

On Bi-Laminar Neural Field Models of Electrical Activity in the Primary Visual Cortex

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Abstract: We investigate the modelling framework for studying electrical activity in the primary visual cortex of the brain based on a bi-laminar neural field equation. The deep layer of the neural field models the orientation-independent electrical activity, whereas the orientation-dependent superficial layer captures the selectivity to spatially oriented stimuli of the orientation columns in the primary visual cortex. We verify the solvability of a Cauchy problem for the bi-laminar neural field equation with both sigmoidal and Heaviside-type neuronal activation. We also construct connections between the solutions that correspond to these types of neuronal activation, which justifies the use of the Heaviside-type neuronal activation functions that is crucial in the problems of computer simulations involving vast ensembles on neurons. We prove the possibility of a correct approximation of the bi-laminar neural field model with a two-layer neuronal network. We also highlight some perspectives opened by the results of the present research related to the studies of travelling waves of evoked electrical activity in the visual cortex as well as the neural activity control problems in the framework of the neurofeedback paradigm.

Keywords: mathematical models of primary visual cortex, bi-laminar neural field models, two-layer neuronal network models, well-posedness, Heaviside activation function

1. INTRODUCTION

Mathematical models of macro- and mesoscopic neuronal activity of the human brain cortex involve the description of electrical activity of vast ensembles of neuronal elements, which can be registered using electro- and magnetoencefalography (EEG and MEG) [1, 2] and indirectly observed in fMRI recordings [3], are usually presented in the form of neural field equations (see e.g. the pioneering work [4] and the review [5]). The most well-known neural field model is the Amari neural field equation (see [4])

$$\partial_t u(t, x) = -\tau u(t, x) + \int_{\Omega} \omega(x, y) g(u(t, y)) dy. \quad (1.1)$$

Here $u(t, x)$ represents the level of electrical activity in the neural field Ω at time t and position x , the so-called connectivity function ω defines the strengths of interneuronal connections in the neural field, the value $g(u)$ determines the probability of activation (firing) of a neuron with electrical activity level u . In the mathematical neuroscience community, the connectivity ω is typically assumed to be an exponentially decaying function symmetric with respect to the vertical axis or a sum of such functions, and the activation function f is taken to be a continuous sigmoidal-shaped function.

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Several extensions of (1.1) relying on the fact that the neural media is not spatially uniform formalize the heterogeneity of the brain cortex in general forms (see e.g. [6–8]). Such mathematical models are rather well-studied, including the issues of well-posedness [8, 9], construction and justification of the schemes for numerical simulations [8–10], studies of special types of solutions that are physiologically relevant [6, 7, 11, 12]. However, none of these neural field models could capture the characteristic features of primary visual cortex, whose elements of microstructure are selective with respect to perceptions of visual stimuli of certain directions, before the introduction of the following model (see [13]):

$$\begin{aligned} \partial_t u_d(t, x) &= -\tau_d u_d(t, x) + \int_{\Omega} \omega_d(x, y) g_d(u(t, y)) dy \\ &\quad + \nu_d \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} g_s(u_s(t, x, \psi)) d\psi, \\ \partial_t u_s(t, x, \varphi) &= -\tau_s u_s(t, x, \varphi) + \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \omega_s(x, \varphi, y, \psi) g_s(u(t, y, \psi)) d\psi dy \\ &\quad + \nu_s g_d(u_d(t, x)). \end{aligned} \tag{1.2}$$

Here $u_d(t, x)$ defines the level of orientation-independent activity in the deep layer and $u_s(t, x, \varphi)$ is the orientation-dependent activity in the superficial layer. The connectivities in the two layers are denoted by ω_d and ω_s , respectively, and the corresponding time constants are given by τ_d and τ_s . We also include vertical inputs from the deep to the superficial layer with the strength ν_d and back from the superficial to the deep layer with the strength ν_s (the latter is averaged with respect to the orientation preference of neurons in the superficial layer). Functions g_d, g_s are probabilistic functions of firing (neuronal activation functions) for the deep layer and the superficial layer, respectively. We refer the reader to the work [13] for more details on the biophysical justification of the modeling framework (1.2).

To the best of our knowledge, the work [13] is the only published study capturing the orientation selectivity in the visual cortex in the framework of the neural field setting. However, several important mathematical issues were overlooked in this study. The aim of the present paper is to fill in these mathematical blank spots in the justification of the modelling framework (1.2). Namely, in Section 2 we verify the solvability of a Cauchy problem for (1.2) and prove the possibility of correct spatially discretized approximation of (1.2). Section 3 deals with the solvability problem for (1.2) in the case when the probabilistic activation functions are replaced with the instant-activation Heaviside-type functions. In Section 4 we establish connections between the modelling approaches of the two previous sections. In Section 5 we highlight some close perspectives opened by the results of the present research.

2. BI-LAMINAR NEURAL FIELD MODEL WITH CONTINUOUS ACTIVATION FUNCTIONS

For convenience of the presentation of the forthcoming material, we introduce the following notations. For any metric space Λ , any $\lambda_0 \in \Lambda$, $S \subset \Lambda$, and $r > 0$, we define $B_{\Lambda}(\lambda_0, r)$ to be the ball in the space Λ of the radius $r > 0$ centered at λ_0 , \bar{S} to be the closure of S in Λ . We denote by \mathbb{R}^m the m -dimensional real vector space with the norm $|\cdot|$ and by Ω – a compact subset of \mathbb{R}^2 . Denote by $L_p(\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}], \mathbb{R}^2)$ and $C_p(\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}], \mathbb{R}^2)$ the Banach spaces of integrable and continuous, respectively, functions from $\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ to \mathbb{R}^2 , which are π -periodic in the second variable. For all $T > 0$, we denote $\Xi_T = [0, T] \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ and

define $BC_p(\Xi_T, \mathbb{R}^2)$ to be the Banach space of bounded continuous functions $\vartheta : \Xi_T \rightarrow \mathbb{R}^2$ π -periodic in the third variable with the norm $\|\vartheta\|_{BC_p(\Xi_T, \mathbb{R}^2)} = \max_{x \in \Xi_T} |\vartheta(x)|$ and $L_{\infty,p}(\Xi_T, \mathbb{R}^{2 \times 2})$ – to be the Banach space of 2×2 matrix functions from Ξ_T to \mathbb{R} with essentially bounded components π -periodic with respect to the third variable.

