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Wave propagation in discrete media

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Abstract. We have considered infinite systems of nonlinear ODEs on the one-dimensional integer lattice which describes the activity in an excitatorily coupled network of excitable cells. For an ideal nonlinearity, we calculated the speed of propagation of an activity and derived the condition for its existence. We also studied the existence and stability of the traveling wave solution and gave, in the simplest case, its explicit expression. We established that some unstable traveling waves lead to propagation with an enlarging profile defined by a front velocity and a wake velocity. We generalized some results to inhomogeneous medium and network with long range connections.

1. Introduction

In neurophysiology, mathematical models use ordinary differential equations to describe the behavior of an isolated neuron or a network of connected neurons through synapses or gap-junctions. The model developed by Hodking and Huxley [12] is an example of such an ODE system which is thoroughly used and studied. Since then, many other models have been developed, based on the biological description of specific electrical currents in cellular structures, or on a mathematical simplification of complete systems. In the present paper, we study a neural network whose neurons are described by a simplified model motivated by biological data on piriform cortex [3]. Our model is composed of interconnected pairs of excitatory and inhibitory neurons described by :

$$\begin{aligned} v' &= -v + c_{ee}\Phi(v)(u_{eq}^{ee} - v) + c_{ie}\Phi(u)(u_{eq}^{ie} - v) \\ u' &= -u + c_{ei}\Phi(v)(u_{eq}^{ei} - u) \end{aligned} \tag{1}$$

where v and u denote the activity of the excitatory and inhibitory neurons, respectively; the positive coefficients c_{ee}, c_{ie}, c_{ei} describe the synaptic connections between excitatory and inhibitory neurons and $u_{eq}^{ee}, u_{eq}^{ie}, u_{eq}^{ei}$ denote the Nernst potential of ions involved in the synaptic current. We assume that $u_{eq}^{ee} > 0, u_{eq}^{ei} > 0, u_{eq}^{ie} < 0$ (throughout this paper, numerical simulations were carried out with $u_{eq}^{ee} = u_{eq}^{ei} = 100$ and $u_{eq}^{ie} = -20$). The function Φ will be clarified later. Model

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(1) is derived from the study of spatially homogeneous solutions of a cortical network model [21]. Such a model is known as a neural oscillator where each neuron stands for a local population of neurons [13].
We were interested in the activity of the neural network composed of neural oscillators described by equation (1) connected through synaptic coupling. The equations are :

$$\begin{aligned} v_k' &= -v_k + \Big(c_{ee,k}\Phi_k(v_k) + \sum_{j\neq k} c_{j,k}\Phi_k(v_j)\Big)(u_{eq,k}^{ee} - v_k) \\ &\quad + c_{ie,k}\Phi_k(u_k)(u_{eq,k}^{ie} - v_k) \\ u_k' &= -u_k + c_{ei,k}\Phi_k(v_k)(u_{eq,k}^{ei} - u_k) \qquad , k \in \mathbb{Z} \end{aligned} \tag{2}$$

where the parameter of the k^{th} component is indexed by k and $c_{i,j} \geq 0$ describes the synaptic connection from i onto j. It should be noted that homogeneous media is obtained when the k^{th} component does not depend on k. We connect neural oscillators into feed forward arrangement and thus take $c_{i,j} = 0$ for $i \geq j$. This idea of connecting the neuronal population into feed forward arrangement is motivated by biological considerations [1], [8]. Moreover, the choice will make for Φ will imply that backward connections neither affects the front of the wave nor its velocity, but, naturally, its shape.
Our purpose is to study the propagation of an activity in the excitable medium described by (2). More precisely, we investigated an excitatory propagation which switches v_k from a rest potential to a subthreshold value. Since v_k stands for the synchronous activity of neurons, which represents the k^{th} neuronal population, our study deals with the propagation of synchronous activity in neural network. We were particularly interested in solutions that travel at constant velocity with fixed shape, known as traveling wave solutions. There is a vast literature on waves in biological systems, particularly in continuous media with a diffusive coupling. Most papers involve the study of reaction-diffusion equations like the FitzHugh-Nagumo [10], [17], [19], [14] or Fisher-KPP [16], [20] equations. For more references see [18], [11] and [22] for a review of results on front propagation in reaction-diffusion-advection equations. In the present work, propagation appears in a discrete medium and the study is substantially more difficult [15], [23], [24], [5]. For a large class of lattice dynamical systems, existence and stabilty results are obtained in [7], nevertheless our model does not complete their assumptions. Beyond the most elementary properties, it is generally difficult to obtain further results, particularly for heterogeneous media. One approach is to consider idealized nonlinearity for the function Φ [17], [2], [5], [6]. In such a case, system (2) will support explicit calculations which can provide some results on propagation and its failure.
This paper is organized as follows. In section (2), we consider a simple network with nearest neighbor coupling which allows us to introduce some definitions and derive some basic properties. We find the conditions for the existence of propagation and derive an analytical expression for its velocity. Specifically, we study traveling waves and give some stability results in a few simpler cases. In section (3) and (4) we extend some results to inhomogeneous media and long range connection respectively. Section (5) is devoted to a discussion.

2. A simple architecture

We consider a network composed of identical neural oscillators which we will call the components of our network. The components are coupled with their nearest neighbor with the same synaptic connection. We study the infinite system of coupled differential equations:

$$\begin{aligned} v_k' &= -v_k + (c_{ee}\Phi(v_k) + c_r\Phi(v_{k-1}))(u_{eq}^{ee} - v_k) + c_{ie}\Phi(u_k)(u_{eq}^{ie} - v_k) \\ u_k' &= -u_k + c_{ei}\Phi(v_k)(u_{eq}^{ei} - u_k) \qquad , k \in \mathbb{Z} \end{aligned} \tag{3}$$

The lattice differential equation (3) is a nonlinear infinite-dimensional problem and it is generally difficult to obtain rigorous results, apart from elementary properties, for such systems with a general nonlinear function Φ. One approach, is to consider idealized nonlinearities which retain the essential feature of our model. Specifically, we chose:

$$\Phi(x) = H(x - u_{th})$$

where H denotes the Heaviside function :

$$H(x) = \begin{cases} 0, & x < 0, \\ 1, & x > 0 \end{cases}$$

and u_{th} is a so-called "detuning" or threshold parameter. Since Φ is discontinuous, it must be stated what is meant by a solution of equation (3). As described in [5], we consider Φ as a set-valued function :

$\Phi(v)$ is a singleton set if $v \neq u_{th}$
$\Phi(u_{th})$ is the compact interval $[0, 1]$

By a solution of (3), we mean $(v(t), u(t)) \in l^\infty(\mathbb{Z}, \mathbb{R}^2)$ for which each coordinates function $(v_k(t), u_k(t))$ is absolutely continuous, and satisfies the differential inclusion :

$$\begin{aligned} v_k'(t) &\in -v_k + (c_{ee}\Phi(v_k) + c_r\Phi(v_{k-1}))(u_{eq}^{ee} - v_k) + c_{ie}\Phi(u_k)(u_{eq}^{ie} - v_k) \\ u_k'(t) &\in -u_k + c_{ei}\Phi(v_k)(u_{eq}^{ei} - u_k) \end{aligned}$$

A traveling wave solution, denoted t.w.s, with velocity $c > 0$, is a bi-infinite sequence $\{(v_k(t), u_k(t))\}_{k=-\infty}^{+\infty}$, solution of (3), for which there is a couple $(S_e, S_i) \in (C^0(\mathbb{R}, \mathbb{R}))^2$ such that :

$$\begin{aligned} v_k(t) &= S_e(k - ct) \\ u_k(t) &= S_i(k - ct) \end{aligned} \tag{4}$$

The conditions at ∞ will be considered later. We denote $\xi = k - ct$. Substitution of (4) into (3) yields :

$$\begin{aligned} -cS_e'(\xi) &= -S_e(\xi) + (c_{ee}\Phi(S_e(\xi)) + c_r\Phi(S_e(\xi - 1)))(u_{eq}^{ee} - S_e(\xi)) \\ &\quad + c_{ie}\Phi(S_i(\xi))(u_{eq}^{ie} - S_e(\xi)) \\ -cS_i'(\xi) &= -S_i(\xi) + c_{ei}\Phi(S_e(\xi))(u_{eq}^{ei} - S_i(\xi)) \end{aligned} \tag{5}$$

This equation may be considered as a differential equation with a delay. One can make a corresponding characterization of a solution as we did for equation (3). For ξ such that $S_e(\xi) = u_{th}$ (or $S_i(\xi) = u_{th}$) , the derivative $S_e'(\xi)$ ($S_i'(\xi)$) has a jump discontinuity; elsewhere the solution is C^1 and satisfies equation (5) in the classical sense.

