2011 International Symposium on Nonlinear Theory and its Applications
NOLTA2011, Kobe, Japan, September 4-7, 2011

Formation of orientation maps by spiral waves in primary visual cortex

Koji Iwayama†‡, Kazuyuki Aihara‡ and Hideyuki Suzuki‡

†FIRST, Aihara Innovative Mathematical Modelling Project, JST
4-6-1 Komaba, Meguro-ku, Tokyo 153-8505, Japan
‡Institute of Industrial Science, University of Tokyo
4-6-1 Komaba, Meguro-ku, Tokyo, 153-8505 Japan
Email: koji@sat.t.u-tokyo.ac.jp

Abstract—Spiral waves have been observed in many systems including the brain cortex. However, the functional role of spiral waves in the cortex is unknown. In the primary visual cortex, neurons are arranged in pinwheel-like patterns according to their orientation selectivities. We show that spiral waves and spike-timing-dependent plasticity of synapses form this pinwheel structure.

1. Introduction

Spiral waves have been observed in many systems. They were also reported in turtle visual cortices [1] and rat neocortical slices [2]. However, their functional role is unknown.

In the sensory cortex, close neurons are selective to similar stimuli and distant neurons are selective to different stimuli. This structure is called "topographic map". The orientation map, a topographic map in the primary visual cortex, consists of neurons selective to the orientation of an edge in the input image. Regions where neurons are selective to similar orientations appear to form patches and arranged in pinwheel-like patterns [3].

It is known that long-term potentiation (LTP) and long-term depression (LTD) of synapses depend on the relative spike times of pre- and postsynaptic neurons [4, 5, 6]. Postsynaptic spikes preceding presynaptic spikes induce LTP, and postsynaptic spikes following presynaptic spikes induce LTD. Moreover, smaller differences between the times of pre- and postsynaptic spikes induce larger synaptic modification. Such synaptic plasticity is called "spike-timing-dependent plasticity" (STDP). It is indicated that STDP can lead to the formation of a topographic map [7] including orientation maps [8]. In these models, close neurons have excitatory connections to each other. These connections propagate activities to near by neurons and induce spikes. Thus close neurons have similar timing of spikes and acquire similar orientation selectivities by STDP. When neural activities are propagated as spiral waves, orientation selectivities would change continuously along traveling direction of spiral waves and the pinwheel structure would develop as a result.

In this paper, we show that when orientation selectivities of neurons are modified by STDP, the propagation of activities as spiral waves can lead to the development of pinwheel-like structures in orientation maps by computer simulations.

2. Model

2.1. Neurons

In our model, 50×50 excitatory neurons were arranged on a square lattice and connected each other. We used the Izhikevich [9] neuron model, which is described by equations

$$\begin{aligned} \frac{\mathrm{d}v_j}{\mathrm{d}t} &= 0.04v_j^2 + 5v_j + 140 - u + I_j^{in} + I_j^{ex}, \\ \frac{\mathrm{d}u_j}{\mathrm{d}t} &= a(bv_j - u), \\ \text{if } v_j \geq 30 & \quad \text{then, } v_j \leftarrow c, u \leftarrow u + d. \end{aligned} \tag{1}$$

Here, a, b, c, and d are dimensionless parameters. In this model, we set parameters $a = 0.02$, $b = 0.2$, $c = -65$, and $d = 8$. The variable v_j is the membrane potential of the jth neuron. The variable u_j represents the recovery variable providing negative feedback to v_j. The variable I_j^{in} and I_j^{ex} represent synaptic currents from other neurons in the network and outside the network, respectively.

The input from neurons in the network to the jth neuron is written as

$$I_j^{in}(t) = \sum_k w_{jk} \exp\left(-\frac{t - t_k}{\tau}\right), \tag{2}$$

where, t_k represents the time of the last spike of kth neuron and τ is the time constant. We used $\tau = 5$ms. Neurons are connected to each other with the synaptic strength w_{jk}:

$$w_{jk} = E \exp\left(\frac{-d_{jk}^2}{\sigma_e^2}\right). \tag{3}$$

Here, d_{jk} is the Euclidean distance on the square lattice between jth and kth neuron. Parameters E and σ_e determine the amplitude and the range of excitatory connections. In our model, we used $E = 3$ and $\sigma_e = 2.5$.

Each neuron has the orientation selectivity and it is represented by one complex number $z_j = |z_j|e^{\mathrm{i}\theta_j}$, where $|z_j|$ means the degree of the orientation selectivity and θ_j is its preferential orientation.

