HOKKAIDO UNIVERSITY

Title	Neural field dynamics for growing brains
Author(s)	Sato, Yuzuru; Shimaoka, Daisuke; Fujimoto, Koichi et al.
Citation	IEEE Nonlinear Theory and its Applications, 7(2), 226-233 https://doi.org/10.1587/nolta.7.226
Issue Date	2016-04-01
Doc URL	https://hdl.handle.net/2115/65396
Rights	Copyright © 2016 The Institute of Electronics, Information and Communication Engineers
Type	journal article
File Information	7_226.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

NOLTA, IEICE

Paper

Neural field dynamics for growing brains

Yuzuru Sato [1,2a)], *Daisuke Shimaoka* [3], *Koichi Fujimoto* [4], *and Gentaro Taga* [5]

[1] *RIES / Department of Mathematics, Hokkaido Univeristy*
Kita 12 Nishi 6, Kita-ku, Sapporo 060-0812, Japan

[2] *London Mathematical Laboratory*
14 Buckingham Street, London, WC2N 6DF, UK

[3] *UCL Institute of Ophthalmology, University College London*
11-43 Bath Street, London EC1V 9EL, UK

[4] *Department of Biological Sciences, Osaka University*
1-1 Machikaneyama-cho, Toyonaka, Osaka 560-0043, Japan

[5] *Graduate School of Education, The University of Tokyo*
7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan

[a)] *ysato@math.sci.hokudai.ac.jp*

Received August 21, 2015; Revised November 24, 2015; Published April 1, 2016

Abstract: We propose an extended framework of two dimensional neural field with network between distant cortical areas as a model of global brain dynamics, and the models whose geometry of the neural field changes depending on the field dynamics as a model for growing brains. As a characteristic pattern with non-local and network interactions in neural field, pulser and memory are constructed. Possible applications to quantitative measurements of cortical activities of mouse and human brain development are briefly discussed.

Key Words: neural field dynamics, neuronal connectome, brain development

1. Introduction

1.1 Two dimensional neural fields

A neural field model describes the dynamics of populational neuronal firing activities [5, 6], which is a spatially continuous-limit of artificial neural networks [1–4]. Let $u(\mathbf{x})$ and $v(\mathbf{x})$ be excitatory and inhibitory variables at position $\mathbf{x} = (x, y)$. The activation-inhibition dynamics is described as,

$$\frac{\partial u(\mathbf{x})}{\partial t} = L_{uu}\left[u(\mathbf{x})\right] + L_{uv}\left[v(\mathbf{x})\right], \tag{1}$$

$$\frac{\partial v(\mathbf{x})}{\partial t} = L_{vu}\left[u(\mathbf{x})\right] + L_{vv}\left[v(\mathbf{x})\right]. \tag{2}$$

where L_{uu}, L_{uv}, L_{vu} and L_{vv} are operators representing interactions of the field variables. The standard reaction-diffusion equation uses the linear Laplacian diffusion for L_{uu} and L_{vv} together

Nonlinear Theory and Its Applications, IEICE, vol. 7, no. 2, pp. 226–233 ©IEICE 2016 DOI: 10.1587/nolta.7.226

with pointwise interactions for L_{uv} and L_{vu} [8], whereas the equation of a neural field uses non-local interactions for L_{uu} and L_{vv} due to the synaptic connections of neurons, represented by a spatial convolution of the type

$$L_{uu}\left[u(\mathbf{x})\right] = \int w\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)\right] d\mathbf{x}', \tag{3}$$

where f is a nonlinear function. The typical equations for a two-dimensional neural field are as follows:

$$\frac{\partial u(\mathbf{x})}{\partial t} = \int w_{ee}\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - \int w_{ie}\left(\mathbf{x}-\mathbf{x}'\right) f\left[v\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - u(\mathbf{x}), \tag{4}$$

$$\frac{\partial v(\mathbf{x})}{\partial t} = \int w_{ei}\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - \int w_{ii}\left(\mathbf{x}-\mathbf{x}'\right) f\left[v\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - \beta v(\mathbf{x}). \tag{5}$$

Here, $u(\mathbf{x})$ and $v(\mathbf{x})$ are the mean potentials of excitatory and inhibitory neurons, respectively, at position $\mathbf{x}$ and time t. The convolutive functions $w_{\cdot}\left(\mathbf{x}-\mathbf{x}'\right)$ represent the synaptic efficacies. The functions f describe the activation functions of neurons together with the threshold h. The mean potentials are activated by $u(\mathbf{x})$ and in turn inhibited by $v(\mathbf{x})$. The parameter β governs the time scale of inhibitory neurons. The two dimensional neural field is homogeneous and rotationally invariant.

