Traveling Waves in a One-Dimensional Global Model of Synaptic Activity in the Cerebral Cortex

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Abstract: - A one-dimensional nonlinear global model of neuronal interaction at cerebral cortex level is here presented, in order to study the dynamics of synaptic excitatory and inhibitory activity of the cortex. We prove that under certain conditions, excitation and inhibition traveling waves appear.

Key-Words: - Traveling waves, Green's principal function, Gâteaux and Fréchet derivatives, cerebral cortex, excitation - inhibition, synapses.

1 Introduction

Traveling waves of chemical, physical and biological activity have been observed in different environments. One important example in neurophysiology is the action potential in a neuron, which is a traveling wave of electric activity that spreads in the axon length. The mathematical model of this phenomenon (The Hodgkin–Huxley's equations) has been widely studied. ([3],[4]) Travelling waves of electric activity have also been observed in the cerebral cortex [6]. Theoretical studies of this phenomenon have been proposed [1].

In order to study the existing relationship between certain physiological states and electroencephalographic states measured at scalp or cortex level, several neuronal interaction models at the cortex thalamus level have been previously proposed.

Local models try to explain the space-time properties of the electroencephalograms(EEG) with respect to the properties at neuronal level, discrete neuronal networks or neuronal networks distributed in the millimeter range.

In global models, the corticortical fiber systems (whose wavelengths are in the centimeter range) and the fact that the cortex is a closed structure are considered important elements. These models consider that the EEG measured at the scalp is essentially the result of cortical neuron interactions through action potentials.

The model takes the column of cerebral cortex as the fundamental unit and tries to describe the interactions between cortical columns through their interconnections as well as the interaction of the cortex with other cerebral structures. It consists of a pair of nonlinear integral equations that relate the synaptic activity in each column of cortex in a given instant of time t to the action potentials produced earlier in other columns of cortex, taking into account propagation velocities of action potentials but ignoring the synaptic delays.

In this article, we will present a global model of neuronal interaction at cerebral cortex level that takes advantage of certain anatomic and physiological characteristics of the cerebral cortex. We argue that this kind of models provides a framework for study the electrical traveling waves at the cerebral cortex.

2 Problem Formulation

The cortex presents certain anatomical and physiological characteristics that allow the elaboration of neuron interaction models whose variables and parameters can be correlated with electroencephalographic measures obtained at the scalp.

Among the important characteristics of the cerebral cortex are:

- 1. It is a stratified system that has 6 horizontal layers.
- 2. It has a columnar organization, that is, the neurons are grouped by cortical columns and cortical macrocolumns.

- 3. It is a densely interconnected system formed by approximately 10^{10} cortical fibers. The interconnections between neurons can also be divided into two groups: the intracortical connections that are short-range (lower than one millimeter) and which can be excitatory or inhibitory, and the corticortical connections, which are large-range (20*cm* long approximately) and are only of the excitatory type.
- 4. The input to the cerebral cortex that come from other cerebral structures are only of the excitatory type.

More information about these points can be found in [5].

2.1 Deduction of the model

With this information it is possible to consider the cortex like a system that involves the dynamic global interaction of approximately 10^6 cortical columns with one external input of the excitatory type and that are modulated by a local process of lateral inhibition.

For the sake of simplicity we will consider the cortex as consisting of only one layer. We will first consider one uniform slice of cortex which will be represented by the set of real numbers.

If we denote by the subindices \pm those related to the synaptic excitatory activity and inhibitory respectively, then the elementary models are:

- a) $h_{\pm}(x,t)$ The active synapses density or synaptic activity, in the column x at time t $(1/cm^2)$.
- b) g(x',t) The total fraction of neurons of column x' that "firing" action potentials in time t (dimensionless).
- c) $R_{\pm}(x', x, v)$ The number of synaptic connections per cm^2 in column x per unit length in x' and per unit velocity (sec/cm^4) . In order to simplify the model, we will consider now that R_{\pm} has the following form

$$R_{\pm}(x, x', v) = \frac{\lambda_{\pm}}{2} S_{\pm}(x) e^{-\lambda_{\pm}|x-x'|} \delta(v - v_{\pm})$$

where v_{\pm} represent the propagation velocities of action potentials of excitatory and inhibitory neurons, respectively; λ_{\pm}^{-1} represents the decreasing scales of synaptic connections, δ is Dirac's delta, and $S_{\pm}(x)$ the synapses density in column x. $(1/cm^2)$.

d) $h^0_{\pm}(x,t)$ – The synaptic input density which is active in column x in time t produced by action potentials that are "fired" in other cerebral structures $(1/cm^2)$.

The density of synaptic activity in column x at instant t produced by action potentials that are "fired" in the inner structures of the cerebral and reach x at instant t, which will be denoted by $h_0(x, t)$. Therefore, we get:

$$h_{+}(x,t) = h_{0}(x,t) + \frac{1}{2}\lambda_{+}S_{+}(x)\int_{-\infty}^{\infty} e^{-\lambda_{+}|x-x'|}g\left(x',t-\frac{|x'-x|}{v_{+}}\right)dx'$$
(1)

$$h_{-}(x,t) = \frac{1}{2}\lambda_{-}S_{-}(x)\int_{x-\epsilon}^{x+\epsilon} e^{-\lambda_{-}|x-x'|}g\left(x',t-\frac{|x-x'|}{v_{-}}\right)dx'.$$
(2)

where the parameter $\epsilon > 0$ is related to the assumption that inhibitory activity has a short range.