We suppose that $\forall k,\ (v_k, u_k) = (v^0, u^0)$ and $(v_k, u_k) = (v^1, u^1)$ are two asymptotically stable fixed points for system (3) (possibly the same). We impose boundary conditions : $\lim_{\xi\to-\infty} S_e(\xi) = v^1$ and $\lim_{\xi\to+\infty} S_e(\xi) = v^0$; similar conditions hold for S_i. In the phase plane (S_e, S_i), these solutions correspond to an heteroclinic or homoclinic orbit.

To determine the fixed points of equation (3), we define four configurations, E_0, E_1, E_2, E_3 which represent a possible fixed point for a given component. Each state stands for a point in $\mathbb{R}^2$:

$$
\begin{aligned}
&E_0 : (0, 0)\\
&E_1 : \begin{cases} \left(\frac{c_{ee}u_{eq}^{ee}}{1+c_{ee}}, \frac{c_{ei}u_{eq}^{ei}}{1+c_{ei}}\right) \\ \left(\frac{c_{ee}u_{eq}^{ee}+c_{ie}u_{eq}^{ie}}{1+c_{ee}+c_{ie}}, \frac{c_{ei}u_{eq}^{ei}}{1+c_{ei}}\right) \end{cases}\\
&E_2 : \left(\frac{c_r u_{eq}^{ee}}{1+c_r}, 0\right)\\
&E_3 : \begin{cases} (v^{1a}, u^{1a}) = \left(\frac{(c_{ee}+c_r)u_{eq}^{ee}}{1+c_{ee}+c_r}, \frac{c_{ei}u_{eq}^{ei}}{1+c_{ei}}\right) \\ (v^{1b}, u^{1b}) = \left(\frac{(c_{ee}+c_r)u_{eq}^{ee}+c_{ie}u_{eq}^{ie}}{1+c_{ee}+c_r+c_{ie}}, \frac{c_{ei}u_{eq}^{ei}}{1+c_{ei}}\right) \end{cases}
\end{aligned}
$$

We give a specific notation for E_3 since it plays an important part in t.w.s characterization. Let us define three boolean conditions C_1, C_2, C_3 associated with the states E_1, E_2, E_3 which ensure the existence of the corresponding fixed point:

$$
\begin{aligned}
&C_1 : \begin{cases} \frac{c_{ee}u_{eq}^{ee}}{1+c_{ee}} > u_{th} & \text{if } c_{ei} < \frac{u_{th}}{u_{eq}^{ei}-u_{th}} \\ \frac{c_{ee}u_{eq}^{ee}+c_{ie}u_{eq}^{ie}}{1+c_{ee}+c_{ie}} > u_{th} & \text{otherwise} \end{cases}\\
&C_2 : \frac{c_r u_{eq}^{ee}}{1+c_r} < u_{th}\\
&C_3 : \begin{cases} v^{1a} > u_{th} & \text{if } c_{ei} < \frac{u_{th}}{u_{eq}^{ei}-u_{th}} \\ v^{1b} > u_{th} & \text{otherwise} \end{cases}
\end{aligned}
$$

The predicate "C_i=true" means "E_i could be taken as a possible fixed point for the component in the chain". Let us consider the graph G depicted in Fig. 1. Given an initial state $s_0 \in G$, we call a trajectory of graph G a double infinite sequence $(\ldots, s_{-k}, \ldots, s_{-1}, s_0, s_1, ..., s_k, ...)$ obtained as follows : according to conditions $(C_i)_{i=1,2,3}$, increasing indexes in the sequence are given by following the black arrows and the decreasing indexes in the sequence are given by following the reverse way in Fig. 1. The following proposition holds:

Proposition 1. *A fixed point of system (3) is a trajectory of graph G. All fixed points are stable.*

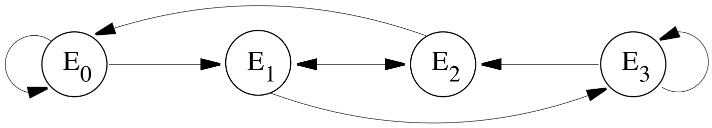

Fig. 1. Graph G to calculate fixed points.

Proof. Taking $\Phi(x) = H(x - u_{th})$ in equation (3) yields the first part of the proposition. Near a fixed point, the system (3) is :

$$v_k'(t) = -v_k(t) + \alpha_k(u_{eq}^{ee} - v_k(t)) + \beta_k(u_{eq}^{ie} - v_k(t))$$
$$u_k'(t) = -u_k(t) + \gamma_k(u_{eq}^{ei} - u_k(t))$$

where $(\alpha_k, \beta_k, \gamma_k) \in \mathbb{R}_+^3$. Hence, the result follows. $\square$

Before investigating t.w.s, we studied the general case of the propagation of an excitatory activity. Initially the system (3) is in its resting state defined as : $\forall k, (v_k(0), u_k(0)) \in E_0$ which reads $v_k(0) = u_k(0) = 0$. It can be seen that the domain $\left\{[\frac{c_{ie}u_{eq}^{ie}}{1+c_{ie}}, u_{th}] \times [0, u_{th}]\right\}_k$ belongs to the domain of attraction of $\{0, 0\}_k$. We prove the following result:

Theorem 1. *A necessary condition for a propagation of excitatory activity is*

$$c_r > \frac{u_{th}}{u_{eq}^{ee} - u_{th}} \tag{6}$$

If $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$*, this condition is sufficient.*
When propagation occurs, the speed of the propagation is :

$$c = \frac{1 + c_r}{\ln\left(\frac{c_r u_{eq}^{ee}}{c_r(u_{eq}^{ee} - u_{th}) - u_{th}}\right)}. \tag{7}$$

Proof. An activity emerges in the network if there is a time t^* and an index i such that $v_i(t^*) > u_{th}$. We may assume, without loss of generality, that $t^* = 0$ and $i = 1$. Let $t_1 \in \overline{\mathbb{R}_+}$ be such that :

$$\forall t \in [0, t_1], v_1(t) > u_{th}$$

Through the synaptic coupling c_r, this component excites a second one. Let v_2 be the activity of this second component such that $(v_2(0), u_2(0)) = (0, 0)$. The excitation propagates if there is $\tilde{t} = \inf\{t,\ v_2(t) > u_{th}\}$.
For $t < t_1$ and while $v_2(t) < u_{th}$, we have:

$$v_2(t) = \frac{c_r u_{eq}^{ee}}{1 + c_r}(1 - e^{-(1+c_r)t})$$

Then a necessary condition for propagation is $\frac{c_r u_{eq}^{ee}}{1+c_r} > u_{th}$ which gives the condition (6). Under this condition, we obtain $\tilde{t} = \frac{1}{c}$ which yields (7). The propagation of the excitation is achieved if $t_1 \geq \frac{1}{c}$. This condition is still fulfilled when the excitatory activity is greater than u_{th} in the wake of the front. If (6) holds and if $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$, we have $v^{1a} > u_{th}$ which implies that E_3 is a fixed point. Then a solution which connects $(0,0)$ to (v^{1a}, u^{1a}) satisfies the condition $t_1 \geq \frac{1}{c}$. In the next paragraph, we give an explicit expression for such a solution which corresponds to a particular t.w.s . $\square$