2.2. External inputs

We suppose that the response of the jth neuron to the visual stimulus with the orientation ϕ is given by

$$r_j(\phi) = \frac{1}{(\sigma_r/|z_j|)^2 \cos^2(\phi - \theta_j) + (|z_j|/\sigma_r)^2 \sin^2(\phi - \theta_j)}. \tag{4}$$

Here, σ_r is the parameter and we used $\sigma_r = 0.1$. The second term of the denominator of eq. 4 is the penalty to strong selectivity; if the jth neuron has strong selectivity to the orientation θ, i.e. $|z_j|$ takes large value, the response of the neuron to other orientations should be small.

The external inputs $I^{ex}(t)$ to the network was generated in the following way.

1. The stimulus orientation ϕ is chosen from the uniform distribution.

2. We find a "winner neuron", whose response (eq. 4) takes the largest value in the network.

3. If the jth neuron is contained in the neighbor of the winner neuron, the external input to the jth neuron is

$$I_j^{ex}(t) = W^{ex} \exp\left(-\frac{t - t^{ex}}{\tau}\right). \tag{5}$$

Here, W^{ex} and t^{ex} are the amplitude and the time of the application of the visual stimulus, respectively. We set $W^{ex} = 30$. Otherwise, the external input to the neuron is 0.

We simulated with following three types of the neighbor of the winner neuron.

Spot The circle with radius 5 (fig. 1(a)). This type of input induces ring-shaped travelling wave.

Bar The half line from the center of the network through the winner neuron with width of 5 (fig. 1(b)). This type of input induces elliptical wave.

Spiral In addition to the "bar", neurons adjacent to the "bar" are inhibited $\Delta t^{in} = 5$ms after excitatory inputs (fig. 1(c)):

$$I_j^{ex} = -W^{in} \exp\left(-\frac{t - t^{ex} - \Delta t^{in}}{\tau}\right), \tag{6}$$

where W^{in} is the amplitude of inhibition and we set $W^{in} = 60$. This type of input induces spiral waves.

2.3. Orientation selectivities and STDP

In our model, orientation selectivities are modified by spike-timing-dependent plasticity (STDP). STDP is typically represented by exponential functions [10]. When pre- and postsynaptic neurons evoked spikes at time t_{pre} and

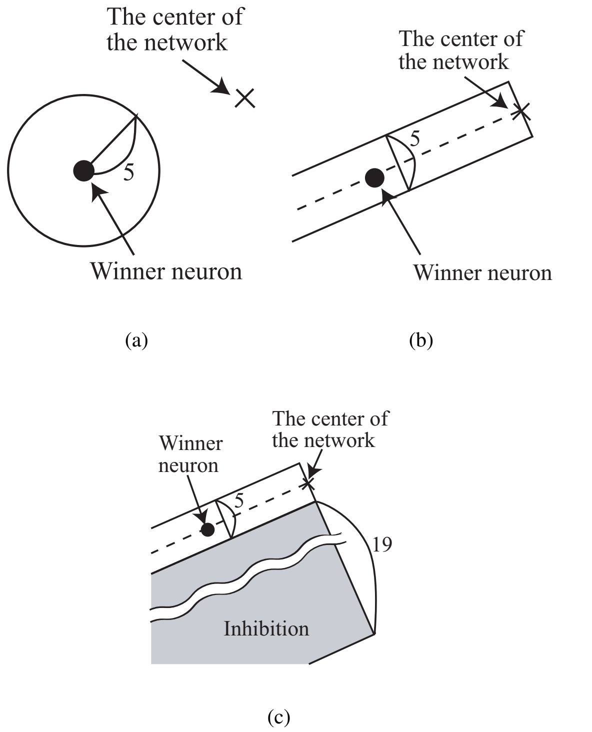


Figure 1: Three types of the neighbor of the winner neuron. (**a**) Spot. The neighbor is a circle with radius 5. (**b**) Bar. The neighbor is a black rectangle. (**c**) Spiral. The neighbor is a black rectangle, and neurons in the gray area are inhibited.

t_{post}, respectively, the synaptic strength w between these neurons are modified by the equation

$$\begin{aligned} w &\leftarrow w + \Delta w, \\ \Delta w &= \begin{cases} A_+ \exp\left(-\frac{t_{post}-t_{pre}}{\tau_+}\right), & \text{if} \quad t_{post} > t_{pre}, \\ -A_- \exp\left(-\frac{t_{pre}-t_{post}}{\tau_-}\right), & \text{if} \quad t_{post} < t_{pre}. \end{cases} \end{aligned}$$

Here, A_+ and A_- are amplitudes of LTP and LTD. τ_+ and τ_- are time constants of LTP and LTD.