2.2 Reduction of the System

We will now define

$$H_{\pm}(x,t) = \frac{h_{\pm}(x,t)}{S_{\pm}(x)}, \quad H_0(x,t) = \frac{h_0(x,t)}{S_{\pm}(x)}$$

Dividing (1) by $S_+(x)$, (2) by $S_-(x)$ and applying the operator $\frac{\partial^2}{\partial x^2}$ on both equations, we obtain the following equivalent system of differential equations:

$$\frac{\partial^2 H_+}{\partial t^2} + 2\lambda_+ v_+ \frac{\partial H_+}{\partial t} + \lambda_+^2 v_+^2 H_+ - v_+^2 \frac{\partial^2 H_+}{\partial x^2}$$

$$= F_0(x,t) + \lambda_+^2 v_+^2 g(x,t) + \lambda_+ v_+ \frac{\partial g}{\partial t}(x,t),$$
(3)

$$\frac{\partial^2 H_-}{\partial t^2} + 2\lambda_- v_- \frac{\partial H_-}{\partial t} + \lambda_-^2 v_-^2 H_- - v_-^2 \frac{\partial^2 H_-}{\partial x^2} = G_0(x, t, \epsilon) , \quad (4)$$

where

$$F_0(x,t) = \frac{\partial^2 H_0}{\partial t^2} + 2\lambda_+ v_+ \frac{\partial H_0}{\partial t} + \lambda_+^2 v_+^2 H_0 - v_+^2 \frac{\partial^2 H_0}{\partial x^2},$$

$$G_0(x,t,\epsilon) = \lambda_-^2 v_-^2 g(x,t) + \lambda_- v_- \frac{\partial g}{\partial t}(x,t)$$

$$\begin{split} &-\frac{1}{2}\lambda_{-}v_{-}e^{-\lambda_{-}\epsilon}\left\{\lambda_{-}v_{-}\left[g\left(x+\epsilon,t-\frac{\epsilon}{v_{-}}\right)\right.\\ &+g\left(x-\epsilon,t-\frac{\epsilon}{v_{-}}\right)\right] \\ &+\left[\frac{\partial g}{\partial t}\left(x+\epsilon,t-\frac{\epsilon}{v_{-}}\right)+\frac{\partial g}{\partial t}\left(x-\epsilon,t-\frac{\epsilon}{v_{-}}\right)\right]\right\} \\ &\left.-\frac{1}{2}\lambda_{-}v_{-}^{2}e^{-\lambda_{-}\epsilon}\left\{\frac{\partial g}{\partial x}\left(x+\epsilon,t-\frac{\epsilon}{v_{-}}\right)\right.\\ &\left.-\frac{\partial g}{\partial x}\left(x-\epsilon,t-\frac{\epsilon}{v_{-}}\right)\right\}. \end{split}$$

Using results of regular perturbation theory of differential equations, we obtain that, when $\epsilon \to 0$, the solutions of (3), (4) have an asymptotical behavior like those of the following system of equations.

$$\frac{\partial^2 H_+}{\partial t^2} + 2\lambda_+ v_+ \frac{\partial H_+}{\partial t} + \lambda_+^2 v_+^2 H_+ - v_+^2 \frac{\partial^2 H_+}{\partial x^2} =$$

$$F_0(x,t) + \lambda_+^2 v_+^2 g(x,t) + \lambda_+ v_+ \frac{\partial g}{\partial t}(x,t) ,$$
(5)

$$\frac{\partial^2 H_{-}}{\partial t^2} + 2\lambda_{-}v_{-}\frac{\partial H_{-}}{\partial t} + \lambda_{-}^2 v_{-}^2 H_{-} - v_{-}^2 \frac{\partial^2 H_{-}}{\partial x^2} = 0.$$
(6)

Since the activity in a column of cortex depends as much of the synaptic excitatory activity as of the inhibitory, we shall introduce the variable

$$u(x,t) = V_{+}H_{+}(x,t) - V_{-}H_{-}(x,t), \qquad (7)$$

where $V \pm$ is the postsypnaptic magnitude potential in one synapse. The variable u will be named as the activation variable.

Doing some algebraic manipulations with equation (7), we obtain:

$$\begin{aligned} \frac{\partial^2 u}{\partial t^2} + 2\lambda_+ v_+ \frac{\partial u}{\partial t} + \lambda_+^2 v_+^2 u - v_+^2 \frac{\partial^2 u}{\partial x^2} \\ = V_+ \lambda_+^2 v_+^2 g(x,t) + V_+ \lambda_+ v_+ \frac{\partial g}{\partial t}(x,t) + V_+ F_0(x,t) \\ - V_- \left[\frac{\partial^2 H_-}{\partial t^2} + 2\lambda_+ v_+ \frac{\partial H_-}{\partial t} \right] \\ + \lambda_+^2 v_+^2 H_- - v_+^2 \frac{\partial^2 H_-}{\partial x^2} \end{aligned}$$
(8)

The function g(x,t) represents, for x fixed, the physiological activity of column x at an instant t. In general, this depends in a very complex way on the synaptic excitatory and inhibitory activity existing in column x. Thus we consider

$$g(x,t) = \overline{g}(u),$$

where, for simplicity we can suppose that \overline{g} is one sigmoid function of activation variable u.