Remark (1) : From the proof, the quantity $\frac{1}{c}$ represents the necessary time for an excitatory population to reach u_{th}. Moreover, for a t.w.s, we have : $u_k(t+\frac{1}{c}) = u_{k-1}(t)$ for all k and t.
Remark (2) : If we excite the excitatory population through an external input, i_s, we find the same condition (6) by changing c_r into i_s.
Remark (3) : In the case $c_r < \frac{u_{th}}{u_{eq}^{ee} - u_{th}}$, no propagation can occur all over the network ; this phenomenon is reported as "propagation failure" [15].
Note that the velocity of a propagation does not depend on its shape; solitary pulse or multiple pulse wave have the same speed. Moreover the velocity is given by initial excitation front and is independent of the inhibition. For large connection strength, expression (7) yields to a linear relationship between speed and synaptic strength. A simple calculation gives:

$$c = \frac{1+c_r}{\ln\left(\frac{u_{eq}^{ee}}{u_{eq}^{ee}-u_{th}}\right)} - \frac{u_{th}}{(u_{eq}^{ee}-u_{th})\left(\ln\left(\frac{u_{eq}^{ee}}{u_{eq}^{ee}-u_{th}}\right)\right)^2} + \epsilon\left(\frac{1}{c_r}\right)$$
$$\text{where} \lim_{c_r \to +\infty} \epsilon\left(\frac{1}{c_r}\right) = 0$$

For small c_r an asymptotic expansion is not relevant since no propagation occurs. We then turn to t.w.s . First, we define more precisely the boundary conditions. We suppose that c_r satisfies (6). Then the condition C_3 is still fulfilled if $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$. From graph G (Fig. 1), the two configurations E_0 and E_3 are of particular interest since only these two configurations are directly connected to themselves. These states define spatially homogeneous elements $(v_k, u_k)_k \in l^\infty(\mathbb{Z}, \mathbb{R}^2)$ by :

$$v_k = u_k = 0 \quad \forall k \in \mathbb{Z}$$
and
$$v_k = \begin{cases} v^{1a} \text{ if } c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - uth} \\ v^{1b} \quad elsewhere \end{cases}, \; u_k = \frac{c_{ei} u_{eq}^{ei}}{1+c_{ei}}, \quad \forall k \in \mathbb{Z}$$

which are stable equilibrium solutions of (3). Then it is natural to impose the boundary condition

$$\lim_{\xi \to +\infty} S_e(\xi) = 0$$
$$\lim_{\xi \to +\infty} S_i(\xi) = 0 \tag{8}$$

The existence of two stable homogeneous states, incites us to consider two types of t.w.s specified in the following statement:

Definition 1. *Wave of type I is a t.w.s such that :* $\begin{cases} \lim\limits_{\xi \to -\infty} S_e(\xi) = 0 \\ \lim\limits_{\xi \to -\infty} S_i(\xi) = 0 \end{cases}$

Wave of type II is a t.w.s such that : $\begin{cases} \lim\limits_{\xi \to -\infty} S_e(\xi) = v^{1a} \text{ or } v^{1b} \\ \lim\limits_{\xi \to -\infty} S_i(\xi) = u^{1a} \text{ or } u^{1b} \end{cases}$

One expects to find wave of type II in bistable medium. More precisely, from theorem 1, the following proposition holds:

Proposition 2. *A wave of type II exists if* $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$. *Otherwise a necessary and sufficient condition for its existence is* $v^{1b} > u_{th}$

We recall that the condition that there be a wave of type I is that the time during which $S_e > u_{th}$ is greater than $\frac{1}{c}$, with c given by (7). Let us examine some simple waves which verify the following property :

Property 1. There are at most two values of ξ such that $S_e(\xi) = u_{th}$.

When property 1 is fulfilled, three cases are possible : standing wave (there is no value for ξ such that $S_e(\xi) = u_{th}$), traveling front (one value such that $S_e(\xi) = u_{th}$) and traveling pulse (two values such that $S_e(\xi) = u_{th}$). We define $(\xi^e_{max}, \xi^e_{min}) \in [-\infty, +\infty]^2$ such that $\xi^e_{max} = \min\{\xi \ : \ S_e(\xi) = u_{th}\}$ and $\xi^e_{min} = \min\{\xi \ : \ \xi > \xi^e_{max}$ and $S_e(\xi) = u_{th}\}$. Because of the translation invariance of t.w.s we may choose $\xi^e_{max} = 0$. Then, type II wave is obtained when $\xi^e_{min} = -\infty$. However, the condition that there be a type I reads $\xi^e_{min} < -1$. To go further, we see that the wave front is given by :

$$\xi \geq 1 : \begin{cases} S_e(\xi) = 0 \\ S_i(\xi) = 0 \end{cases} ; \quad 0 \leq \xi \leq 1 : \begin{cases} S_e(\xi) = (u_{th} - \frac{c_r u_{eq}^{ee}}{1+c_r}) e^{\frac{1+c_r}{c}\xi} + \frac{c_r u_{eq}^{ee}}{1+c_r} \\ S_i(\xi) = 0 \end{cases} \tag{9}$$

where we assume that $\xi^e_{min} \leq -1$; otherwise there is no wave since the continuity of the solution at $\xi = \xi^e_{min} + 1$ cannot be to obtained. Such a wave is reported as a traveling excitation of sharp type since $S_e'(1^+) = 0$ and $S_e'(1^-) \neq 0$. Using the continuity of S_e at $\xi = 1$ and writing $S_e(0) = u_{th}$, we again find formula (7) for the wave speed and the necessary condition of existence (6). c is evaluated from the wave front and its value does not depend on (v_1, u_1). Relations (9) give the general expression for an excitatory propagation even if it does not correspond to a t.w.s $\{S_e(j - ct), S_i(j - ct)\}_j$.
We explicitly calculate in the appendix all possible cases for the t.w.s which verify property 1. This is illustrated in Fig. 2a–f.
Remark (1) : For waves of type I, the retrieval time is parameterized by the wave speed c. More precisely, the time for halving the activities is $c \ln 2$.
Remark (2) : The different expressions found for the wave equation in the appendix underline the importance of the potential parameters $u_{eq}^{ee}, u_{eq}^{ie}, u_{eq}^{ei}$ associated with the weight into the following combinations: (c_r, u_{eq}^{ee}), (c_{ee}, u_{eq}^{ee}), $(c_{ee} + c_r, u_{eq}^{ee})$,