The neural field model can be regarded as a special case of the field equation with excitation and inhibition mechanisms. While reaction-diffusion equations are restricted within local interactions due to the diffusion term, the neural field model has a non-local interactions. We introduce inhomogeneous network structure to the kernels $w_{\cdot}$ in the later sections. In the two dimensional two-component reaction-diffusion equation, the existence of spatially localized traveling objects has not been reported with local operators [9]. It is known that global operators added to two-component systems may induce a single stable traveling bump, but may not induce multiple bumps [10]. On the other hand, many three component systems with local operators show multiple travelling bumps [12].

An example of multiple stable traveling bumps in a two dimensional neural field model is presented in [7]. The spatial convolution term plays the role of the third component to stabilize the bump, which supports existence of multiple bumps [7].

1.2 Stable traveling bumps and their collisions

Numerical experiments of the following simple equations [11] suggest that the field can be tri-stable, admitting the quiescent state, a stable traveling bump with a characteristic length Fig. 1, and a traveling band solution growing to infinite length [7].

$$\frac{\partial u(\mathbf{x})}{\partial t} = \int w_{ee}\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - u(\mathbf{x}) \tag{6}$$

$$\frac{\partial v(\mathbf{x})}{\partial t} = \alpha u(\mathbf{x}) - \beta v(\mathbf{x}), \tag{7}$$

where $\alpha = 0.6$, $\beta = 0.8/3$, $h = 3.0$, and

$$w_{ee}(\mathbf{x}) = 7.32e^{-\frac{x^2+y^2}{2}}, \quad f[u] = \frac{1}{1+e^{-2(u-4)}}, \tag{8}$$

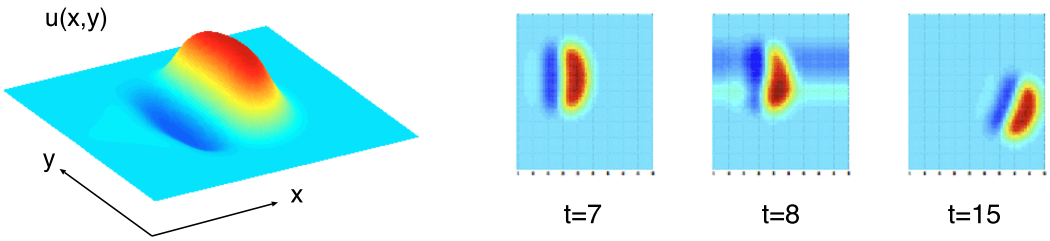

Fig. 1. A stable traveling bump (left) and controlling directions of motion of it (right) in two dimensional neural field. When $t = 8$, an external perturbation added to change the direction of motion of the traveling bump. The bumps may travel at arbitrary angle because of the radial symmetry of the system.

where the initial conditions at time $t = 0$ are given as

$$u(\mathbf{x}) = \begin{cases} 15e^{(x-0.5)^2/5} & (y \in [15, 23.9]) \\ 0 & \text{Otherwise.} \end{cases}$$
$$v(\mathbf{x}) = \begin{cases} 10e^{(x-0.3)^2/5} & (y \in [15, 23.9]) \\ 0 & \text{Otherwise.} \end{cases} \tag{9}$$

The parameter α represents the pointwise effect from an excitatory neuron to an inhibitory neuron at point $\mathbf{x}$.

The traveling bumps in this neural field is structurally and orbitally stable. Because the basin measure to generate the traveling bump is positive without any boundary conditions, the bump is a robust attracting set. A number of traveling bumps may coexist in the field, and they strongly interact when they are close. When two bumps collide, they fuse into a single bump. The resulting bump converges to one of the tri-stable states depending on the collision angle. When the angle is small, the two bumps disappear after collision, when it is large, they merge to the band solution. The numerically estimated critical threshold angle is $\sim \frac{3}{8}\pi$ for which bumps survives after collision [7]. We use external inputs to control directions of motion of traveling bumps to adjust the collision angle. There are no standing patterns other than the traveling bumps in the parameter settings because of the lack of diffusion terms, so that even with complex collisions, the resulting output is thought to be only one of the following: (i) quiescent state, (ii) stable traveling bump, or (iii) growing band solution, implying that the field is "clean" without complex after effects. As for complex transitory collision phenomena, see [12] for the various collision and scattering phenomena of traveling spots in the reaction-diffusion systems with three components. Multiple bumps in neural field can be applied to study informational functions of brains such as working memory and fast learning [13, 14].