In our model, we represent the orientation selectivity not by the distribution of synaptic strengths, but one complex number z_j. Hence, we modified the equation of STDP. When the jth neuron generated a spike at time t_j, its orientation selectivity is modified as:

$$z_j \leftarrow z_j + A \exp\left(-\frac{t_j - t^{ex}}{\tau_s}\right) \Delta z \tag{7}$$

$$\Delta z = \cos^2(\phi - \theta_j)(\exp(\mathrm{i}\phi) - z_j) - \sin^2(\phi - \theta_j) z_j. \tag{8}$$

Here, A and τ_s are the scaling parameter of modification and the time constant of STDP. We used $A = 0.1$ and $\tau_s = 20$ms. In eq. 7, the amount of modification is determined by the exponential function of the time difference. When the input orientation and the preferential orientation are different significantly, the selectivity to the current preferential orientation is reduced by the second term of eq. 8.

3. Simulation results

We simulated the network model for 100sec. Every 100ms, we generated external inputs I^{ex} and reset membrane potentials v and inputs I^{in} of the network neurons.

Snapshots (at $10, 20, 30, 40$ms) of the neuronal activities in the network are illustrated in fig. 2. For each kth neuron, $\exp(-(t - t_k)/\tau)$ in eq. 2 is represented by color. Red pixels mean neurons which evoked spikes at the time. Inputs of "spot" induced ring-shaped traveling waves of activities (fig. 2(a)). Activities of neurons were propagated elliptically with inputs of "bar" (fig. 2(b)). Spiral waves were appeared only with inputs of "spiral" (fig. 2(c)).

Orientation maps generated with three types of inputs are illustrated in fig. 3, where similar orientation selectivities are represented by similar colors. The relationship between orientation selectivities and colors is shown in fig. 3(a). In the map of "spot", neurons which are selective to similar orientations formed patches(fig. 3(b)). However, the center of pinwheel, which is surrounded by continuously changing orientation selectivities, does not appear. Inputs of "bar" did not form patches of similar orientation selectivities(fig. 3(c)). On the other hand, the orientation selectivity changes continuously around the center of the network in the map of "spiral"(fig. 3(d)). Only the input of "spiral" could generate the pinwheel structure.

4. Conclusion

Although spiral waves have been observed in the cortex, those roles have yet to be revealed. We simulated the development of orientation maps by spike-timing-dependent plasticity when neural activities propagate as spiral waves.

We showed that spiral waves contribute to the development of the pinwheel structure in the primary visual cortex. This result implies a possible role of spiral waves in the cortex. It is known that the structure of the orientation map relates to contextual modulation by surrounding stimuli in a receptive field [11]. Hence, the spiral wave may also contribute to contextual modulation.

Acknowledgments

This research is partially supported by the Aihara Innovative Mathematical Modelling Project, the Japan Society for the Promotion of Science (JSPS) through the "Funding Program for World-Leading Innovative R&D on Science and Technology (FIRST Program)," initiated by the Council for Science and Technology Policy (CSTP).

References

[1] J. C. Prechtl, et al., "Visual stimuli induce waves of electrical activity in turtle cortex", *P. Natl. Acad. Sci. USA*, vol.94, pp.7621–7626, 1997.

[2] X. Huang, et al., "Spiral waves in disinhibited mammalian neocortex", *J. Neurosci.*, vol.24, no.44, pp.9897–9902, 2004.

[3] T. Bonhoeffer, et al., "Iso-orientation domains in cat visual cortex are arranged in pinwheel-like patterns", Nature, vol.353, no.6343, pp.429–431, 1991.

[4] C. C. Bell, et al., "Synaptic plasticity in a cerebellum-like structure depends on temporal order", vol.387, no.6630, pp.278–281, 1997.

[5] B. G. Poo, et al., "Synaptic modifi cations in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type" *J. Neurosci.*, vol.18 no.24, pp.10464–10472, 1998.

[6] L. I. Zhang, "A critical window for cooperation and competition among developing retinotectal synapses", vol.395, no.6697, pp.37–44, 1998.

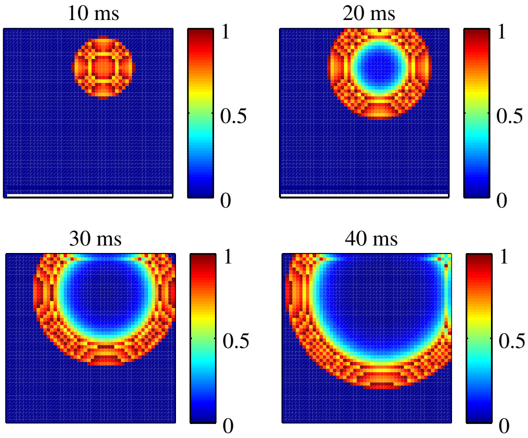
[7] S. Song, et al., "Cortical development and remapping through spike-timing-dependent plasticity", *Neuron*, vol.32, pp.339-350, 2001.