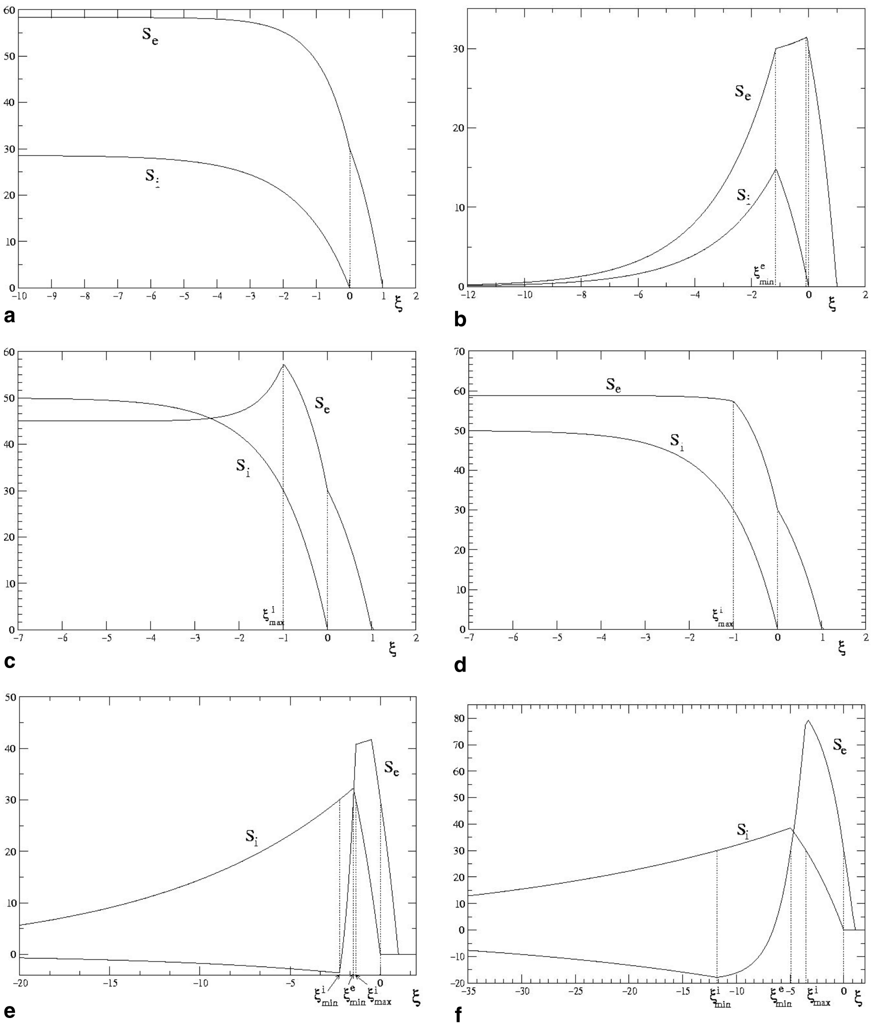

Fig. 2a–f. The different shapes of t.w.s $(v_k(t), u_k(t)) = (S_e(k - ct), S_i(k - ct))$. The dotted lines represent the characteristic points underlined in the wave analysis. The threshold, u_{th}, is equal to 30 and parameters $(c_r, c_{ee}, c_{ie}, c_{ei})$ are equal to $(1, 0.4, 0.4, 0.4)$ (**a** and **b**), $(1, 1, 1, 1)$ (**c**), $(1, 1, 0.3, 1)$ (**d**), $(4, 0.5, 15, 3)$ (**e**), $(10, 2, 15, 3)$ (**f**). These wave patterns correspond to the different kinds of t.w.s obtained from equation (5). The derivation of these solutions is given in the appendix.

(c_{ei}, u_{eq}^{ie}), (c_{ei}, u_{eq}^{ei}) and $(1, 0)$ (the last one corresponds to the relaxation dynamics). The difference between the barycentre of some of them and u_{th} give the classification of the different wave behavior obtained in the appendix.

From the appendix, we note that although cases 1 and 2 are exclusive, subcases 1.1 and 1.2 or 2.1, 2.2 and 2.2 may occur simultaneously (see Fig. 2a and Fig. 2b). This means that bistable medium supports traveling front, which is not surprising,

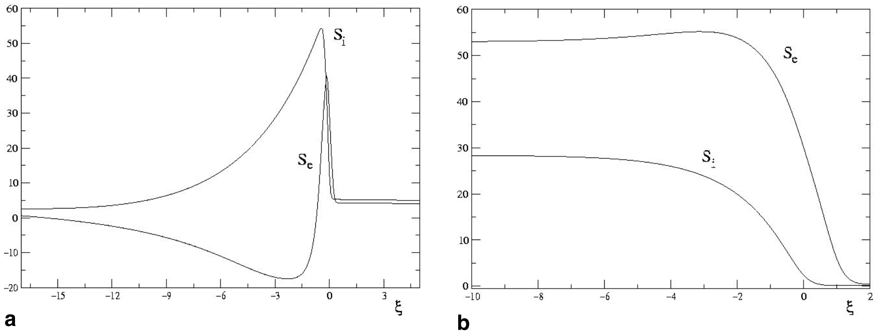

Fig. 3a, b. Traveling wave solution with: $\Phi(x) = \frac{1}{1+e^{\lambda(x-u_{th})}}$; $u_{th} = 30$, $\lambda = 0.2$. Parameters $(c_r, c_{ee}, c_{ie}, c_{ei})$ are equal to (5, 6, 10, 10) (**a**), (1, 0.4, 0.4, 0.4) (**b**). This figure illustrates continuous t.w.s similar to those depicted Fig. 2a.

but it also supports traveling pulse. It is also noted that for waves of type II (i.e $\xi^e_{min} = -\infty$) the traveling wave is not necessarily monotone (see Fig. 2c).
One may wonder what happens in a more regular case for the function Φ. Numerical simulations show that similar t.w.s occurs. In Fig. 3a, Fig. 3b, we depicted the wave of type I and type II, respectively, obtained for $\Phi(x) = \frac{1}{1+e^{\lambda(x-u_{th})}}$. It can be shown that these solutions are C^∞.

Depending on initial conditions and parameters, more complex waves may appear. Such waves do not verify property (1) since there are more than two values for ξ such that $S_e = u_{th}$ (or $S_i = u_{th}$). In these configurations, an oscillatory behavior in the wake of the wave (Fig. 4a) or multiple pulses (three pulses in Fig. 4b) occur. In Fig. 4a the excitation of the inhibitory population allows it to reach u_{th}. However, since c_{ei} is close to $\frac{u_{th}}{u^{ei}_{eq}-u_{th}}$, the inhibitory population does not retain a high activity level and cannot inhibit the excitatory population enough. Therefore no second pulse occurs. In Fig. 4b, inhibition is strong enough to produce wave trains and other numerical simulations reveal periodic wave trains. The relative strength of the parameter c_{ie} implies a fast recovery time which gives birth to complex wave patterns.

Moreover, apart from the cases studied, there are propagations which are not t.w.s. Such propagations present a profile that evolves during time. We obtain the following results :

Proposition 3. – *For $c_{ei} < \frac{u_{th}}{u^{ee}_{eq}-u_{th}}$, wave of type I is unstable. In this case, there is a propagation of a "growing pulse" such that (i) the velocity of the front is given by (7) and (ii) the velocity of the wake is asymptotically given by :*

$$\tilde{c} = \frac{1 + c_{ee}}{\ln\left(\frac{v^{1a}-v^{1c}}{u_{th}-v^{1c}}\right)} \tag{10}$$

where $v^{1c} = \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}}$

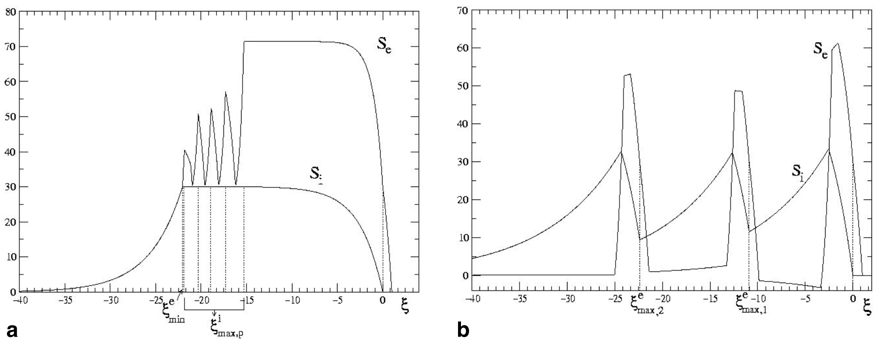

Fig. 4a, b. Complex wave pattern. Parameters $(c_r, c_{ee}, c_{ie}, c_{ei})$ are equal to : (1.5, 1, 4, 0.43) (**a**), (3, 1, 10, 1.5) (**b**). In **a**, the equality $S_i = u_{th}$ is verified ten times, for $\xi \in [-24, -15]$. We only represent the ones where $S_i' > 0$. In **b**, there are six values for ξ such that $S_e = u_{th}$ (and $S_i = u_{th}$). We represent three of them, 0, $\xi^e_{max,2}$, $\xi^e_{max,3}$, which correspond to $S_e' > 0$.