Considering this new function and introducing the non dimensional variables

$$\tau = \lambda_+ \upsilon_+ t, \quad y = \lambda_+ x,$$

we get the following equivalent simplified equation to (8):

$$\frac{\partial^2 u}{\partial \tau^2} + 2\frac{\partial u}{\partial \tau} + u - \frac{\partial^2 u}{\partial y^2} =$$

$$V_+ \left[\bar{g}(u) + \bar{g}'(u) \frac{\partial u}{\partial \tau} \right] + f_0(y,\tau) + C_0(y,\tau)$$
(9)

where

$$f_0(y,\tau) = \frac{V_+}{\lambda_+^2 v_+^2} F_0\left(\frac{y}{\lambda_+}, \frac{\tau}{\lambda_+ v_+}\right)$$
(10)

$$C_0(y,\tau) = -V_{-} \left[\frac{\partial^2 H_{-}}{\partial \tau^2} + 2 \frac{\partial H_{-}}{\partial \tau} + H_{-} - \frac{\partial^2 H_{-}}{\partial y^2} \right].$$
Note that in model (10) (11) we have the follow:

Note that in model (10), (11) we have the following facts:

- 1. $f_0(y, \tau)$ is associated to the excitatory input of inner brain structures to the cortex.
- 2. $C_0(y,\tau)$ is associated to the control produced by the lateral inhibitory activity.

3 Problem solution

Traveling waves are waves that spread through the physical medium without losing their shape.

In this section, we shall study under which conditions equation (9) yields traveling waves.

3.1 Preliminary lemmas

Before beginning this analysis, we shall prove some important results for our aims.

We suppose that the inhibitory control is such that

$$f_0(y,\tau) + C_0(y,\tau) \equiv 0.$$

It is easy to proof the following lemma,

Lemma 1 Let $f : \mathbb{R}^2 \to \mathbb{R}^2$ be continuous, and suppose that the differential equation

$$\frac{dx}{dt} = f(x), \qquad x \in \mathbb{R}^2 \tag{12}$$

has one and only one stationary-point x_0 , which is a saddle-point. Then, the necessary and sufficient condition for the existence of a homoclinic solution of the equation (12) that is it has one nontrivial bounded solution in \mathbb{R} .

We will search under which conditions the partial differential equation

$$\frac{\partial^2 u}{\partial \tau^2} + 2\frac{\partial u}{\partial \tau} + u - \frac{\partial^2 u}{\partial y^2} = V_+ \left[\bar{g}(u) + \bar{g}'(u)\frac{\partial u}{\partial t} \right] .$$
(13)

has solutions of the form

$$u(y,\tau) = \phi(y - c\tau) = \phi(s)$$
, where $s = y - c\tau$ (14)

which also satisfy the condition

$$\lim_{s \to \pm \infty} \phi(s) = \phi_0 \,, \tag{15}$$

where ϕ_0 is a constant.

If one solution of equation (13) exists, it has the form (14) and since it has to satisfy condition (15), it has to satisfy the ordinary differential equation

$$(c^{2}-1)\frac{d^{2}\phi}{ds^{2}} + c(V_{+}\bar{g}'(\phi)-2)\frac{d\phi}{ds} + (\phi - V_{+}\bar{g}(\phi)) = 0.$$
(16)

Conversely, if ϕ is a solution of (16) which satisfies condition (15), then the function

$$u(y,\tau) = \phi(y - c\tau)$$

is a solution of equation (13).

Note:

In the following we will suppose that 0 < c < 1, such that it corresponds to the real propagation velocity, cv_+ , which cannot be greater than the action potential spread velocities.

We have that equation (16) is equivalent to the first order equation system:

$$\frac{d}{dt} \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ \frac{1}{1-c^2} & \frac{-2c}{1-c^2} \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix} + \frac{V_+}{1-c^2} \begin{pmatrix} 0 \\ c\bar{g}'(\phi)\psi - \bar{g}(\phi) \end{pmatrix}, \quad (17)$$

where $\psi(s) = \frac{d\phi}{ds}$

The existence of traveling waves for the equation (13) is equivalent to the existence of homoclinic solutions of system (17) at some value of $c \in (0, 1)$, and

due to Lemma 1, The existence of homoclinic solutions of (17) is equivalent to the existence of nontrivial bounded solutions in \mathbb{R} of (17) in case (17) satisfies the conditions of Lemma 1.

From (16) it is evident that for c = 1 there are not homoclinic solutions to this equation.

In the following we shall suppose that

$$\bar{g}'(\phi) < \frac{1}{V_+} \text{ for each } \phi \in \mathbb{R}.$$
 (18)

With this condition we shall see that system (17) has only one stationary-point for every value of constant c that satisfies 0 < c < 1.

In addition, this stationary point is independent of c and is a saddle-point of the system. With this result, the problem of finding homoclinic solutions for the system (17) is reduced to searching bounded solutions in \mathbb{R} , different from the trivial solution for this system.

The stationary solutions of (17) have the form $\binom{\phi_0}{0}$, where ϕ_0 is the root of the equation

$$\phi - V_+ \bar{g}(\phi) = 0.$$

Therefore, from the condition $V_+\bar{g}'(\phi) < \frac{1}{V_+}$, we conclude that this equation has only one solution ϕ_0 , which belongs to only one stationary solution of (17).

