to stability of periodic orbits, an interesting question would be to determine what kind of piece-wise monotone solutions for the activity are stable in the excitatory case and if exponential convergence to this type of profile arises. We conjecture that the stable solutions correspond to those with few jump discontinuities in general.

Acknowledgements

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