– *For $c_{ei} > \frac{u_{th}}{u^{ee}_{eq} - u_{th}}$, there is c_r^* such that : $\forall c_r > c_r^*$, wave of type I does not exist . In this case, there is a propagation of a "growing pulse" such that (i) the velocity of the front is given by (7) and (ii) the velocity of the wake is asymptotically given by :*

$$\tilde{c} = \frac{1 + c_{ee} + c_{ie}}{\ln\left(\frac{v^{1b} - v^{1d}}{u_{th} - v^{1d}}\right)} \tag{11}$$

where $v^{1d} = \frac{c_{ee}u^{ee}_{eq} + c_{ie}u^{ie}_{eq}}{1 + c_{ee} + c_{ie}}$

Proof. We are interested in propagation corresponding to a single pulse. Let us introduce Δ_k the time during which $v_k(t) > u_{th}$. First, we note that for a wave of type I, one must have $\forall k,\ \Delta_k = \Delta_0$. Let t_k be the time at which v_k returns to u_{th}. From theorem 1, we have :

$$t_k = \Delta_k + \frac{k}{c}$$

Let us consider the case $c_{ei} < \frac{u_{th}}{u^{ee}_{eq} - u_{th}}$. The inhibitory population does not affect the excitatory one and we have :

$$\begin{aligned} &\text{for } t \in [\tfrac{k}{c}, t_{k-1}],\quad v_k(t) = (u_{th} - v^{1a})e^{-(1+c_r+c_{ee})(t-\frac{k}{c})} + v^{1a} \\ &\text{for } t \in [t_{k-1}, t_k],\ v_k(t) = (u_{th} - \tfrac{c_{ee}u^{ee}_{eq}}{1+c_{ee}})e^{-(1+c_{ee})(t-t_k)} + \tfrac{c_{ee}u^{ee}_{eq}}{1+c_{ee}} \end{aligned}$$

Such a propagation exists if $\frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}} < u_{th}$. The continuity of v_k at t_{k-1} gives the recurrence formula :

$$\Delta_k = f(\Delta_{k-1})$$

where:

$$f(x) = x + \frac{1}{1 + c_{ee}} \ln\left(\frac{(u_{th} - v^{1a})e^{-(1+c_r+c_{ee})(x-\frac{1}{c})} + v^{1a} - \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}}}{u_{th} - \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}}}\right) - \frac{1}{c}$$

for a given $\Delta_0 > \frac{1}{c}$ and $k \geq 1$. As already mentioned, no propagation occurs when $\Delta_0 < \frac{1}{c}$.
Let

$$\Delta^* = \frac{1}{c} + \frac{1}{1+c_{ee}+c_r} \ln \left(\frac{(1+c_{ee})(v^{1a}-u_{th})}{(c_{ee}u^{ee}_{eq} - (1+c_{ee})u_{th})e^{\frac{1+c_{ee}}{c}} + (1+c_{ee})v^{1a} - c_{ee}u^{ee}_{eq}} \right)$$

Note that Δ^* is well defined and one has $\Delta^* > \frac{1}{c}$.
Taking $\Delta_0 = \Delta^*$ yields $\forall k,\ \Delta_k = \Delta^*$. This solution corresponds to a wave of type I. It remains to be checked that this solution is unstable. Consider the function $g(x) = f(x) - x$. It is seen that g is strictly increasing and $g(\Delta^*) = 0$. This implies:

$$\begin{array}{l} \text{Let } \Delta_0 = \Delta^* + \delta \\ \text{if } \delta > 0,\ \lim\limits_{k \to +\infty} \Delta_k = +\infty \\ \text{if } \delta < 0,\ \lim\limits_{k \to +\infty} \Delta_k = -\infty \end{array}$$

Then the wave of type I is unstable. If $\delta > 0$, a propagation with a profile that evolves during time occurs. To be more precise, let $s_k = g(\Delta_{k-1})$. This quantity represents the increase of excitation duration from component $k-1$ to component k. We have

$$\lim_{k \to +\infty} s_k = \tilde{s} = \frac{1}{1+c_{ee}} \ln \left(\frac{v^{1a} - \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}}}{u_{th} - \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}}} \right) - \frac{1}{c}$$

The speed of the recovery is asymptotically given by $\tilde{c} = \frac{1}{\tilde{s}+\frac{1}{c}}$.
The point (i) follows from theorem 1.
We consider the case $c_{ei} > \frac{u_{th}}{u^{ei}_{eq}-u_{th}}$. With the same notations, we have :

$$\Delta_k = \Delta_{k-1} + g(\Delta_{k-1})$$

where:

$$g(x) = \frac{1}{1+c_{ee}+c_{ie}} \ln \left(\frac{\mu e^{-(1+c_r+c_{ee}+c_{ie})x} + v^{1b} - v^{1d}}{u_{th} - v^{1d}} \right) - \frac{1}{c}$$

with:

$$\mu = \left(v^{1a} - v^{1b} + (u_{th} - v^{1a})(1 - \frac{u_{th}}{u^{1b}})^{\frac{1+c_{ee}+c_r}{1+c_{ei}}} \right) e^{(1+c_r+c_{ee}+c_{ie})(\frac{1}{c} + \frac{1}{1+c_{ei}} \ln \frac{u^{1b}}{u^{1b}-u_{th}})}$$

We assumed that $t_{k-1} - \frac{k}{c} > \frac{1}{1+c_{ei}} \ln(\frac{u^{1b}}{u^{1b}-u_{th}})$ (the other case is similar). This condition ensures that the inhibitory population of the k^{th} component is excited before the excitatory population of component $k-1$ returns below u_{th}.
Let Δ^* be such that $g(\Delta^*) = 0$ (this case corresponds to a t.w.s). Then Δ^* verifies:

$$\mu e^{-(1+c_r+c_{ee}+c_{ie})\Delta^*} = (u_{th} - v^{1d})e^{\frac{1+c_{ee}+c_{ie}}{c}} + v^{1d} - v^{1b}$$

Since $\mu > 0$ and $v^{1d} - v^{1b} < 0$, Δ^* does not exist for large c_r. Therefore, there is c_r^* such that for $c_r > c_r^*$, t.w.s of type I do not exist. Moreover, from the variation of f it can be obtained that: $\lim_{k \to +\infty} \Delta_k = +\infty$. Taking the limits of g gives expression (11) $\square$

Remark (1) : Let us examine the case where $c_{ei} > \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$ and Δ^* exists. We calculate :

$$g'(\Delta^*) = -\frac{1 + c_r + c_{ee} + c_{ie}}{1 + c_{ee} + c_{ie}} \left(1 + \frac{v^{1d} - v^{1b}}{u_{th} - v^{1d}} e^{-\frac{1+c_{ee}+c_{ie}}{c}} \right)$$

Since $-2 < g'(\Delta^*) < 0$, therefore Δ^* is a stable fixed point of the discrete iteration.