To determine if the stationary point is a saddlepoint, we will study the linear approximation to the system in a vicinity of a stationary point.

Calculating the right hand side derivative of (17) in the stationary point and making some operations, we obtain that the linear approximation of the system in the vicinity of a stationary point is:

$$\frac{d}{dt} \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ \frac{1}{c^2 - 1} (V_+ \bar{g}'(\phi_0) - 1) & \frac{c}{c^2 - 1} (2 - V_+ \bar{g}'(\phi_0)) \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}.$$
(19)

and the roots of its characteristical equation are :

$$\lambda_{\pm} = \frac{\frac{c}{c^2 - 1} (2 - V_{\pm} \bar{g}'(\phi_0))}{2} \\ \pm \frac{\sqrt{\left(\frac{c}{c^2 - 1} (2 - V_{\pm} \bar{g}'(\phi_0))^2 + \frac{1}{c^2 - 1} (V_{\pm} \bar{g}'(\phi_0) - 1)\right)}}{2}.$$
(20)

Now, since $V_+\bar{g}'(\phi_0) < 1$ and 0 < c < 1, we obtain $0 < \lambda_+$ and $\lambda_- < 0$.

Therefore, $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}$ is one saddle-point of (19) for every value of 0 < c < 1.

According to Lemma 1, the existence of homoclinic solutions of (17) is equivalent to the existence of bounded solutions different from the trivial solution $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}$.

We know that the bounded solutions of differential equation (17) coincide with the bounded solutions of the nonlinear integral equation

$$\begin{pmatrix} \phi \\ \psi \end{pmatrix} = \frac{V_+}{1-c^2} \int_{-\infty}^{\infty} G(t-\tau,c) \begin{pmatrix} 0 \\ c\bar{g}'(\phi(\tau)\psi(\tau) - \bar{g}(\tau) \end{pmatrix} d\tau ,$$
(21)

where G(t, c) is the corresponding Green's principal function ([1], p. 81) of the equation (17).

Now, we shall study under which conditions the integral equation (21) have bounded solutions in \mathbb{R} .

Lemma 2 Green's principal function of A_c is

$$G(t,c) = \begin{cases} \frac{1}{2}e^{\frac{t}{c-1}} \begin{pmatrix} 1-c & c^2-1\\ -1 & 1+c \end{pmatrix}, & si \ t > 0\\ \\ -\frac{1}{2}e^{\frac{t}{c+1}} \begin{pmatrix} 1+c & 1-c^2\\ 1 & 1-c \end{pmatrix}, & if \ t < 0. \end{cases}$$
(22)

Proof:

We know that Green's principal function is defined by

$$G(t,c) = \begin{cases} e^{A_c t} P_{-}, & t > 0\\ -e^{A_c t} P_{+}, & t < 0 \end{cases}$$
(23)

So, we need to calculate $e^{A_c t}$ and the projectors P_+, P_- .

Using Jordan's canonical form A_c , and after some manipulations, which we will not show here, we obtain

$$e^{A_{c}t} = \frac{1}{2}e^{\frac{t}{1+c}} \begin{pmatrix} 1+c & 1-c^{2} \\ 1 & 1-c \end{pmatrix} + \frac{1}{2}e^{\frac{t}{c-1}} \begin{pmatrix} 1-c & c^{2}-1 \\ -1 & 1+c \end{pmatrix} = e^{\frac{t}{1+c}}P_{+} + e^{\frac{t}{c-1}}P_{-} \quad (24)$$

Substituting (24) in (23), we come to (22). \blacksquare

Lemma 3

$$|G(t)| \le (1+c)e^{\frac{-|t|}{1+c}}$$
. (25)

Proof:

The proof is immediate from lemma 2.

In order to obtain simpler estimates of the integrand in the integral equation (21), we suppose that $\bar{g}(u)$ is the sigmoid function.

$$\bar{g}(u) = \frac{1}{1 + e^{-\alpha u + \beta}}$$
 with $\alpha > 0, \ \beta > 0.$ (26)

Obtaining the first and second derivative of expression (26), we obtain

$$\mid \bar{g}' \mid \le \alpha \,, \tag{27}$$

$$|\bar{g}''| \le 2\alpha^2 \,. \tag{28}$$

From (27) and (28), we immediately obtain

Lemma 4 Let $\rho > 0$. For all $\begin{pmatrix} \phi \\ \psi \end{pmatrix} \in B[0,\rho]$, and $\begin{pmatrix} \phi_i \\ \psi_i \end{pmatrix} \in B[0,\rho]$, i = 1, 2, we get the following estimated values

$$|c\bar{g}'(\phi)\psi - \bar{g}(\phi)| \le c\alpha\rho + 1, \qquad (29)$$

$$| (c\bar{g}'(\phi_1)\psi_1 - \bar{g}(\phi_1)) - (c\bar{g}'(\phi_2)\psi_2 - \bar{g}(\phi_2)) | \leq 2\alpha(\alpha\rho c + 1).$$
 (30)

3.2 The existence of traveling waves

In the Theorem 1 we state the conditions that guarantee the existence of traveling waves in our model.