In this section we consider the solvability of a Cauchy problem for the bi-laminar neural field equation (1.2) in the case of continuous activation functions (i.e. $g_d = f_d, g_s = f_s$) and justify the possibility to approximate the bi-laminar model (1.2) with a two-layered neuronal network. We start out with the system

$$\begin{aligned} \partial_t u_d(t, x) &= -\tau_d u_d(t, x) + \int_{\Omega} \omega_d(x, y) f_d(u_d(t, y)) dy \\ &\quad + \nu_d \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} f_s(u_s(t, x, \psi)) d\psi, \\ \partial_t u_s(t, x, \varphi) &= -\tau_s u_s(t, x, \varphi) + \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \omega_s(x, \varphi, y, \psi) f_s(u_s(t, y, \psi)) d\psi dy \\ &\quad + \nu_s f_d(u_d(t, x)) \end{aligned} \tag{2.3}$$

together with the initial condition

$$u_d(0, x) = \hat{u}_d(x), \quad u_s(0, x, \varphi) = \hat{u}_s(x, \varphi) \tag{2.4}$$

where $\hat{u}_d : \Omega \rightarrow \mathbb{R}$, $\hat{u}_s : \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}] \rightarrow \mathbb{R}$ are continuous and $\lim_{\varphi \rightarrow -\frac{\pi}{2}} \hat{u}_s(x, \varphi) = \hat{u}_s(x, \frac{\pi}{2})$.

Assume that

- (A $_{\omega}$) The neuronal connectivity functions $\omega_d, \omega_s : \Omega \times \Omega \rightarrow \mathbb{R}^n$ are continuous;
- (A $_f$) The neuronal activation functions $f_d, f_s : \mathbb{R}^2 \rightarrow [0, 1]$ are Lipschitz continuous;

Theorem 2.1:

Let assumptions (A $_{\omega}$) and (A $_f$) be satisfied. Then there exists a unique solution of the problem (2.3), (2.4), which is a continuous function from $[0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ to \mathbb{R}^2 .

Proof

The system (2.3) can be written as

$$\partial_t u(t, x, \varphi) = -\tau u(t, x, \varphi) + \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} V(x, y, \varphi, \psi) F(u(t, x, \varphi)) d\psi dy, \tag{2.5}$$

where

$$F(u) = \begin{pmatrix} f_d(u_d) \\ f_s(u_s) \end{pmatrix}, \quad V(x, y, \varphi, \psi) = \begin{pmatrix} \omega_d(x, y)/\pi & \nu_s \delta(x - y) \\ \nu_d \delta(x - y)/\pi & \omega_s(x, \varphi, y, \psi) \end{pmatrix}.$$

We will consider the problem of solvability of the system (2.3), (2.4) in a more general setting that reads as follows:

$$u(t, x, \varphi) = \hat{u}(x, \psi) + \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) F(u(s, y, \psi)) \mu^1(d\psi) \mu^2(dy) ds \tag{2.6}$$

where

$$u(t, x, \varphi) = \begin{pmatrix} u_d(t, x) \\ u_s(t, x, \varphi) \end{pmatrix}, \hat{u}(x, \varphi) = \begin{pmatrix} \hat{u}_d(x) \\ \hat{u}_s(x, \varphi) \end{pmatrix},$$

$$W(t, s, x, y, \varphi, \psi) = \begin{pmatrix} \exp(-\tau_d(t-s)) & 0 \\ 0 & \exp(-\tau_s(t-s)) \end{pmatrix} V(x, y, \varphi, \psi),$$

and μ^1 and μ^2 are complete σ -additive measures defined on \mathbb{R} and \mathbb{R}^2 , respectively, and finite on bounded subsets of their ranges of definition.

Introduce the following two conditions:

- (\mathbf{A}_W) For any $T > 0$ and any $(t, x, \varphi) \in \Xi_T$, the function $W(t, \cdot, x, \cdot, \varphi, \cdot)$ belongs to $L_{\infty, p}(\Xi_T, \mathbb{R}^{2 \times 2})$, the function $(t, x, \varphi) \mapsto \|W(t, \cdot, x, \cdot, \varphi, \cdot)\|_{L_{\infty, p}(\Xi_T, \mathbb{R}^{2 \times 2})}$ is bounded, and for any measurable set $\mathbb{I} \subset \Xi_T$ and any $(t_0, x_0, \varphi_0) \in \Xi_T$, it holds true that

$$\lim_{(t, x, \varphi) \rightarrow (t_0, x_0, \varphi_0)} \int_{\mathbb{I} \cap ([0, t] \times \Omega)} \int \int W(t, s, x, y, \varphi, \psi) \mu^1(d\psi) \mu^2(dy) ds$$

$$= \int_{\mathbb{I} \cap ([0, t_0] \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}))} \int \int W(t_0, s, x_0, y, \varphi_0, \psi) \mu^1(d\psi) \mu^2(dy) ds.$$

- (\mathbf{A}_F) The function $F : \mathbb{R}^2 \rightarrow [0, 1]^2$ is Lipschitz continuous (hereinafter, we denote $[0, 1]^2 = [0, 1] \times [0, 1]$).