[8] K. Iwayama, et al., "Self-organization of orientation-selective and ocular-dominance maps through spike-timing-dependent plasticity", *Artif. Life Robotics*, vol.14, pp.371–374, 2009.

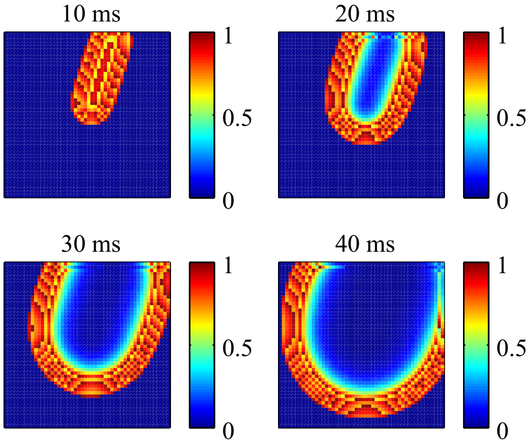
[9] E. M. Izhikevich, "Simple model of spiking neurons". *IEEE T. Neural Networ.*, vol.14, no.6, pp.1569–1572, 2003.

[10] S. Song, et al., "Competitive hebbian learning through spike-timing-dependent-synaptic plasticity", Nat. Neurosci., vol.3, no.9, pp.919–926, 2000.

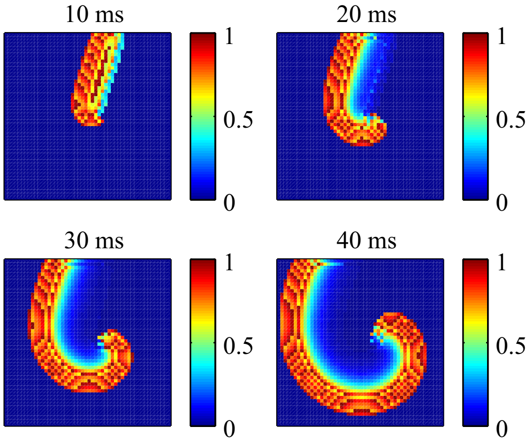
[11] T. Okamoto, et al., "An explanation of comtextual modulation by short-range isotropic connections and orientation map geometry in the primary visual cortex", Biol. Cybern., vol.91, pp.396–407, 2004.



(a)

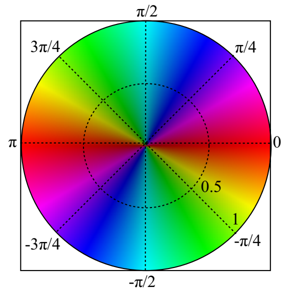


(b)

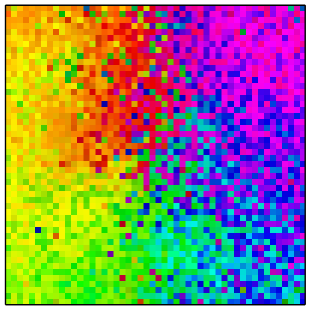


(c)

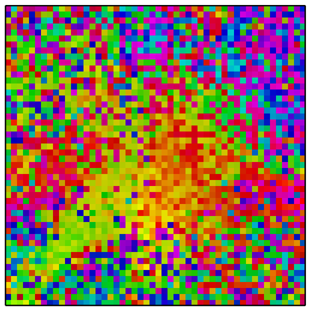
Figure 2: Snapshots of the neuronal activities in the network. (**a**) Spot. (**b**) Bar. (**c**) Spiral.



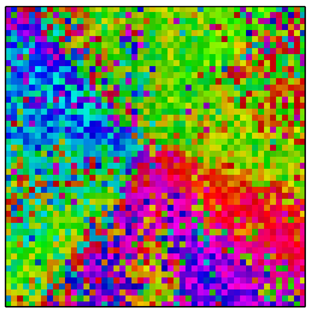
(a)



(b)



(c)



(d)

Figure 3: Orientation maps obtained by simulations. (**a**) The relationship between orientation selectivities and colors in the maps is illustrated. (**b**) Spot. (**c**) Bar. (**d**) Spiral.