Proposition 1 We suppose that in system (17) the function \bar{g} has the form (26). Let $\begin{pmatrix} \phi \\ 0 \end{pmatrix}$ be the stationary solution of (17).

We also suppose that $V_{+}\alpha < \frac{1}{4}$. Then, for each $\rho > \max\{\phi_0, \frac{1}{2\alpha}\}$ there exists one and only one bounded solution of the system (17) contained in $B[0, \rho]$, which is the stationary-solution $\binom{\phi_0}{0}$. In addition $c(\rho)$ is given by

$$c(\rho) = -\frac{\left(1 + \frac{1}{\alpha\rho} + \frac{1}{4\alpha^{2}\rho V_{+}}\right)}{2} + \frac{\sqrt{\left(1 + \frac{1}{\alpha\rho} + \frac{1}{4\alpha^{2}\rho V_{+}}\right)^{2} - 4\left(\frac{1}{\alpha\rho} - \frac{1}{4\alpha^{2}\rho V_{+}}\right)}}{2}.$$
 (31)

Proof:

We begin by proving that under the conditions of this proposition, system (17) satisfies the conditions of the Theorem of the appendix, and therefore has only one bounded solution u contained in $B[0, \rho]$. Since $\binom{\phi_0}{0}$ is a bounded solution of the system contained in the same closed-ball, we have $\binom{\phi_0}{0}$ is the only solution of (17) in this closed ball.

The eigenvalues of matrix are

$$\frac{1}{1+c}, \quad \frac{1}{c-1}$$

therefore A_c satisfies condition (52).

By lemma 4 we get, for $\begin{pmatrix} \phi \\ \psi \end{pmatrix} \in B[0, \rho],$

$$\frac{V_+}{1-c^2} \left| \begin{pmatrix} 0\\ c\bar{g}'(\phi)\psi - \bar{g}(\phi) \end{pmatrix} \right| \le \frac{V_+}{1-c^2}(c\alpha\rho+1)$$

and

$$\frac{V_{+}}{1-c^{2}} \left| \begin{pmatrix} 0\\ c\bar{g}'(\phi_{1}) - \bar{g}(\phi_{1}) - (c\bar{g}'(\phi_{2})\psi_{2} - \bar{g}(\phi_{2})) \end{pmatrix} \right|$$
$$\leq \frac{V_{+}}{1-c^{2}} 2\alpha(\alpha\rho c + 1) \left| \begin{pmatrix} \phi_{1}\\ \psi_{1} \end{pmatrix} - \begin{pmatrix} \phi_{2}\\ \psi_{2} \end{pmatrix} \right|$$

when $\begin{pmatrix} \phi_i \\ \psi_i \end{pmatrix} \in B[0,\rho] \quad i=1,2.$

Therefore, system (17) satisfies the conditions (53), (54), where

$$M = (c\alpha\rho + 1)\frac{V_+}{1 - c^2}, \quad q = 2\alpha(\alpha\rho c + 1)\frac{V_+}{1 - c^2}.$$

By lemmas 2 and 3, Green's principal function, G(t,c), of A_c satisfies

$$|G(t,c)| \le (1+c)e^{\frac{-|t|}{1+c}},$$

therefore, system (17) also satisfies (55) with

$$N = 1 + c$$
 y $r = \frac{1}{1 + c}$.

We only have to prove condition (56) holds, that is, we need to prove with conditions of the proposition 1, its satisfied

$$\frac{(c\alpha\rho+1)V_+}{1-c^2} \le \frac{\rho}{2(1+c)^2},$$
(32)

$$\frac{2\alpha(\alpha\rho c+1)V_+}{1-c^2} < \frac{1}{2(1+c)^2}.$$
 (33)

Performing some operations and reordering the terms we obtain that the system (32), (33) is equivalent to the system

$$P_1(c) = c^2 + \left(1 + \frac{1}{\alpha\rho} + \frac{1}{2\alpha V_+}\right)c + \frac{1}{\alpha\rho} - \frac{1}{2\alpha V_+} \le 0, \quad (34)$$

$$P_{2}(c) = c^{2} + \left(1 + \frac{1}{\alpha\rho} + \frac{1}{4\alpha^{2}\rho V_{+}}\right)c + \left(\frac{1}{\alpha\rho} - \frac{1}{4\alpha^{2}\rho V_{+}}\right) < 0.$$
(35)

That's why we need to prove (34) and (35). To prove this, we need to obtain the polynomial square roots $P_1(c)$, $P_2(c)$.

The roots of P_1 are

$$c_{\pm}^{1}(\rho) = \frac{-\left(1 + \frac{1}{\alpha\rho} + \frac{1}{2\alpha V_{+}}\right)}{2} \\ \pm \frac{\sqrt{\left(1 + \frac{1}{\alpha\rho} + \frac{1}{2\alpha V_{+}}\right)^{2} - 4\left(\frac{1}{\alpha\rho} - \frac{1}{2\alpha V_{+}}\right)}}{2} .$$
 (36)

The roots of P_2 are

$$c_{\pm}^{2}(\rho) = \frac{-\left(1 + \frac{1}{\alpha\rho} + \frac{1}{4\rho\alpha^{2}V_{\pm}}\right)}{2} \\ \pm \frac{\sqrt{\left(1 + \frac{1}{\alpha\rho} + \frac{1}{4\rho\alpha^{2}V_{\pm}}\right)^{2} - 4\left(\frac{1}{\alpha\rho} - \frac{1}{4\alpha^{2}\rho V_{\pm}}\right)}}{2}.$$
 (37)

Since, by hypothesis, $\alpha V_+ < \frac{1}{4}$ and $\rho > \frac{1}{2\alpha}$ we have

$$\frac{1}{\alpha\rho} - \frac{1}{4\alpha^2\rho V_+} < 0 \,,$$

therefore the roots of $P_1(c)$ are real, one negative, $c_{-}^1(\rho)$, and the other positive $c_{+}^1(\rho)$. The same happens with $P_2(c)$.