2. Neural field dynamics with network interactions

2.1 Pattern construction in neural fields

In the mammalian cortex such as mouse isocortex, a population of neurons in one cortical area receive synaptic inputs from adjacent microcircuits, and from distant cortical and subcortical areas. To study how such non-local and network interactions form mesoscale cortical dynamics, we here extend the neural field model by adding long-range connection terms with a kernel K_{ee} and K_{ei} as follows.

$$\frac{\partial u(\mathbf{x})}{\partial t} = \int w_{ee}\left(\mathbf{x}-\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' f\left[v\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' + \int K_{ee}\left(\mathbf{x},\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - u(\mathbf{x}), \tag{10}$$

$$\frac{\partial v(\mathbf{x})}{\partial t} = \alpha u(\mathbf{x}) - \beta v(\mathbf{x}) + \int K_{ei}\left(\mathbf{x},\mathbf{x}'\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}'. \tag{11}$$

The networks $K_{ee}\left(\mathbf{x},\mathbf{x}'\right)$ and $K_{ei}\left(\mathbf{x},\mathbf{x}'\right)$ can be given based on the mice brain connectome data [15]. Also, the coarse-grained geometry of isocortex of mouse can be extracted from Allen Brain Atlas (http://connectivity.brain-map.org/). In addition, neuronal activity at this spatial scale has been observed in the mouse using millisecond-timescale imaging of voltage-sensitive dye [17] and genetically-encoded voltage indicator [16]. The nonlinear wave phenomena observed in the experiments [16] can be discussed with the detailed network models.

When we have the data-based detailed network model of neural field, what can be qualitative change of spatio-temporal dynamics in the neural field? Here we consider this problem theoretically. In general, mathematical framework of network interactions are given by designed kernels $w_{\cdot}$ and $K_{\cdot}$. We discuss the effect of non-local coupling and networks. The schematic views of the type of the kernels for (A) local, (B) global, (C) non-local, (D) non-local and network interactions are shown in Fig. 2.

In Fig. 3, examples of pattern construction for pulser and memory are exhibited. The robust information carriers are realized by the stable traveling bumps. The bumps may travel at arbitrary

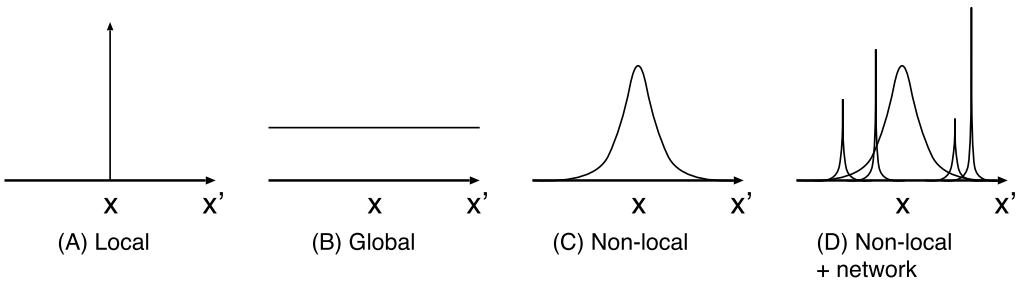

Fig. 2. The kernels for (A) local, (B) global, (C) non-local, (D) non-local and network interactions.

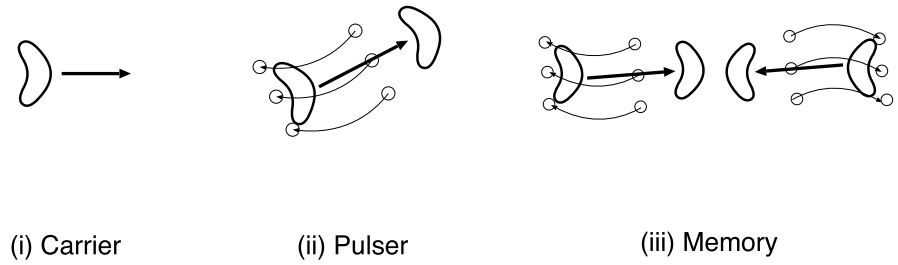

Fig. 3. Possible pattern construction with non-local and network interactions; (i) Robust information carriers, (ii) pulser, (iii) memory. The circle and the arrows represent non-local and network interactions, respectively.