Remark (2) : From the above proposition, and given a time $t > 0$, the number of excited components is given by : $E(ct) - E(\tilde{c}t)$, where $E(x)$ is the integer part of x.

We note that the inhibitory population allows a stable type I wave. However, when the effect of the inhibitory population is absent, or for a large synaptic connection, propagation with an enlarging profile appears. In other words, traveling pulse tends toward a stable traveling front.

3. Inhomogeneous excitable medium

From the above study, we generalized some of the results to a network composed of disparate components connected through different synaptic connections strength. The integer k indexes the parameters of the k^{th} component and we note c_k the connection strength from $k-1$ onto k. We studied the infinite dimensional system:

$$\begin{aligned} v_k' &= -v_k + (c_{ee,k}\Phi_k(v_k) + c_k \Phi_k(v_{k-1}))(u_{eq,k}^{ee} - v_k) \\ &\quad + c_{ie,k}\Phi_k(u_k)(u_{eq,k}^{ie} - v_k) \\ u_k' &= -u_k + c_{ei,k}\Phi_k(v_k)(u_{eq,k}^{ei} - u_k) \qquad , k \in \mathbb{Z} \end{aligned} \tag{12}$$

where $\Phi_k(x) = H(x - u_{th,k})$ and $\forall k,\ (v_k(0), u_k(0)) = (0, 0)$.

The constraints on parameters are $u_{th,k}^{ie} < 0$, $0 < u_{th,k} < u_{eq,k}^{ee}$ and $u_{th,k} < u_{eq,k}^{ei}$.

We easily generalize proposition 1 by indexing the parameters in the definition of E_i and C_i and we note (v_k^{1a}, u_k^{1a}) , (v_k^{1b}, u_k^{1b}) the two points previously introduced. The following theorem can be proved:

Theorem 2. *A necessary condition for an excitatory propagation to exist reads :*

$$\forall k, \quad c_k > \frac{u_{th,k}}{u_{eq,k}^{ee} - u_{th,k}} \tag{13}$$

If $\forall k,\ c_{ei,k} < \frac{u_{th,k}}{u_{eq,k}^{ei} - u_{th,k}}$ *this condition is sufficient.*

When propagation occurs, the necessary time to cross n *components* $\{1, .., n\}$ *is :*

$$t_n = \sum_{k=1}^{k=n-1} \frac{1}{1 + c_k} \ln \Big(\frac{c_k u_{eq,k}^{ee}}{c_k(u_{eq,k}^{ee} - u_{th,k}) - u_{th,k}} \Big) \tag{14}$$

Proof. This can be obtained following a method similar to that given in theorem 1. We note that the time t_k for the component indexed by k for reaching $u_{th,k}$ is given by :

$$\frac{c_k u^{ee}_{eq,k}}{1+c_k}(1-e^{-(1+c_k)t_k}) = u_{th,k}$$

and then $t_n = \sum_{k=1}^{k=n-1} t_k$. □

Looking for t.w.s is not relevant since the medium is nonhomogeneous. We then generalize definition 1:

Definition 2. *A propagation of type II is a propagation of an excitatory activity which connects* $\{(0,0)\}_k$ *to* $\{(v^1_k, u^1_k)\}_k$ *with* $v^1_k > u_{th,k}$

For the sake of simplicity we do not consider the case where there is k such that $v^1_k < u_{th,k}$. For the two cases :

$$\begin{array}{lll} \text{Case } (a) & \forall k, & c_{ei,k} < \frac{u_{th,k}}{u^{ei}_{eq,k}-u_{th,k}} \\ \text{Case } (b) & \forall k, & c_{ei,k} > \frac{u_{th,k}}{u^{ei}_{eq,k}-u_{th,k}} \end{array}$$

we derive the following proposition :

Proposition 4. *In case (a), propagation of type II still exists; in case (b) a necessary and sufficient condition for propagation reads :* $\forall k,\ v^{1b}_k > u_{th,k}$

Proof. Since we are interested in propagation of type II, let $(k-1)$ be a component such that $\forall t > 0,\ v_{k-1}(t) > u_{th}$. In the proof of theorem 2, we have shown that there is t_k such that $v_k(t_k) = u_{th,k}$ (with $v_k(0) = 0$). We shall show that $\forall t > t_k,\ v_k(t) > u_{th,k}$; and proposition 4 will then follow by induction.
For $t \geq t_k$ and while $u_k(t) < u_{th,k}$, the k^{th} component verifies :

$$\begin{aligned} v'_k(t) &= -v_k(t) + (c_{ee,k} + c_k)(u^{ee}_{eq,k} - v_k) \\ u'_k(t) &= -u_k(t) + c_{ei,k}(u^{ei}_{eq,k} - u_k) \end{aligned}$$

which gives, by integration:

$$\begin{aligned} v_k(t) &= (u_{th,k} - v^{1a}_k)e^{-(1+c_{ee,k}+c_k)(t-t_k)} + v^{1a}_k \\ u_k(t) &= u^{1a}_k(1 - e^{-(1+c_{ei,k})(t-t_k)}) \end{aligned}$$

In case (a), we obtain $\forall t \geq 0,\ u_k(t) < u_{th,k}$ and $\lim_{t\to+\infty} v_k(t) = v^{1a,k}$. Since (13) holds and $u^{ee}_{eq,k} > u_{th,k}$ we have $v^{1a}_k > u_{th,k}$ and thus we have determined a propagation which connects $(0,0)_k$ to (v^{1a}_k, u^{1a}_k).
In case (b) there is t'_k such that $u_k(t'_k) = u_{th,k}$ and for $t \geq t'_k$, we have :

$$v_k(t) = r_k e^{-(1+c_k+c_{ee,k}+c_{ie,k})t} + v^{1b}_k$$

The continuity of $v_k(t)$ at $t = t'_k$ gives r_k.
We show that $v_k(t)$ is monotone on $[t'_k, +\infty[$ and since $\lim_{t\to+\infty} v_k(t) = v^{1b,k} > u_{th,k}$, it is derived that $\forall t > t_k$, $v_k(t) > u_{th,k}$. We have thus determined a propagation of type II which connects $(0,0)_k$ to $(v^{1b}_k, u^{1b}_k)_k$. □

4. Long range connection

In this part, we study the case where there is more than one connection from one component to another. We go back to a homogeneous chain and we place our study in the general framework where a component may be connected to p others through identical connection strengths $c_1, c_2, \dots, c_p$. The equations are :

$$\begin{aligned} -cS_e'(\xi) &= -S_e(\xi) + c_{ie}\Phi(S_i(\xi))(u_{eq}^{ie} - S_e(\xi)) + (c_{ee}\Phi(S_e(\xi)) \\ &\quad + c_1\Phi(S_e(\xi-1)) + c_2\Phi(S_e(\xi-2)) \\ &\quad + \dots + c_p\Phi(S_e(\xi-p)))(u_{eq}^{ee} - S_e(\xi)) \\ -cS_i'(\xi) &= -S_i(\xi) + c_{ei}\Phi(S_e(\xi))(u_{eq}^{ei} - S_i(\xi)) \end{aligned} \tag{15}$$

For the reasons previously given, a necessary condition of wave existence reads $\xi_{min}^e < -1$. For simplicity, we assume that $\xi_{min}^e < -p$. Such an assumption also includes the case of type II wave which verifies $\xi_{min}^e = -\infty$. Let us define $S_j = 1 + \sum_{r=j}^{p} c_r$ and $S_{p+1} = 1$. The following general theorem is then proved :

Theorem 3. *A necessary condition for the existence of an excitatory propagation is:*

$$\left(1 - \frac{1}{S_1}\right) u_{eq}^{ee} > u_{th} \tag{16}$$

If $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$ this condition is sufficient. For type II wave, the wave speed is given by solving :

$$-\sum_{k=1}^{p} \frac{c_k u_{eq}^{ee}}{S_k S_{k+1}} e^{\frac{1}{c}(-kS_k - \sum_{r=1}^{k-1} r c_r)} = u_{th} - \left(1 - \frac{1}{S_1}\right) u_{eq}^{ee} \tag{17}$$

Equation (17) admits a solution if and only if (16) holds.