Then

$$P_1(c) \le 0 \text{ for } c_-^1(\rho) \le c \le c_+^1(\rho),$$
 (38)

$$P_2(c) < 0 \text{ for } c_-^1(\rho) < c < c_+^2(\rho).$$
 (39)

In addition,

$$c_{+}^{2}(\rho) < c_{+}^{1}(\rho),$$
 (40)

This final part follows from each of the expressions for every one of them and from the fact that

$$4\alpha^2 \rho V_+ = 2\alpha \rho (2\alpha V_+) > (2\alpha V_+) \text{ since } \rho > \frac{1}{2\alpha}.$$

It is also easy to prove that $c_+^1(\rho) < 1$. Thus, if we take $0 < c(\rho) = c_+^2(\rho) < 1$, then, for every $0 < c < c(\rho)$, we have

$$P_1(c) \le 0$$
,
 $P_2(c) < 0$.

Summarizing, under the conditions of proposition 1, system (17) satisfies the conditions of the theorem of the appendix, for every $0 < c < c(\rho)$. This is what we wanted to prove.

With proposition 1, we have proved that if $\alpha V_+ < \frac{1}{4}$, $\rho > \max\{\phi_0, \frac{1}{2\alpha}\}$, then system (17) cannot have homoclinic solutions in $0 < c < c(\rho)$. Then, the traveling waves do not exist for the equation (13), where $0 < c < c(\rho)$.

Now, we continue to analyze what happens when we take $\rho > \max\{\phi_0, \frac{1}{2\alpha}\}$ and $c(\rho) < c < 1$.

We consider for $\rho > \max\{\phi_0, \frac{1}{2\alpha}\}$ the β_{ρ} space,

$$\beta_{\rho} = \left\{ \begin{pmatrix} \phi \\ \psi \end{pmatrix} : \mathbb{R} \longrightarrow \mathbb{R}^2 : \begin{pmatrix} \phi \\ \psi \end{pmatrix} \text{ is continuous,} \\ \| \phi \|_{\infty}^2 + \| \psi \|_{\infty}^2 \le \rho^2 \right\}.$$
(41)

We know that β_{ρ} is a Banach space. We consider the family of integral operators $\mathbf{F}\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right)$ defined by

$$\mathbf{F}\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right) = \begin{pmatrix}\phi\\\psi\end{pmatrix} - \mathbf{F}_1\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right),\qquad(42)$$

where

$$\mathbf{F}_{1}\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right) = \frac{V_{+}}{1-c^{2}}$$
$$\int_{-\infty}^{\infty} G(t-\tau,c) \begin{pmatrix}0\\c\bar{g}'(\phi(\tau))\psi(\tau) - \bar{g}(\phi(\tau))\end{pmatrix} d\tau.$$
(43)

In order that $\mathbf{F}\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right)$ can act from β_{ρ} to β_{ρ} , c it should satisfy the condition (34). From this we can conclude that those values of c for which it is possible to find homoclinic solutions of system (17), satisfy

$$c_+^2(\rho) < c < c_+^1(\rho)$$
.

So we consider

$$\mathbf{F}:\beta_{\rho}\times(c_{+}^{2}(\rho),c_{+}^{1}(\rho))\longrightarrow\beta_{\rho}$$
 defined by (42) .

Since $\binom{\phi_0}{0}$ is a stationary point of system (17) for each 0 < c < 1, we have the following expression:

$$\mathbf{F}\left(\binom{\phi}{0}, c\right) = 0 \text{ for each } c_+^2(\rho) < c < c_+^1(\rho).$$

So, if we can prove that $D\mathbf{F}\left(\binom{\phi_0}{0}, c\right)$ is invertible, and that it satisfies the other conditions of the

implicit function theorem in a vicinity of $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}, c \end{pmatrix}$, we shall conclude that there exist U, V vicinities of $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}$ and c respectively, such that for each $c^* \in V$ one and only one $\mathcal{L}(c^*) = \begin{pmatrix} \phi \\ \psi \end{pmatrix} \in U$ exists that satisfies:

$$\mathbf{F}\left(\binom{\phi}{\psi}, c^*\right) = 0\,,$$

but, $\binom{\phi}{\psi}$ would be one nontrivial bounded solution in \mathbb{R} , of system (17) and by lemma 1, a homoclinic solution of this system, to this would correspond one traveling wave of equation (13) with velocity c^* .

So, now we will prove that the integral operator **F** with $c^1_+(\rho) < c < c^2_+(\rho)$, satisfies the conditions of the implicit function theorem.