angle because of the radial symmetry of the system. The robust pulser of the traveling bumps can be constructed by a feedback within the networks (Fig. 4, top). When the traveling bump passes an area in the neural field connected to the other points, the initial conditions of the traveling bumps is regenerated at that area. In this neural field, the bumps are sustainable if a bump in the u space followed by a smaller bump in the v spaces. Thus, to generate a stable bump, we need the network from the u space to the u and v spaces with network kernels K_{ee} and K_{ei}. If the network connections is a feedback to an area on the pathway of the traveling bumps, they works as an autonomous pulser which repeatedly generates the identical traveling bumps (Fig. 4, bottom).

We give an example of the pulser based on the Eqs. (9) and (10) with

$$K_{ee}\left(\mathbf{x},\mathbf{x}'\right)=\begin{cases}60 & (\mathbf{x}=(15,y),\ \mathbf{x}'=(x',y),\ x'\in[3,4],\ y\in[15,26.9])\\ 0 & \text{Otherwise.}\end{cases} \tag{12}$$

$$K_{ei}\left(\mathbf{x},\mathbf{x}'\right)=\begin{cases}1 & (\mathbf{x}=(15,y),\ \mathbf{x}'=(x',y),\ x'\in[1.8,2.8],\ y\in[15,26.9])\\ 0 & \text{Otherwise.}\end{cases} \tag{13}$$

where the other parameters follows the Eqs. (6)–(8). The frequency of the pulser is governed by v/l, where v is the velocity of the center of mass of bumps [7] and l is the length of the feedback network.

In this neural field, we have no stable standing patterns without network structure. However, with network structure, we can construct a standing oscillatory pattern by coupled pulsers with a head-on collision which can work as "memory." This oscillatory pattern is sustainable unless it is disturbed by internal or external perturbations. Many other spatial pattern constructions were proposed in [18]. Other phenomenology based on local and global interactions was discussed, for instance, in the model of muscle [19]. It is not possible to construct these patterns on neither cellular automata/reaction diffusion systems which consist of only short range interactions, nor coupled dynamical systems/artificial neural networks which do not have spatial structure.

3. Neural field dynamics for growing brains

3.1 Geometry of growing cortex

We extend the neural field model considering the geometry of brains with spherical coordinate. The surface of human adult cortex is a highly folded sheet. The previous studies with the structural MRI (magnetic resonance imaging) have demonstrated that the folded surface of each hemisphere can be