Proof. Let $1, \dots p+1$ the indexes of the components such that

$$\forall i \in \{1, \dots, p\}, \forall t > 0,\ v_i(t) > u_{th} \text{ and } v_{p+1}(0) = 0$$

While $v_{p+1}(t) < u_{th}$:

$$v_{p+1}(t) = (1 - \frac{1}{S_1}) u_{eq}^{ee} (1 - e^{-S_1 t})$$

Then, there is t_{p+1} such that $v_{p+1}(t_{p+1}) = u_{th}$ if and only if $(1 - \frac{1}{S_1}) u_{eq}^{ee} > u_{th}$ this gives (16). If $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$, we have :

$$\forall t > t_{p+1}, v_{p+1}(t) = (u_{th} - (1 - \frac{1}{S_1}) u_{eq}^{ee}) e^{-S_1(t - t_{p+1})} + (1 - \frac{1}{S_1}) u_{eq}^{ee}$$

and then $\forall t > t_{p+1},\ v_{p+1}(t) > u_{th}$. By induction, it is proved that a propagation of type II still exists.

For the second part, we turn to equation (15) and calculate the wave expression for $\xi \geq 0$:

$$\begin{aligned}&\text{for } i-1 \leq \xi \leq i :\\ &S_e(\xi) = \lambda_i e^{\frac{1+c_i+\cdots+c_p}{c}\xi} + \frac{c_i+\cdots+c_p}{1+c_i+\cdots+c_p} u_{eq}^{ee}\\ &\text{where } i \in \{1, .., p\}\end{aligned}$$

The continuity of S_e at i leads to the recurrent formula for λ_i :

$$\begin{aligned}\lambda_p &= -\frac{c_p u_{eq}^{ee}}{1+c_p} e^{-\frac{1+c_p}{c}p}\\ \lambda_i &= -\frac{c_i u_{eq}^{ee}}{S_i S_{i+1}} e^{-\frac{S_i}{c}i} + \lambda_{i+1} e^{-\frac{ic_i}{c}}\end{aligned}$$

and we deduce:

$$\lambda_1 = -\sum_{k=1}^{p} \frac{c_k u_{eq}^{ee}}{S_k S_{k+1}} e^{\frac{1}{c}(-kS_k - \sum\limits_{r=1}^{k-1} r c_r)}$$

Using $S_e(0) = u_{th}$, we infer that the wave speed c is given by solving the equation:

$$f(\frac{1}{c}) = -\sum_{k=1}^{p} \frac{c_k u_{eq}^{ee}}{S_k S_{k+1}} e^{\frac{1}{c}(-kS_k - \sum\limits_{r=1}^{k-1} r c_r)} = u_{th} - (1 - \frac{1}{S_1}) u_{eq}^{ee}$$

The function f is strictly increasing, continuous and satisfies $\forall x,\ f(x) < 0$, $\lim\limits_{x\to+\infty} f(x) = 0$. Using $c_k = S_k - S_{k+1}$, we calculate :

$$f(0) = -u_{eq}^{ee} \sum_{k=1}^{p} \frac{1}{S_{k+1}} - \frac{1}{S_k} = -u_{eq}^{ee}(1 - \frac{1}{S_1})$$

this implies $f(0) < u_{th} - (1 - \frac{1}{S_1}) u_{eq}^{ee}$. Then c exists if and only if $\frac{S_1 - 1}{S_1} u_{eq}^{ee} > u_{th}$. In this case, c is unique. □

We note that the front of the wave is monotone since, from the proof of theorem 3 $\forall i \in \{1, \ldots, p\}$, $\lambda_i < 0$.

5. Discussion

Our study was devoted to excitatory propagation in a neural network with discrete components. Specifically, we investigated traveling wave solutions which leads to a nonlinear differential difference equation. For a general nonlinearity, our model appears to be mathematically intractable and we then considered an idealized nonlinearity. We derived conditions for the existence of propagation and found the general expression for its velocity. In some simple cases, we gave the explicit expression of traveling wave solutions and the necessary and sufficient conditions for their existence. We found that traveling pulse and traveling front can coexist in a bistable medium. Moreover, under some conditions, we showed that some traveling pulses are unstable and lead to a propagation with two distinct velocities: one for the front and one for the wake. Asymptotically, such a wave solution tends towards

a traveling front. We found other interesting phenomena such as: (i) a sharp initial profile which did not allow further propagation, (ii) an inhibitory population which allowed stabilization of the traveling wave solution in some conditions. We generalized some results for inhomogeneous medium and long range connections.
Although much work has been done on continuous models, some results are already known concerning traveling waves for discrete equations. Most of them concern the discrete Nagumo equation [15], [23], [24]. Discrete models present a much richer and more complex set of dynamical phenomena than would occur in the continuous counterpart. Specifically, they give rise to : (i) propagation failure, (ii) threshold properties and (iii) bounds for the propagation velocity. Analytical results can be obtained following different techniques : (i) averaging or perturbation method [6], [9], which allows a reduction of a complex system into a simpler one, (ii) use of an idealized nonlinearity (typically the Heaviside function) , which allows direct calculations and (iii) a specific form for the synaptic gating variables. In our work, we used a Heaviside function and an analogous approach is to take a synaptic gating variables of the form $s_k(t) = \chi_{[\frac{k}{c},\frac{k}{c}+\alpha]}(t)$, where c is the velocity of the wave, α its duration and χ is the characteristic function. All these approaches show that the velocity is well approximated by the initial excitation front and is rather independant of the inhibition [9]. We reported similar results and have shown that the velocity of the propagation depends on the integration rise time from resting potential to threshold and does not depend on the global shape of the wave. As already reported [15], [9], [4], we showed that (i) propagation occurs if the synaptic weight of neuronal interactions exceeds some threshold, (ii) for strong coupling, velocity scales linearly with the coupling strenght , and (iii) multiple wave patterns can propagate for the same set of parameter values.
The study of traveling wave on a discrete lattice leads to a mixed type differential equation. Development of the theory of such equations may provide insight into the study of traveling wave for a smooth nonlinearity Φ.

Appendix

We give the explicit expression of t.w.s which verifies property 1. We derive necessary and sufficient conditions for their existence. Following the definition of ξ_e^{min}, we define ξ^i_{max}, ξ^i_{min} which verify $S_i(\xi) = u_{th}$ and $\xi^i_{max} > \xi^i_{min}$.
First, we note that for $\xi \geq 0$, the wave expression is given by equations (9).
We split the study into two parts:

1 If $c_{ei} < \frac{u_{th}}{u_{eq}^{ei} - u_{th}}$ then $\xi^i_{min} = -\infty$ and we have the two cases :

1.1 $\xi^e_{min} = -\infty$. We obtain :

$$\text{for } \xi \leq 0 : \begin{cases} S_e(\xi) = (u_{th} - v^{1a})e^{\frac{1+c_r+c_{ee}}{c}\xi} + v^{1a} \\ S_i(\xi) = u^{1a}(1 - e^{\frac{1+c_{ei}}{c}\xi}) \end{cases} \tag{18}$$

A necessary and sufficient condition for this wave to exist is $v^{1a} > u_{th}$. When (6) holds this condition is fulfilled. In the phase plane (S_e, S_i), this trajectory corresponds to a heteroclinic orbit which connects $(0, 0)$ to (v^{1a}, u^{1a}). Such a wave is depicted in Fig. 2a.