Lemma 5 Under the conditions of proposition 1, the integral operator **F** defined in (42), is of the C^1 class in one vicinity of $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}, c \end{pmatrix}$. In addition the Fréchet's partial derivative of **F** with respect to $\begin{pmatrix} \phi \\ \psi \end{pmatrix}$, which is denoted by $D\mathbf{F}\left(\begin{pmatrix} \phi \\ \psi \end{pmatrix}, c\right)$, is given by

$$D\mathbf{F}\left(\binom{\phi}{\psi}, c\right) = I - D\mathbf{F}_1\left(\binom{\phi}{\psi}, c\right).$$
(44)

with

$$D\mathbf{F}_1\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},0\right) = \delta_{\phi}\mathbf{F}_1\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right) + \delta_{\psi}\mathbf{F}_1\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right)$$
(45)

where the Gâteaux 's derivatives with respect to ϕ and ψ that appear in the right-hand side of equation (45) are given by the expressions

$$\begin{split} \delta_{\phi} \mathbf{F}_{1} \left(\begin{pmatrix} \phi \\ \psi \end{pmatrix}, c \right) (h) &= \frac{-V_{+}}{2} \left\{ \frac{e^{\frac{t}{c+1}}}{1+c} \int_{t}^{\infty} \right. \\ \left[e^{\frac{-\tau}{c+1}} \binom{c+1}{1} [c \bar{g}''(\phi(\tau))\psi(\tau) - \bar{g}'(\phi(\tau)]h(\tau) \right] d\tau \end{split}$$

$$+\frac{e^{\frac{t}{c-1}}}{c+1}\int_{-\infty}^{t}\left[e^{\frac{-\tau}{c-1}}\binom{c-1}{1}\left[c\bar{g}''(\phi(\tau))\psi(\tau)-\bar{g}'(\phi(\tau))\right]h(\tau)\right]d\tau\right]d\tau\right\},$$
 (46)

$$\delta_{\psi} \mathbf{F}_{1} \left(\begin{pmatrix} \phi \\ \psi \end{pmatrix}, c \right) (k) = -\frac{V_{+}c}{2} \left\{ \frac{e^{\frac{t}{c+1}}}{1+c} \int_{t}^{\infty} e^{\frac{-\tau}{c+1}} \binom{c+1}{1} \bar{g}'(\phi(\tau))k(\tau) d\tau + \frac{e^{\frac{t}{c-1}}}{1+c} \int_{-\infty}^{t} e^{\frac{-\tau}{c-1}} \binom{c-1}{1} \bar{g}'(\phi(\tau))k(\tau) d\tau \right\}.$$
(47)

Proof.

The Gâteaux's derivative is obtained in a direct way. \blacksquare

Lemma 6 Under the conditions of proposition 1, $D\mathbf{F}\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right)$ is an invertible operator.

Proof:

Since

$$D\mathbf{F}\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right) = I - D\mathbf{F}_1\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right)$$

it suffices to prove that

$$\left\| D\mathbf{F}_1\left(\binom{\phi_0}{0}, c\right) \right\| < 1$$

Evaluating (45) in $\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}$, $c \end{pmatrix}$ and calculating its norm, we obtain

$$\begin{aligned} \left\| D\mathbf{F}_{1}\left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) \begin{pmatrix} h \\ k \end{pmatrix} \right\|_{\infty} \\ \leq \left\| \delta_{\phi} \mathbf{F}_{1}\left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) (h) \right\|_{\infty} \\ + \left\| \delta_{\psi} \mathbf{F}_{1}\left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) (k) \right\|_{\infty}. \end{aligned}$$
(48)

We obtain values for

$$\left\|\delta_{\phi}\mathbf{F}_{1}\left(\begin{pmatrix}\phi_{0}\\0\end{pmatrix},c\right)\right\|_{\infty},\quad\left\|\delta_{\psi}\mathbf{F}_{1}\left(\begin{pmatrix}\phi_{0}\\0\end{pmatrix},c\right)\right\|_{\infty}.$$

Evaluating (46) in $\binom{\phi_0}{0}, c$ and calculating its norm, we obtain:

$$\left\| \delta_{\phi} \mathbf{F}_{1} \left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) (h) \right\|_{\infty}$$

$$\leq \frac{V_{+} \bar{g}(\phi_{0})}{2} \left(\sqrt{c^{2} + 2c + 2} + \sqrt{c^{2} - 2c + 2} \right) \parallel h \parallel_{\infty} .$$

For 0 < c < 1 we have that

$$\sqrt{c^2 + 2c + 2}$$
 is increasing,
 $\sqrt{c^2 + 2c - 2}$ is decreasing.

Therefore, we have that

$$\left\| \delta_{\phi} \mathbf{F}_{1} \left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) (h) \right\|_{\infty} \leq \frac{V_{+} \bar{g}'(\phi_{0})}{2} \left(\sqrt{5} + \sqrt{2} \right) \parallel h \parallel_{\infty} .$$
 (49)

In a similar way we obtain

$$\left\| \delta_{\psi} \mathbf{F}_{1} \left(\begin{pmatrix} \phi_{0} \\ 0 \end{pmatrix}, c \right) (k) \right\|_{\infty}$$

$$\leq \frac{V_{+} \bar{g}'(\phi_{0}) c}{2} \left(\sqrt{5} + \sqrt{2} \right) \parallel k \parallel_{\infty} .$$
 (50)

Substituting (49) and (50) in (48), we obtain

$$\left\| D\mathbf{F}_1\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right)\begin{pmatrix}h\\k\end{pmatrix}\right\| \le \frac{V_+\bar{g}'(\phi_0)}{2}(1+c)\left(\sqrt{5}+\sqrt{2}\right)\left(\sqrt{\parallel h\parallel_{\infty}^2+\parallel k\parallel_{\infty}^2}\right).$$

Since 0 < c < 1 and $V_+ \alpha < \frac{1}{4}$ we obtain

$$\left\| D\mathbf{F}\left(\begin{pmatrix} \phi_0 \\ 0 \end{pmatrix}, c \right) \begin{pmatrix} h \\ k \end{pmatrix} \right\| < 1,$$

and this is what we wanted to prove. Finally, we have the main theorem.