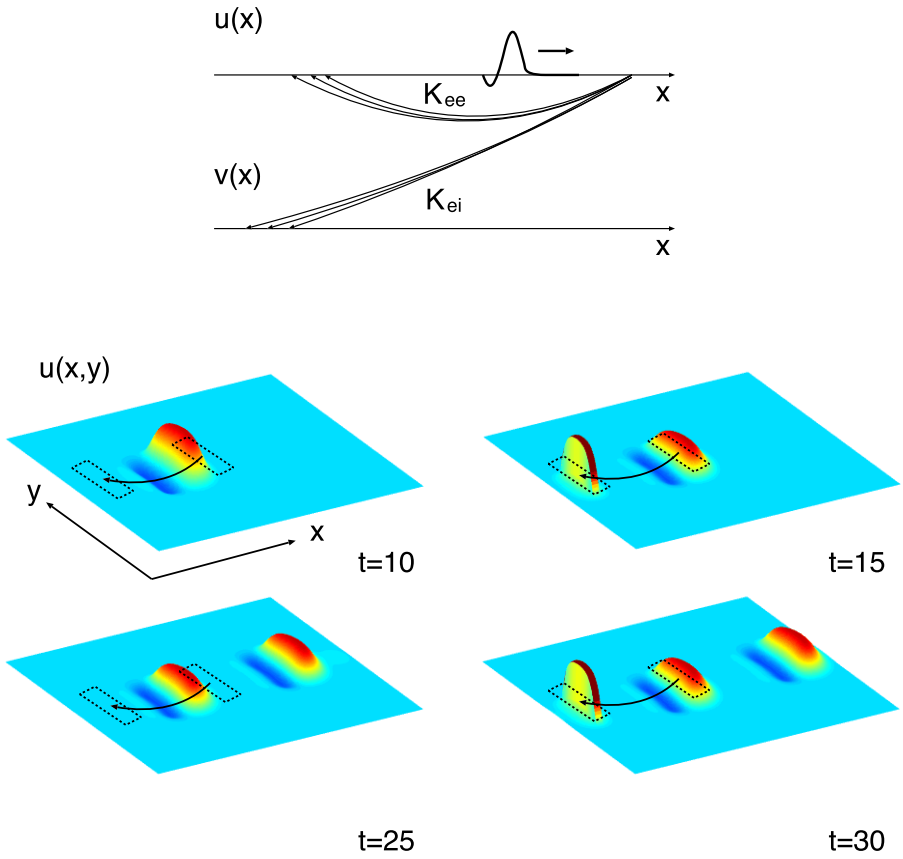

Fig. 4. A construction of a network working as a pulser (top). If the network connections are feedbacks to an area on the pathway of the traveling bumps, they works as an autonomous pulser which repeatedly generates the identical traveling bumps (bottom). The squares with dotted lines denote the connected areas and the arrow represents the feedback networks.

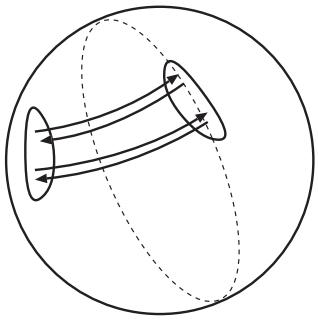

Fig. 5. Neural field model on a sphere.

inflated and transformed onto a sphere [20, 21]. This surface-based representation of the cortex will have a great advantage to analyze spatio-temporal pattern of cortical activation on 2D sheet [22]. In addition to the continuous short-range connectivity, separate regions of the cortex are connected by the white matter fiber tracts, which can be visualized as a diffusion tensor imaging and represented as a connectivity matrix [23]. Thus, the long-range connectivity between specific regions of the cortex can be added in the neural field model on a spherical coordinate. Furthermore, the thalamo-cortical connectivity can be added to the model in a form of another long range connectivity, thereby the effect of sensory input to the cortex is examined.

3.2 Network formation in the brain

Gyrification is an important step for the development of the brain. The human cortical surface grows from a smooth structure into a convoluted structure during the third trimester of fetal period.

Although a number of hypotheses have been proposed on the mechanism of cortical folding during fetal period [24, 25], the neural field model will provide an useful framework for analyzing activity-dependent structural development of the brain.

The neural field model can be extended to describe network formation underlying neuronal growth and differentiation as well. We introduce new variables $\rho_c(\mathbf{x})$, $\rho_s(\mathbf{x})$, which represent two types of neuron densities at position $\mathbf{x}$. The density $\rho_\cdot(\mathbf{x})$ is governed by an equation of growth $V_\cdot(\cdot)$ and random migration $\Delta\rho_\cdot(\mathbf{x})$ of neurons. We couple it with neural field through the kernel w_{ee}, w_{ie} and K_{ee}.

$$\begin{aligned}\frac{\partial u(\mathbf{x})}{\partial t} &= \int w_{ee}\left(\mathbf{x}-\mathbf{x}', \rho_s(\mathbf{x}), \rho_s(\mathbf{x}')\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' \\ &\quad - \int w_{ie}\left(\mathbf{x}-\mathbf{x}', \rho_s(\mathbf{x}), \rho_s(\mathbf{x}')\right) f\left[v\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' \\ &\quad + \int K_{ee}\left(\mathbf{x}, \mathbf{x}', \rho_c(\mathbf{x}), \rho_c(\mathbf{x}')\right) f\left[u\left(\mathbf{x}'\right)-h\right] d\mathbf{x}' - u(\mathbf{x}), \qquad (14)\end{aligned}$$

$$\frac{\partial v(\mathbf{x})}{\partial t} = \alpha u(\mathbf{x}) - \beta v(\mathbf{x}), \qquad (15)$$

$$\frac{\partial \rho_c(\mathbf{x})}{\partial t} = V_c[\rho_c(\mathbf{x}), \rho_s(\mathbf{x}), u(\mathbf{x}), v(\mathbf{x})] + D_c\Delta\rho_c(\mathbf{x}), \qquad (16)$$

$$\frac{\partial \rho_s(\mathbf{x})}{\partial t} = V_s[\rho_c(\mathbf{x}), \rho_s(\mathbf{x}), u(\mathbf{x}), v(\mathbf{x})] + D_s\Delta\rho_s(\mathbf{x}), \qquad (17)$$