1.2 $\xi^e_{min} \in \mathbb{R}^-$. We have :

$$\text{for } \xi^e_{min}+1 \leq \xi \leq 0: \text{ equation (18)}$$

$$\text{for } \xi^e_{min} \leq \xi \leq \xi^e_{min}+1: \begin{cases} S_e(\xi) = \lambda e^{\frac{1+c_{ee}}{c}\xi} + \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}} \\ S_i(\xi) = u^{1a}(1-e^{\frac{1+c_{ei}}{c}\xi}) \end{cases} \quad (19)$$

$$\text{for } \xi \leq \xi^e_{min}: \begin{cases} S_e(\xi) = u_{th}e^{\frac{\xi-\xi^e_{min}}{c}} \\ S_i(\xi) = \beta e^{\frac{\xi}{c}} \end{cases} \quad (20)$$

where $\lambda = (u_{th} - \frac{c_{ee}u^{ee}_{eq}}{1+c_{ee}})e^{-\frac{1+c_{ee}}{c}\xi^e_{min}}$. The continuity of S_e (S_i) at $\xi^e_{min}+1$ (ξ_{min}) gives ξ^e_{min} (β). Such a wave exists if and only if ξ_{min} exists and $\xi^e_{min} < -1$. The first condition leads to $\lambda > 0$ which gives $c_{ee} < \frac{u_{th}}{u^{ee}_{eq}-u_{th}}$. The second condition does not lead to a tractable expression. In the phase plane (S_e, S_i), such a wave is a homoclinic orbit based in $(0,0)$. The shape of such a wave is depicted in Fig. 2b. We show, in proposition 3, that this t.w.s is unstable.

2 If $c_{ei} > \frac{u_{th}}{u^{ei}_{eq}-u_{th}}$ then ξ^i_{max} still exists and is given by $\xi^i_{max} = \frac{c}{1+c_{ei}}\ln(1 - \frac{u_{th}(1+c_{ei})}{c_{ei}u^{ei}_{eq}})$. We distinguish the two cases:

2.1 $\xi^e_{min} = -\infty$, we have :

$$\text{for } \xi^i_{max} \leq \xi \leq 0: (18)$$

$$\text{for } \xi \leq \xi^i_{max}: \begin{cases} S_e(\xi) = \gamma e^{\frac{1+c_r+c_{ee}+c_{ie}}{c}\xi} + v^{1b} \\ S_i(\xi) = u^{1b}(1-e^{\frac{1+c_{ei}}{c}\xi}) \end{cases} \quad (22)$$

The continuity of S_e at ξ^i_{max} gives γ. This wave exists as long as $v^{1b} > u_{th}$ and corresponds to a heteroclinic orbit from $(0,0)$ to (v^{1b}, u^{1b}). Such a wave is depicted Fig. 2c (for $\gamma > 0$) and Fig. 2d (for $\gamma < 0$).

2.2 $\xi^e_{min} \in \mathbb{R}^-$. Depending on the relative position between ξ^i_{max} and $\xi^e_{min}+1$, we split the study into two cases:

2.2.1 $\xi^e_{min}+1 > \xi^i_{max}$. We obtain :

$$\text{for } \xi^e_{min}+1 \leq \xi \leq 0: \text{equation (18)}$$

$$\text{for } \xi^i_{max} \leq \xi \leq \xi^e_{min}+1: \text{equation (19) with a different } \lambda$$

for $\xi^e_{min} \leq \xi \leq \xi^i_{max}$:

$$\begin{cases} S_e(\xi) = (u_{th} - \frac{c_{ee}u^{ee}_{eq}+c_{ie}u^{ie}_{eq}}{1+c_{ee}+c_{ie}})e^{\frac{1+c_{ee}+c_{ie}}{c}\xi-\xi^e_{min}} + \frac{c_{ee}u^{ee}_{eq}+c_{ie}u^{ie}_{eq}}{1+c_{ee}+c_{ie}} \\ S_i(\xi) = \frac{c_{ei}u^{ei}_{eq}}{1+c_{ei}}(1-e^{\frac{1+c_{ei}}{c}\xi}) \end{cases} \quad (23)$$

$$\text{for } \xi^i_{min} \leq \xi \leq \xi^e_{min}: \begin{cases} S_e(\xi) = (u_{th} - \frac{c_{ie}u^{ie}_{eq}}{1+c_{ie}})e^{\frac{1+c_{ie}}{c}\xi-\xi^e_{min}} + \frac{c_{ie}u^{ie}_{eq}}{1+c_{ie}} \\ S_i(\xi) = u_{th}e^{\frac{\xi-\xi^i_{min}}{c}} \end{cases} \quad (24)$$

$$\text{for } \xi \leq \xi^i_{min} : \begin{cases} S_e(\xi) = \alpha e^{\frac{\xi}{c}} \\ S_i(\xi) = u_{th} e^{\frac{\xi - \xi^i_{min}}{c}} \end{cases} \tag{25}$$

The continuity of S_e at $\xi^e_{min}+1$ gives $\lambda(\xi^e_{min})$ (as a function of ξ^e_{min}). The continuity of S_e at ξ^i_{max} gives an equation whose solution is ξ^e_{min}. The continuity of S_i at ξ^e_{min} gives ξ^i_{min} and the continuity of S_e at ξ^i_{min} gives α. Therefore, the wave is entirely determined. The necessary and sufficient conditions of existence are : (i) ξ^{min}_e exists (ii) $\xi^{min}_e+1 < 0$ (iii) $\xi^{min}_e+1 > \xi^i_{max}$. Condition (i) implies $\frac{c_{ee}u^{ee}_{eq}+c_{ie}u^{ie}_{eq}}{1+c_{ee}+c_{ie}} < u_{th}$ and conditions (ii), (iii) do not lead to tractable expressions. Depending on the sign of λ and α, four shapes for this wave may be obtained. We depicted the case $\lambda > 0$ and $\alpha < 0$ in Fig. 2e.

2.2.2 $\xi^e_{min} + 1 < \xi^i_{max}$. We calculate :

$$\text{for } \xi^i_{max} \leq \xi \leq 0 : \text{ equation (18)}$$

$$\text{for } \xi^e_{min} + 1 \leq \xi \leq \xi^i_{max} : \begin{cases} S_e(\xi) = \mu e^{\frac{1+c_r+c_{ee}+c_{ie}}{c}\xi} + v^{1b} \\ S_i(\xi) = u^{1b}(1 - e^{\frac{1+c_{ei}}{c}\xi}) \end{cases} \tag{26}$$

$$\text{for } \xi^e_{min} \leq \xi \leq \xi^e_{min} + 1 : \text{ equation (23) .}$$

$$\text{for } \xi < \xi^e_{min} : \text{ equations (24) and (25) .}$$

The continuity of S_e at ξ^i_{max} gives μ and the continuity at $\xi^e_{min}+1$ gives ξ^e_{min}. As in 2.2.1, we derived the necessary condition of existence : $\frac{c_{ee}u^{ee}_{eq}+c_{ie}u^{ie}_{eq}}{1+c_{ee}+c_{ie}} < u_{th}$. Depending on the sign of μ and α (see (25)) four shapes may be obtained. In Fig. 2f, we depicted the case $\lambda > 0$ and $\alpha < 0$.

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