Theorem 1 Suppose that in system (17), the function \bar{g} has the form (26) and $\alpha V_+ < \frac{1}{4}$. Then, for every $\rho > \max\{\phi_0, \frac{1}{2\alpha}\}$, there exist $c_1(\rho), c_2(\rho)$ with $0 < c_1(\rho) < c_2(\rho) < 1$, such that, for each c, satisfying $0 < c < c_1(\rho)$, the only bounded solution of this system, contained in the closed-ball $B[0, \rho]$, is the stationary solution $\binom{\phi_0}{0}$. On the other hand, for every c, with $c_1(\rho) \leq c \leq c_2(\rho)$, there exists one nontrivial bounded solution, of the system, which is also a homoclinic solution, which corresponds one traveling wave of equation (13) with velocity c. The real translation velocity of this traveling wave is cv_+ . In addition $c_1(\rho), c_2(\rho)$ are the positive roots of the quadratic polynomials defined in (36), (37).

Proof:

The existence of $c_1(\rho)$, was proved in proposition 1. By lemmas 5 and 6 the integral operator **F** defined in (42) satisfies the conditions of the implicit function theorem in one vicinity of $\left(\binom{\phi_0}{0}, c\right)$, which means $\mathbf{F}\left(\begin{pmatrix}\phi\\\psi\end{pmatrix},c\right)$ is of the C' class in one vicinity of $\begin{pmatrix}\begin{pmatrix}\phi_0\\0\end{pmatrix},0\end{pmatrix}$, $\mathbf{F}\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right) = 0$ and $D\mathbf{F}\left(\begin{pmatrix}\phi_0\\0\end{pmatrix},c\right)$ is invertible. Then, there exist vicinities U and V of $\begin{pmatrix}\phi_0\\0\end{pmatrix}$ and c respectively such that, for each $c^* \in V$, one and only nontrivial element $\begin{pmatrix}\phi\\\psi\end{pmatrix} \in U$ exists such that

$$\mathbf{F}\left(\binom{\phi}{\psi}, c^*\right) = 0$$

Then, $\begin{pmatrix} \phi \\ \psi \end{pmatrix}$ is a nontrivial bounded solution of (21) and thus, $\begin{pmatrix} \phi \\ \psi \end{pmatrix}$ is a bounded nontrivial solution of system (17), which, by lemma 1, is a homoclinic solution of system (17).

4 Conclusions

In the model we propose, we have included strong simplifications such as the fact that it is a one dimensional model, not taking into account the curvature of the cortex. Also, we consider that the distribution of connections only depends on the distance between columns and the decreasing scales of the connexions do not depend on the cortical regions considered. Finally, we did not explicitly take into account neurochemical activity. The model we have studied, notwithstanding its important simplifications, has allowed us to obtain analytical results that may motivate experimental analysis. Note the relative simplicity of the proposed model and the immediate possibility to include, although partially, some elements not yet considered in the model, such as decreasing scales that depend on the regions of cortex considered, a generation function of action potentials \bar{q} that depends on the location of the column and the activation function, and the possibility to build a bi dimensional mathematical model of the cerebral cortex that would also include, albeit partially, the real cerebral cortex geometry.

5 Appendix

Theorem (see [1]) Let the equation

$$\frac{du}{dt} = Au + f(t, u) \tag{51}$$

with u(t) in \mathbb{R}^n and suppose that it satisfies the following conditions

1. A is a $n \times n$ matrix, such that

$$\sigma(A) \cap (\{0\} \times \mathbb{R}) = \emptyset.$$
 (52)

2. f is continuous and f(t, 0) = 0

- 3. Let $\rho > 0$ we suppose exist M > 0 such that $|f(t, u)| \le M$ for $t \in \mathbb{R}$ and $|u| \le \rho$. (53)
- 4. There exists q > 0 such that

$$|f(t, u_1) - f(t, u_2| \le q | u_1 - u_2 |$$
 (54)

for $|u_1| \leq \rho$ and $|u_2| \leq \rho$.

5. There exists N > 0 and r > 0 such that

$$G(t) \mid \leq N e^{-r|t|} \text{ for each } t \in \mathbb{R}$$
 (55)

where G(t) is the Green's principal function of the equation (51).

6. M and q such that satisfies

$$M \le \frac{\rho r}{2N}$$
 and $q < \frac{r}{2N}$. (56)

Then, equation (51) has one and only one bounded solution in \mathbb{R} , such that

$$|u(t)| \le \rho \text{ for each } t \in \mathbb{R}.$$
(57)

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