This model could be consistent with early development of human fetal cortex. The cell density ρ_c and ρ_s could represent the neuronal populations of cortical and subplate layers, respectively. The subplate neurons show spontaneous electrical activity in human fetal cortex [26]. In addition, in this developmental stage, subplate neurons are not only electrically connected, represented by the excitatory and inhibitory non-local interaction, but also connected in a long range via the white matter fibers, represented by the excitatory network interaction. Thus, we assume that these two interaction strength depend on the cell density ρ_c and ρ_s, and that white matter fiber grows from one area with a large $\rho_c(\mathbf{x})$ to other area with a large $\rho_c(\mathbf{x}')$.

Proliferation and differentiation between the cortical and the subplate neurons are regulated by several genes, whose expression level can be localized in the cortex [27] by a reaction-diffusion mechanism. The functions V_s and V_c are represented by the growth and the differentiation of neurons depending on the gene activity. The feedback of neuronal activity into the growth and differentiation dynamics can be introduced when V_s and V_c are the functions of u and v. The details depend on the system, but these interaction nature are not negligible, and would rather be explicitly taken into account to study developmental stages of brains. The schematic view of this model is given in Fig. 6., which will be studied based on further details elsewhere.

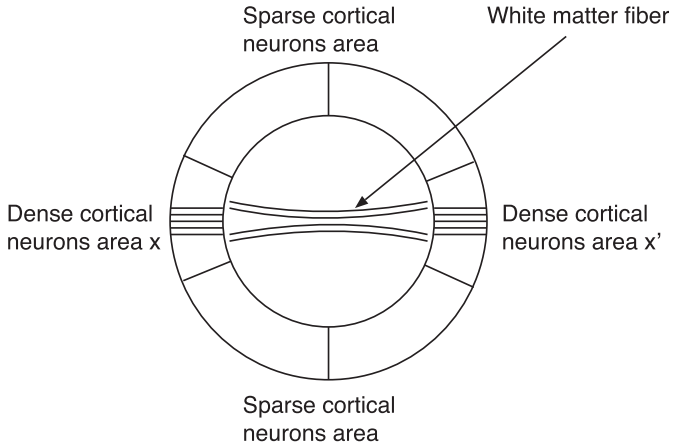

Fig. 6. White matter fiber grows from one area with a large $\rho_c(\mathbf{x})$ to other area with a large $\rho_c(\mathbf{x}')$.

4. Summary

We presented a framework for a detailed network model of whole brains and a neural field model for growing brains. As a characteristic pattern with non-local and network interactions in neural field, pulser and memory are constructed. Possible applications to quantitative measurements of cortical activities of mouse and human brain development are briefly discussed. The data driven model implementations and its phenomenology will be studied elsewhere. The presented framework for neural computation with spatial structure may shed light on the design principle of whole brains.

Acknowledgments

Y. Sato is supported by the platform grant at Imperial College London, External fellowship at London Mathematical Laboratory, and JSPS Grant-in-Aid for Scientific Research (C) No. 26520201. Y. Sato, K. Fujimoto, and G. Taga are supported by JSPS Grant-in-Aid for Scientific Research (S) No. 26220044. D. Shimaoka would like to thank Prof. Thomas Knopfel at Imperial College London for help with preliminary experiments that motivated this study.

References

[1] W.S. McCulloch and W. Pitts, "A logical calculus of the ideas immanent in nervous activity," *Bulletin of Mathematical Biophysics*, vol. 5, pp. 115–133, 1943.

[2] J. von Neumann, "Probabilistic logics and the synthesis of reliable organisms from unreliable components," *Automata Studies*, Princeton University Press, pp. 43–98, 1956.

[3] S. Amari, "Characteristics of randomly connected threshold-element networks and network systems," *IEEE Proceedings*, vol. 59, no. 1, pp. 35–47, 1971.

[4] J.J. Hopfield, "Neural network and physical systems with emergent collective computational abilities," *Proceedings of the National Academy of Sciences*, vol. 79, no. 8, pp. 2554–2558, 1982.

[5] H.R. Wilson and J.D. Cowan, "A mathematical theory of the functional dynamics of cortical and thalomic tissue," *Kybernetik*, vol. 13, pp. 55–80, 1973.