Choose $T > 0$. We define $u_T \in BC_p(\Xi_T, \mathbb{R}^2)$ to be a T -local solution to (2.6) if u_T satisfies the equation (2.6) on the set Ξ_T . We consider a continuous function $u_\infty : [0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}) \rightarrow \mathbb{R}^2$ to be a global solution to (2.6) if for any $T > 0$, the restriction of u_∞ to Ξ_T is a T -local solution to (2.6).

Let us formulate the statement on solvability of the integral equation (2.6) in terms of the definitions given above.

Lemma 2.1:

Let assumptions (\mathbf{A}_W) and (\mathbf{A}_F) be satisfied. Then for any $T > 0$, the equation (2.6) has a unique T -local solution that is the restriction to Ξ_T of the unique global solution to (2.6).

Proof of Lemma 2.1

We choose arbitrary $T > 0$ and take any two functions $u_1, u_2 \in BC_p(\Xi_T, \mathbb{R}^2)$. We estimate $\|\mathfrak{J}_T N_T u_1 - \mathfrak{J}_T N_T u_2\|_{BC_p(\Xi_T, \mathbb{R}^2)} = \max_{(t, x, \varphi) \in \Xi_T} |(\mathfrak{J}_T N_T u_1)(t, x, \varphi) - (\mathfrak{J}_T N_T u_2)(t, x, \varphi)|$,

where for any $\xi \in BC_p(\Xi_T, \mathbb{R}^2)$, the operator \mathfrak{J}_T is defined by the relation

$$(\mathfrak{J}_T \xi)(t, x, \varphi) = \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) \xi(s, y, \psi) \mu^1(d\psi) \mu^2(dy) ds \quad (2.7)$$

and, due to condition (\mathbf{A}_W), has the image in $BC_p(\Xi_T, \mathbb{R}^2)$ (see e.g. [14], Chapter 3, § 5.5); the operator N_T defined as $(N_T \xi)(t, x, \varphi) = F(\xi(t, x, \varphi))$ acts from the space $BC_p(\Xi_T, \mathbb{R}^2)$ to itself due to (\mathbf{A}_F). By the virtue of (\mathbf{A}_F), we have

$$\max_{(t, x, \varphi) \in \Xi_T} |(\mathfrak{J}_T N_T u_1)(t, x, \varphi) - (\mathfrak{J}_T N_T u_2)(t, x, \varphi)|$$

$$\begin{aligned}
 &= \max_{(t,x,\varphi) \in \Xi_T} \left| \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t,s,x,y,\varphi,\psi) F(u_1(s,y,\psi)) \mu^1(d\psi) \mu^2(dy) ds \right. \\
 &\quad \left. - \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t,s,x,y,\varphi,\psi) F(u_2(s,y,\psi)) \mu^1(d\psi) \mu^2(dy) ds \right| \\
 &\leq \max_{(t,x,\varphi) \in \Xi_T} \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} |W(t,s,x,y,\varphi,\psi)| |F(u_1(s,y,\psi)) - F(u_2(s,y,\psi))| \mu^1(d\psi) \mu^2(dy) ds \\
 &\leq \max_{(t,x,\varphi) \in \Xi_T} \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} |W(t,s,x,y,\varphi,\psi)| l_f |u_1(s,y,\psi) - u_2(s,y,\psi)| \mu^1(d\psi) \mu^2(dy) ds \\
 &\leq l_f \max_{(t,x,\varphi) \in \Xi_T} \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} |W(t,s,x,y,\varphi,\psi)| \mu^1(d\psi) \mu^2(dy) ds \|u_1(s,y,\psi) - u_2(s,y,\psi)\|
 \end{aligned}$$

where $l_f > 0$ is the Lipschitz constant of F . By choosing $T = T_1 > 0$ in a way that

$$l_f \max_{(t,x,\varphi) \in \Xi_{T_1}} \int_0^{T_1} \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} |W(t,s,x,y,\varphi,\psi)| \mu^1(d\psi) \mu^2(dy) ds < 1$$

and applying Banach fixed point theorem (see e.g. [15], Chapter 2, § 14) to the problem

$$u = \mathfrak{J}_{T_1} N_{T_1} u \tag{2.8}$$

in the space $BC_p(\Xi_{T_1}, \mathbb{R}^2)$ we prove the existence of a unique solution $u_{T_1} \in BC_p(\Xi_{T_1}, \mathbb{R}^2)$ of (2.8), which is a unique T_1 -local solution of the integral equation (2.6).

We introduce a new time-variable $t' = t - T_1$. Now we consider the problem (2.6) with $t = t'$. We will refer to this new problem as (2.6)' (with the initial problem $u'_d(-T_1, x) = \hat{u}'_d(x)$, $u'_s(-T_1, x, \varphi) = \hat{u}'_s(x, \varphi)$). We apply the procedure described above and prove the existence of a T'_1 -local solution $u_{T'_1}$ to (2.6)' for some $T'_1 > 0$. We thus obtain a T_2 -local

solution u_{T_2} to (2.6) where $T_2 = T_1 + T'_1$, $u = \begin{cases} u_{T_1} & t \in [0, T_1] \\ u_{T'_1} & t \in [T_1, T_2] \end{cases}$. The T_2 -local solution u_{T_2}

is continuous at (T_1, x) for any $x \in \Omega$, that is, $u_{T_2} \in C$. On the next step, we choose any T_2 -local solution $u_{T_2} \in C$ to the equation (2.6). We introduce a new time-variable $t'' = T - T_2$ and repeat the procedure

We thus obtain a strictly increasing sequence $\{T_i\}, i = 1, 2, \dots$ and the corresponding sequence of local solutions $u_{T_i}, i = 1, 2, \dots$ such that for any $i_1 < i_2$, $u_{T_{i_1}}$ is the restriction of $u_{T_{i_2}} \in BC_P(\Xi_{T_{i_2}}, \mathbb{R}^2)$ to the set $\Xi_{T_{i_1}}$. We find $\lim_{i \rightarrow \infty} T_i = \hat{T}$. Take any $t^* \in (0, \hat{T})$. For some number $i, t \in (T_{i-1}, T_i)$ and u_{t^*} therefore is a t^* -local solution. We have constructed the mapping $t^* \mapsto u_{t^*}$. Prove that $\{T_i\}, i = 1, 2, \dots$ is not bounded. Indeed, assuming the contrary, we get $T_i < T^*$ for some $T^* < \infty$ and all $i = 1, 2, \dots$, so that the norms of the

corresponding solutions satisfy the relation $\lim_{T \rightarrow T^* - 0} \|u_T\|_{BC_p(\Xi_T, \mathbb{R}^2)} = \infty$ which contradicts to (A_W) . We thus proved that $\{T_i\}, i = 1, 2, \dots$ is not bounded and, hence that the sequence of local solutions constructed in the proof has a unique limit that is a global solution to (2.6). Thus, Lemma 2.1 is proved. \square

Note that the validity of conditions (A_ω) and (A_f) naturally provides the fulfillment of (A_W) and (A_F) .

Now, applying Lemma 2.1 to (2.6) in the case when $\mu^1(d\psi)$ is the Lebesgue measure on \mathbb{R} $\mu^2(dy)$ is the Lebesgue measure on \mathbb{R}^2 , we prove the theorem.

The validity of the following statement is implied by Lemma 2.1.

Remark 2.1:

For any $T > 0$, the restriction of the unique (global) solution obtained in Theorem 2.1 to the set Ξ_T is the unique solution to the problem (2.3), (2.4) on the set Ξ_T .

Consider now a two-layer neural network

$$\begin{aligned} \partial_t v_d^i(t, n) &= -\tau_d v_d^i(t, n) + \sum_{j=1}^n \omega_d^{ij}(n) f_d(v_d^j(t, n)) + \nu_d \sum_{l=1}^m f_s(v_s^{il}(t, m)), \\ \partial_t v_s^{it}(t, n, m) &= -\tau_s v_s^{it}(t, n, m) + \sum_{j=1}^n \sum_{l=1}^m \omega_s^{ijlt}(n, m) f_s(v_s^{jl}(t, n, m)) + \nu_s f_d(v_d^i(t, n)) \end{aligned} \tag{2.9}$$

having n "spatial" elements in each of the layers and m "directions" in the orientation columns layer, and parameterized by the dimensions n and m of its layers. For any natural n and m , the values $v_d^i(t, n), v_s^{it}(t, n, m)$ correspond to the neuronal activity of the deep layer and the superficial layer in the network, the constants $\omega_d^{ij}(n), \omega_s^{ijlt}(n, m)$ define the strengths of connections inside each of the layers, and the constants ν_d, ν_s define the strengths of connections between the layers.

The following statement establishes correspondence between the bi-laminar neural field model (2.3) and the two-layer neuronal network (2.9).

Proposition 2.1:

Let assumptions $(A_\omega), (A_f)$ be satisfied. For each natural m and n , let $\{\delta_\xi^1(m), \xi = 1, \dots, m\}$ and $\{\delta_i^2(n), i = 1, \dots, n\}$ be finite families of open subsets of \mathbb{R} and \mathbb{R}^2 , respectively, satisfying the conditions

$$\bigcup_{\xi=1}^m \overline{\delta_\xi^1(m)} = \left(-\frac{\pi}{2}, \frac{\pi}{2}\right], \quad \bigcup_{i=1}^n \overline{\delta_i^2(n)} = \Omega,$$

$$\lim_{m \rightarrow \infty} \max_{\xi=1, \dots, m} \text{mes}(\delta_\xi^1(m)) = 0, \quad \lim_{n \rightarrow \infty} \max_{i=1, \dots, n} \text{mes}(\delta_i^2(n)) = 0,$$

where $\text{mes}(\cdot)$ denotes the Lebesgue measure. Let $\psi_\xi(m)$ and $y_i(n)$ ($\xi = 1, \dots, m, i = 1, \dots, n$) be arbitrary points in $\delta_\xi^1(m)$ and $\delta_i^2(n)$, respectively.

Then for each natural n and m and any $\alpha(n, m) \in \mathbb{R}^{nm+n}$, there exists a unique continuous solution to the system (2.9) considered together with the initial conditions

$$(v_d^i(n))(0) = \alpha_d^i(n), \quad (v_s^{it}(n, m))(0) = \alpha_s^{it}(n, m), \tag{2.10}$$

which is a function $v(n, m) = (v_d(n), v_s(n, m))$ from $[0, \infty)$ to \mathbb{R}^{nm+n} .

Moreover, the sequence of solutions $v^{it}(n, m) = (v_d^i(n), v_s^{it}(n, m))$ to the initial value problem (2.9), (2.9), where

$$\begin{aligned} \omega_d^{ij}(n) &= \text{mes}(\delta_i^2(n))\omega_d(y_i(n), y_j(n)), \\ \omega_s^{ijt}(n, m) &= \text{mes}(\delta_i^2(n))\text{mes}(\delta_t^1(m))\omega_s(y_i(n), y_j(n), \psi_t(m), \psi_l(m)), \\ \alpha_d^{it}(n) &= \hat{u}_d(0, y_i(n)), \quad \alpha_s^{it}(n, m) = \hat{u}_s(0, y_i(n), \psi_t(m)) \end{aligned} \tag{2.11}$$

converges to the solution $u(t, x, \varphi)$ ($t \geq 0, x \in \Omega, \varphi \in (-\frac{\pi}{2}, \frac{\pi}{2}]$) of the initial value problem (2.3), (2.4), as $n, m \rightarrow \infty$, in the following sense:

$$\lim_{\substack{n \rightarrow \infty \\ m \rightarrow \infty}} \max_{t \in [0, T]} \left(\sup_{\substack{1 \leq i \leq n \\ 1 \leq t \leq m}} \left(\sup_{\substack{x \in \delta_i^2(n) \\ \varphi \in \delta_t^1(m)}} |u(t, x, \varphi) - (v^{it}(n, m))(t)| \right) \right) = 0 \tag{2.12}$$

for any $T > 0$.