[6] S. Amari, "Dynamics of pattern formation in lateral-inhibition type neural fields," *Biological Cybernetics*, vol. 27, pp. 77–87, 1977.

[7] Y. Lu, Y. Sato, and S. Amari, "Traveling bumps and thier collisions in two-dimensional neural field," *Neural Computation*, vol. 23, no. 5, pp. 1248–1260, 2011.

[8] A.M. Turing, "The chemical basis of morphogenesis," *Philosophical Transactions of the Royal Society of London*, vol. B 237, pp. 37–72, 1952.

[9] V.K. Vanag and I.R. Epstein, "Localized patterns in reaction-diffusion systems," *Chaos*, vol. 17, 037110, 2007.

[10] C.P. Schenk, M. Or-Guil, M. Bode, and H.G. Purwins, "Interacting pulses in three-component reaction-diffusion systems on two-dimensional domains," *Physical Review Letters*, vol. 78, pp. 3781–3784, 1997.

[11] D.J. Pinto and G.B. Ermentrout, "Spatially structured activity in synaptically coupled neuronal networks: I. Traveling waves fronts and pulses," *SIAM Journal on Applied Mathematics*, vol. 62, pp. 206–225, 2001.

[12] Y. Nishiura, T. Teramoto, and K. Ueda, "Scattering of traveling spots in dissipative systems," *Chaos*, vol. 15, 047509, 2005.

[13] Y. Sato and S. Amari, "Robust computation in two dimensional neural field," *Advances in Cognitive Neurodynamics*, pp. 123–129, 2013.

[14] C.R. Laing, W.C. Troy, B. Gutkin, and G.B. Ermentrout, "Multiple bumps in a neuronal model of working memory," *SIAM Journal on Applied Mathematics*, vol. 63, pp. 62–97, 2002.

[15] S.W. Oh et al., "A mesoscale connectome of the mouse brain," *Nature*, vol. 508, pp. 207–214, 2014.

[16] D. Shimaoka, W. Akemann, H. Mutoh, and T. Knopfel, "Analysis of membrane potential waves during recovery from anesthesia in mice using VSFP-based imaging," *36th Annual meeting of the Japan Neuroscience Society*, 2013.

[17] M.H. Mohajerani et al., "Spontaneous cortical activity alternates between motifs defined by regional axonal projections," *Nature Neuroscience*, vol. 16, pp. 1426–1435, 2013.
[18] Y. Sato, "Robust pattern construction in two-dimensional neural field," *Proc. of AFCA*, to appear.
[19] K. Sato, Y. Kuramoto, M. Ohtaki, Y. Shimamoto, and S. Ishiwata, "Locally and globally coupled oscillators in muscle," *Physical Review Letters*, vol. 111, 108104, 2013.
[20] B. Fischl, M.I. Sereno, and A.M. Dale, "Cortical surface-based analysis: II: inflation, flattening, and a surface-based coordinate system," *Neuroimage*, vol. 9, no. 2, pp. 195–207, 1999.
[21] D.C. van Essen, "A population-average, landmark-and surface-based (PALS) atlas of human cerebral cortex," *Neuroimage*, vol. 28, no. 3, pp. 635–662, 2005.
[22] V.K. Jirsa et al., "Spatiotemporal forward solution of the EEG and MEG using network modeling," *IEEE Trans. Medical Imaging*, vol. 21, no. 5, pp. 493–504, 2002.
[23] A. Haimovici et al., "Brain organization into resting state networks emerges at criticality on a model of the human connectome," *Physical Review Letters*, vol. 110, no. 17, 178101, 2013.
[24] T. Tallinen et al., "Gyrification from constrained cortical expansion," *Proceedings of the National Academy of Sciences*, vol. 111, no. 35, pp. 12667–12672, 2014.
[25] J. Lefevre and J.F. Mangin, "A reaction-diffusion model of the human brain development," *PLoS Computational Biology*, vol. 6, no. 4, e1000749, 2010.
[26] A.R. Moore, W.L. Zhou, I. Jakovcevski, N. Zecevic, and S.D. Antic, "Spontaneous electrical activity in the human fetal cortex in vitro," *Journal of Neuroscience*, vol. 31, no. 7, pp. 2391–2398, 2011.
[27] V. Borrell and M. Götz, "Role of radial glial cells in cerebral cortex folding," *Current Opinion in Neurobiology*, vol. 27, pp. 39–46, 2014.