Proof

By a reasoning similar to the one applied in the proof of Theorem 2.1, we can conclude that for any natural n and m , the problem (2.9), (2.10) is equivalent to the equation (2.6) with $\mu^1 = \mu_{1/m}^1, \mu^2 = \mu_{1/n}^2$, where $\mu_{1/m}^1$ and $\mu_{1/n}^2$ are the sums of m Dirac point measures concentrated at the points $\psi_t(m) \in (-\frac{\pi}{2}, \frac{\pi}{2}]$ and n Dirac point measures at the points $y_i(n) \in \Omega$, respectively. We define μ_0^1 and μ_0^2 to be the Lebesgue measures on \mathbb{R} and \mathbb{R}^2 , respectively. Therefore, solvability of (2.9), (2.10) for each natural n and m follows from Theorem 2.1. The proposition conditions imply that the measures $\mu_{(\cdot)}^1$ and $\mu_{(\cdot)}^2$ are weakly right-continuous at 0 on the sets $(-\frac{\pi}{2}, \frac{\pi}{2}]$ and Ω , respectively. Indeed, for any continuous function $\Upsilon(x, \varphi) : (-\frac{\pi}{2}, \frac{\pi}{2}] \times \Omega \rightarrow \mathbb{R}^2$,

$$\begin{aligned} & \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \Upsilon(y, \psi) \mu_{1/m}^1(d\psi) \mu_{1/n}^2(dy) \\ &= \sum_{i=1}^n \sum_{t=1}^m \Upsilon(y_i(n), \psi_t(m)) \text{mes}(\delta_t^1(m)) \text{mes}(\delta_i^2(n)) \\ &= \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \Upsilon(y, \psi) \mu_0^1(d\psi) \mu_0^2(dy) \end{aligned} \tag{2.13}$$

as $n, m \rightarrow \infty$. Finally, assumptions $(A_\omega), (A_f)$, together with the relations (2.11) and the property (2.13) provide the convergence (2.12). \square

3. BI-LAMINAR NEURAL FIELD MODEL WITH HEAVISIDE-TYPE ACTIVATION FUNCTIONS

In this section we derive conditions for solvability of (1.2) in the case of discontinuous Heaviside-type activation functions (i.e., $g_d = H_d$, $g_s = H_s$):

$$\begin{aligned} \partial_t u_d(t, x) = & -\tau_d u_d(t, x) + \int_{\Omega} \omega_d(x, y) H_d(u_d(t, y)) dy \\ & + \nu_d \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} H_s(u_s(t, x, \psi)) d\psi, \end{aligned} \quad (3.14)$$

$$\begin{aligned} \partial_t u_s(t, x, \varphi) = & -\tau_s u_s(t, x, \varphi) + \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \omega_s(x, \varphi, y, \psi) H_s(u_s(t, y, \psi)) d\psi dy \\ & + \nu_s H_d(u_d(t, x)) \end{aligned}$$

where

(\mathbf{A}_H) The components of the neuronal activation function $H = (H_d, H_s)$, $H : \mathbb{R}^2 \rightarrow \{0, 1\}$ are Heaviside-type activation functions:

$$H_k(u) = \begin{cases} 0, & u \leq h_k, \\ 1, & u > h_k, \end{cases}$$

where h_k is the threshold of activation, $k = d, s$.

Following the procedure described in the proof of Theorem 2.1 we rewrite the problem (3.14), (2.4) as follows:

$$u(t, x, \varphi) = \hat{u}(x, \psi) + \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) H(u(s, y, \psi)) d\psi dy ds \quad (3.15)$$

where $H = \begin{pmatrix} H_d \\ H_s \end{pmatrix}$. Using the ideas of A.F. Filippov (see [16], Chapter 2, § 4), we address the problem of solvability of the integral equation (3.15) and, hence, the problem (3.14), (2.4), in the sense of the so-called generalized solutions. We define a *generalized solution* to the problem (3.14), (2.4) to be a continuous function from $[0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ to \mathbb{R}^2 , which satisfies the inclusion

$$u(t, x, \varphi) \in \hat{u}(x, \psi) + \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) \mathcal{H}(u(s, y, \psi)) d\psi dy ds \quad (3.16)$$

where

($\mathbf{A}_{\mathcal{H}}$) The set-valued function $\mathcal{H} : \mathbb{R}^2 \rightrightarrows [0, 1]^2$ is defined as

$$\mathcal{H} = (\mathcal{H}_d, \mathcal{H}_s), \quad \mathcal{H}_k(u) = \begin{cases} 0, & u < h_k, \\ [0, 1], & u = h_k, \\ 1, & u > h_k, \end{cases} \quad k = d, s \text{ (} h_k \text{ are the same as in } (\mathbf{A}_H)\text{)}.$$

Theorem 3.1:

Let assumptions (A_ω) and (A_H) be satisfied. Then there exists a generalized solution to the problem (3.14), (2.4), which is a continuous function from $[0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ to \mathbb{R}^2 ,

Proof

We start out with proving the solvability of the inclusion (3.16) in the following sense. For any $T > 0$, we define $u_T \in BC_p(\Xi_T, \mathbb{R}^2)$ to be a T -local solution to (3.16) if u_T satisfies the inclusion (3.16) on the set Ξ_T . We say that a continuous function $u_\infty : [0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}] \rightarrow \mathbb{R}^2$ is a global solution to (3.16) if for any $T > 0$, the restriction of u_∞ to Ξ_T is a T -local solution to the inclusion (3.16).

Lemma 3.1:

Let assumptions (A_W) and $(A_{\mathcal{H}})$ be satisfied. Then, for any $T > 0$, the inclusion (3.16) has a T -local solution. Any T -local solution can be extended to a global solution to (3.16).

Proof of Lemma 3.1

We choose arbitrary $T > 0$ and represent the mapping on the right-hand side of (3.16) as follows:

$$(\mathfrak{J}_T \mathcal{N}_T u)(t, x, \varphi) = \int_0^t \int_\Omega \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) \mathcal{H}(u(s, y, \psi)) d\psi dy ds$$

where $\mathfrak{J}_T : BC_p(\Xi_T, \mathbb{R}^2) \rightarrow BC_p(\Xi_T, \mathbb{R}^2)$ is defined by (2.7) and for any $\xi \in BC_p(\Xi_T, \mathbb{R}^2)$, $(\mathcal{N}_T \xi)(t, x, \varphi) = \mathcal{H}(\xi(t, x, \varphi))$.

By the virtue of (A_W) we have that \mathfrak{J}_T is a continuous operator. The operator \mathcal{H} is upper-semicontinuous due to $(A_{\mathcal{H}})$. As \mathcal{H} is upper-semicontinuous and \mathfrak{J}_T is a linear continuous operator, for $\mathbb{M}_r^\xi = BC(\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}], \mathbb{R}^2)(\xi, r)$, the composition $\mathfrak{J}_T \mathcal{N}_T \xi : \mathbb{M}_r^\xi \rightarrow C(\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}], \mathbb{R}^2)$ is a convex valued mapping. Show that the composition $\mathfrak{J}_T \mathcal{N}_T \xi$ is upper-semicontinuous and closed. Choose u_i and ϑ such that $\vartheta \in \mathfrak{J} \mathcal{N} u_i$ and

$$\|u_i - u_0\|_{BC_p(\Xi_T, \mathbb{R}^2)} \rightarrow 0, \quad \|\vartheta_i - \vartheta_0\|_{BC_p(\Xi_T, \mathbb{R}^2)} \rightarrow 0$$

where $u_0 \in BC_p(\Xi_T, \mathbb{R}^2)$, $\vartheta_0 \in BC_p(\Xi_T, \mathbb{R}^2)$ are some limit points and $v_i \rightarrow v_0 \in BC_p(\Xi_T, \mathbb{R}^2)$. Choose also $w_i \in \mathcal{N} v_i$ such that $\vartheta_i = \mathfrak{J} w_i$.

Consider the sequence $\{w_i\} \subset L$ as the sequence of Bochner integrable mappings $w_i : [0, T] \rightarrow L(\Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}])$. By the virtue of condition $(A_{\mathcal{H}})$ and convergence $v_i \rightarrow v_0$ we can apply Kolmogorov-Riesz compactness theorem [17] and consequently Proposition 4.2.1 [18], and conclude that $w_i \rightarrow w_0$ weakly, $w_0 \in L$. Further, using Mazur's lemma (see [19], Section

5.1, Theorem 2) we have $\hat{w}_i = \sum_{j=i}^\infty \beta_{ij} w_j$ such that

$$\|\hat{w}_i - w_0\| \rightarrow 0 \tag{3.17}$$

where the coefficients β_{ij} satisfy the following conditions:

- $\sum_{j=i}^\infty \beta_{ij} = 1$ for all $i = 1, 2, \dots$;
- one can find a number j_0 such that $\beta_{ij} = 0$ for all $j > j_0$ and for each $i = 1, 2, \dots$

The relation (3.17) implies (see Section 41, Theorem 4 [15]) the existence of a subsequence of the sequence \hat{w}_i converging to w_0 almost everywhere.

Due to upper semicontinuity of \mathcal{H} , for almost all $(t, x, \varphi) \in \Xi_T$ and for any $\varepsilon > 0$ there exists a number $i_0 = i_0(t, x, \varphi, \varepsilon)$ such that for all $i > i_0$ it holds true that

$$\mathcal{H}(t, x, \varphi, v_i) \subset B((\mathcal{H}(t, x, \varphi_0))(t, x, \varphi), \varepsilon)$$

We thus have $w_i \in B((\mathcal{H}(t, x, \varphi_0))(t, x, \varphi), \varepsilon)$. As an ε -neighborhood of a convex set is convex, we obtain $\hat{w}_i \in B((\mathcal{H}(t, x, \varphi_0))(t, x, \varphi), \varepsilon)$. By the virtue of the closedness of \mathcal{H} , the latter relation implies that $w_0 \in B((\mathcal{H}(t, x, \varphi_0))(t, x, \varphi), \varepsilon)$ so that $w_0 \in \mathcal{N}u_0$. Putting

$$\hat{v}_i = \mathfrak{I}_T \hat{w}_i = \mathfrak{I}_T \sum_{j=i}^{\infty} \beta_{ij} w_j = \sum_{j=i}^{\infty} \beta_{ij} \mathfrak{I}_T w_j = \sum_{j=i}^{\infty} \beta_{ij} \vartheta_j$$

we obtain $\|\hat{v}_i - \vartheta\| \rightarrow 0$, which due to the continuity of \mathfrak{I}_T implies that

$$\vartheta = \mathfrak{I}_T w_0 \in \mathfrak{I}_T \mathcal{N}u_0.$$

Thus, the closedness and, consequently, the upper semicontinuity of the composition $\mathfrak{I}_T \mathcal{N}_T$ is proved.

Now we choose some sufficiently large $T > 0$ and put $r = 2 \max(\hat{u})$. Using (A_W) and $(A_{\mathcal{H}})$, find the maximal $T_1 \in (0, T]$ such that

$$\max_{(t,x,\varphi) \in \Xi_{T_1}} \left| \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) \xi_r(s, x, \psi) - \hat{u}(x, \varphi) d\psi dy ds \right| \leq r.$$

Thus, we have $\mathfrak{I}_{T_1} \mathcal{N}_{T_1}(\mathbb{M}_r^\xi) \subset \mathbb{M}_r^\xi$, we apply Bohnenblust–Karlin theorem and prove the existence of a fixed point $u_{T_1} \in \Xi_{T_1}$ that is a T_1 -local solution to the problem (3.16).

Choose any T_1 -local solution u_{T_1} to problem (3.16). We introduce a new time-variable $t_1 = t - T_1$. Now, we consider the problem (3.16) with $t = t_1$. We apply the procedure described above and prove the existence of a T'_1 -local solution $u'_{T'_1}$ to (3.16) for some $T'_1 > 0$. We thus obtain a T_2 -local solution u_{T_2} to (3.16), where $T_2 = T_1 + T'_1$. $u = \begin{cases} u_{T_1} & t \in [0, T_1] \\ u'_{T'_1} & t \in [T_1, T_2] \end{cases}$. The T_2 -local solution u_{T_2} is continuous at (T_2, x, φ) .

In the next step, we select any T_2 -local solution u_{T_2} to the problem (3.15), (2.4). We introduce a new time-variable $t_2 = t - T_2$ and repeat the procedure above. We thus obtain a strictly increasing sequence $\{T_i\}, i = 1, 2, \dots$ and the corresponding sequence of local solutions $u_{T_i}, i = 1, 2, \dots$ such that for any $i_1 < i_2$, $u_{T_{i_1}}$ is the restriction of $u_{T_{i_2}} \in BC_P(\Xi_{T_{i_2}}, \mathbb{R}^2)$ to the set $\Xi_{T_{i_1}}$. We find $\lim_{i \rightarrow \infty} T_i = \hat{T}$. Take any $t^* \in (0, \hat{T})$. For some number $i, t \in (T_{i-1}, T_i)$ and u_{t^*} therefore is a t^* -local solution. We have constructed the mapping $t^* \mapsto u_{t^*}$. Prove that $\{T_i\}, i = 1, 2, \dots$ is not bounded. Indeed, assuming the contrary, we get $T_i < T^*$ for some $T^* < \infty$ and all $i = 1, 2, \dots$, so that the norms of the corresponding solutions satisfy the relation $\lim_{T \rightarrow T^*-0} \|u_T\|_{BC_P(\Xi_T, \mathbb{R}^2)} = \infty$ which contradicts to (A_W) . We thus proved that $\{T_i\}, i = 1, 2, \dots$ is not bounded and, hence that the sequence of local solutions constructed in the proof has a unique limit that is a global solution to (2.6). Thus, Lemma 3.1 is proved. \square

Lemma 3.1 implies that the problem (3.14), (2.4) possesses a generalized solution, which proves the theorem.

4. CONTINUOUS DEPENDENCE OF SOLUTIONS TO BI-LAMINAR NEURAL FIELD MODEL UNDER THE TRANSITION FROM CONTINUOUS TO HEAVISIDE-TYPE NEURONAL ACTIVATION

We introduce here the following parameterized version of (2.3)

$$\begin{aligned} \partial_t u_d(t, x) &= -\tau_d u_d(t, x) + \int_{\Omega} \omega_d(x, y) f_d^i(u_d(t, y)) dy \\ &\quad + \nu_d \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} f_s^i(u_s(t, x, \psi)) d\psi, \\ \partial_t u_s(t, x, \varphi) &= -\tau_s u_s(t, x, \varphi) + \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} \omega_s(x, \varphi, y, \psi) f_s^i(u_s(t, y, \psi)) d\psi dy \\ &\quad + \nu_s f_d^i(u_d(t, x)) \end{aligned} \tag{4.18}$$

with a natural parameter i .

The next statement presents the main result of this section.

Theorem 4.1:

Let assumption (A_{ω}) be fulfilled and for all natural i , the functions $f_d^i, f_s^i : \mathbb{R} \rightarrow [0, 1]$ satisfy assumption (A_f) .

Then for any natural i , there exists a unique solution, say u^i , to the equations (4.18) with the initial condition (2.4), which is a continuous function from $[0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}]$ to \mathbb{R}^2 . Moreover, if for any $\varepsilon > 0$, one can find a number i_{ε} such that

$$|f_k^i(u) - H_k(u)| < \varepsilon, \quad u \in \mathbb{R} \setminus \overline{B_{\mathbb{R}}(h_k, \varepsilon)}, \quad i > i_{\varepsilon}, \quad k = d, s, \tag{4.19}$$

a continuous function $u^0 : [0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}] \rightarrow \mathbb{R}^2$, $u^0 = (u_d^0, u_s^0)$, obtained from the relation

$$\lim_{T \rightarrow \infty} \lim_{i \rightarrow \infty} \max_{(t, x, \varphi) \in \Xi_T} |u^i(t, x, \varphi) - u^0(t, x, \varphi)| = 0$$

in the case if it satisfies the condition

$$\begin{aligned} &\text{mes}(\{(t, x) \in [0, \infty) \times \Omega, u_d^0(t, x) = h_d, u_s^0(t, x, \varphi) = h_s\} \\ &\cup \{(t, x, \varphi) \in [0, \infty) \times \Omega \times (-\frac{\pi}{2}, \frac{\pi}{2}], u_d^0(t, x) = h_d, u_s^0(t, x, \varphi) = h_s\}) = 0, \end{aligned} \tag{4.20}$$

is a generalized solution to the problem (3.14), (2.4).

Proof

Similarly to the previous sections we can rewrite (4.18) as

$$u(t, x, \varphi) = \hat{u}(x, \psi) + \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) (\mathcal{F}(u, \frac{1}{i}))(s, y, \psi) d\psi dy ds, \tag{4.21}$$

where

$$\mathcal{F}(u, \frac{1}{i}) = \begin{pmatrix} f_d^i(u_d) \\ f_s^i(u_s) \end{pmatrix}.$$

Unique solvability of the problem (4.18), (2.4) for all natural i follows from Theorem 2.1. Choose arbitrary $T > 0$. Assumptions (A_ω) and (A_f) imply that the set

$$\bigcup_{i=1}^{\infty} \int_0^t \int_{\Omega} \int_{-\frac{\pi}{2}}^{\frac{\pi}{2}} W(t, s, x, y, \varphi, \psi) (\mathcal{F}_T(BC_p(\Xi_T, \mathbb{R}^2), \frac{1}{i})) (s, y, \psi) d\psi dy ds$$

and, hence, the set of solutions to the problem (4.18), (2.4) defined on the set Ξ_T , say u_T^i , (for all natural i) is relatively compact in $BC_p(\Xi_T, \mathbb{R}^2)$. Choose any limit point, say $u_T^0 \in BC_p(\Xi_T, \mathbb{R}^2)$, of the set $\bigcup_{i=1}^{\infty} u_T^i$. Denoting

$$\mathcal{F}_T(u, 0) = \begin{pmatrix} \mathcal{H}_d(u_d) \\ \mathcal{H}_s(u_s) \end{pmatrix}$$

we notice that the relations (4.19), (4.20) and the properties of set-valued integral (see e.g. [20], §1.5.1) provide that for any $\varepsilon > 0$, there exists a number i_ε such that

$$\mathfrak{J}_T \mathcal{F}_T(u^i, \frac{1}{i}) \in B_{BC_p(\Xi_T, \mathbb{R}^2)}(\mathfrak{J}_T \mathcal{F}(u^0, 0), \varepsilon)$$

for all $i > i_\varepsilon$. The latter allows to get the following relation:

$$B_{BC_p(\Xi_T, \mathbb{R}^2)}(u^0, \varepsilon/2) \ni u^i = \mathfrak{J}_T \mathcal{F}(u^i, \frac{1}{i}) \in B_{BC_p(\Xi_T, \mathbb{R}^2)}(\mathfrak{J}_T \mathcal{F}(u^0, 0), \varepsilon/2),$$

which means that u^0 is a limit point of $\mathfrak{J}_T \mathcal{F}_T(u^0, 0) = \mathfrak{J}_T \mathcal{N}_T u^0$ (see Section 3). Noticing that the values of $\mathfrak{J}_T \mathcal{F}_T$ are closed (see e.g. the proof of Lemma 3.1), we prove that $u^0 \in BC_p(\Xi_T, \mathbb{R}^2)$ is a generalized solution of the problem (3.14), (2.4) on the set Ξ_T . Taking into account the arbitrary choice of $T > 0$, we finalize the proof. \square

5. CONCLUSIONS AND OUTLOOK

In this research we established fundamental properties of the mathematical model for the macro- and meso-scale electrical activity in the primary visual cortex based on the neural field concept. This opens several perspectives of further applications of the modelling framework (1.2).

In recent studies of the human brain travelling waves, which are the most well-identified phenomenon of the brain electrical activity, underlying the brain functioning in both normal regime and in various pathological states (such as e.g. epilepsy and Parkinson's disease), the neural field equation (1.1) was successfully used in the simulations of travelling waves in the sensorimotor cortex [21]. The model (1.1) was supplemented by an extra component formalizing a slow negative feedback in the neural media due to the presence of the inhibitory neurons (see e.g. [22]). A much more intriguing problem from the point of view of neurophysiology is to investigate and model the interaction of travelling waves in the visual cortex with the orientation columns under a presentation of spatially oriented stimuli. In a similar way to (1.1), the models (2.3) and (3.14) can be equipped with the corresponding negative feedback components for mathematical modelling in the framework of the aforementioned studies. Moreover, the presentation of spatially oriented stimuli can be treated as an impulse control problem for the modelling system (1.2), which can be studied e.g. based on the ideas developed in [23].

The models of the form (1.2) can be used in the framework of the neurofeedback paradigm, where the target characteristics of the brain activity are converted into human-interpretable visual, auditory or tactile stimuli [24, 25]. For example, a person undergoing a neurofeedback session learns to regulate the activity of his own central nervous system by performing task of maintaining the stimulus in a certain state trying to keep the angle of a rotating arrow displayed on the monitor screen within certain limits, which corresponds to maintaining the target characteristic of brain activity in the required range. This paradigm is used both for the correction of the psycho-emotional state, and for training to improve the efficiency of cognitive functions, as well as the treatment of a wide range of neurodegenerative diseases, including epilepsy [26].

Another paradigm involves stimulation and alteration (transcranial magnetic, using direct or alternating current) of brain activity, depending on the current state of the central nervous system [27, 28]. It is aimed at suppressing pathological activity or inducing a specific behavioral response, which is used e.g. to suppress tremor in patients with Parkinsonism or reduce the probability of an epileptic seizure.

The paradigms described can be related to minimization problems constructed based on the mathematical framework (3.14), as it is more suitable for computer simulations compared to the model (2.3). In these minimization problems, the discontinuity in the nonlinear activation functions implies difficulties in using the standard theory that relies on the smoothness of the mappings involved. However, we conjecture that due to the presence of the Heaviside-type activation functions in (3.14), one can construct isotone operators acting in an appropriate ordered space and apply the results on minimization of functionals in partially ordered spaces developed in [29] to prove the solvability of the minimization problem.

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