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Self-Organization of Orientation Selective and Ocular Dominance Maps through Spike-Timing-Dependent Plasticity

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Abstract

In the primary visual cortex, there are orientation selective map and ocular dominance map. These maps correlate with each other. Though many models which explain the formation of the orientation selective map and the ocular dominance map have been proposed, these models contain a physiologically implausible process. It is indicated that spike-timing-dependent plasticity (STDP) can yield "topographic map" without any constraints. We show that large STDP time constants yield the orientation selective map, and small STDP time constants yield the ocular dominance map. This result suggests the relationship between the orientation selective and the ocular dominance maps can be explained by modulation of STDP time constants.

Keywords :Orientations selective map, Ocular Dominance Map, Spike-timing-dependent plasticity

1 Introduction

In sensory cortex, the selective map called " topographic map " consists of stimulus-selective neurons, in which close neurons are selective to a similar stimulus and distant neurons are selective to a different stimulus. In the primary visual cortex, there are orientation selective map and ocular dominance map [1]. Orientation selective map consists of neurons selective to orientation of edge in the input image. Ocular dominance map consists of neurons selective to whether the input comes from the right eye or the left one. These maps have spatial relationships [2]. The borders between different orientation selectivities are tend to intersect the borders between different ocular dominance at right angles. Moreover, many intersections of the borders between different orientation selectivities are in the middle of the regions with same ocular dominance. These relationships indicate two maps have negative correlation.

Correlations between inputs are important for formation of topographic maps. In the primary visual cortex, neurons receive inputs from lateral geniculate nucleus (LGN). LGN has eve-specific layers and their respective ON/OFF sublaminae. In eye-specific layers, neurons are selective to inputs from the contralateral or the ipsilateral eye. ON/OFF sublaminae consist of ON-Center and OFF-Center neurons, respectively. Activities show correlations between neurons in the same sublamina and different sublaminae [3]. Correlation in the same sublamina is the strongest and correlation in the same eye-specific layer is stronger than in different eye-specific layers. Cross-correlation functions within the same and between different evespecific layers show unimodal distribution and strong peak at zero. However, in finer time scale, central peaks are wider and more peaks at nonzero are observed between different eye-specific layers. These differrences of correlations between neurons in the same sublamina and different sublaminae lead to formation of orientation selective and ocular dominance map.

Many models based on correlation learning which modify synaptic strengths depending on the correlation of pre- and postsynaptic activities explain formation of topographic maps [4] [5] [6]. These models contain, however, physiologically implausible constraints. For example, Malsberg's model normalizes synaptic strength to keep constant sum of synaptic strengths subject to one neuron.

It is indicated that long-term potentiation (LTP) and long-term depression (LTD) of synapses depend on relative spike timing of pre- and post-synaptic neurons [7]. Postsynaptic spikes preceding presynaptic spikes induce LTP and postsynaptic spikes following presynaptic spikes induce LTD. Smaller difference between 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 formation of topographic map [8].

There is no model that explains formation of orientation selective and ocular dominance maps without implausible constraints. For unified explanation of formation of orientation selective and ocular dominance maps by STDP, we show that we can switch between formation of orientation selective and ocular dominance maps by modulating time constants of STDP.

2 Model

2.1 Synaptic strengths and STDP

The model network consists of the LGN and the primary visual cortex. Each of the LGN neurons has projections to all of the cortical neurons. All of the cortical neurons are connected to each other with synaptic strengths w^{cor} :

$$w^{cor} = E \exp\left(-\frac{d}{\sigma_e^2}\right) - I \exp\left(-\frac{d}{\sigma_i^2}\right),$$
 (1)

where d is the distance between neurons, and E, I, σ_e , σ_i are parameters.

Synaptic strengths $w^{E,C}$ of projections from the LGN eye-specific layer $E \in \{con, ips\}$ whose center type is $C \in \{on, off\}$ to the cortex is modified by STDP as follows:

$$w^{E,C} \leftarrow w^{E,C} + \Delta w^{E,C},$$

$$\Delta w^{E,C} = \begin{cases} A_{+} \exp\left(-\frac{\Delta t}{\tau_{+}}\right) & (\Delta t \ge 0), \\ -A_{-} \exp\left(\frac{\Delta t}{\tau_{-}}\right) & (\Delta t < 0), \end{cases}$$
(2)

when pre- and postsynaptic spikes occur at t_{pre} and t_{post} . Here, $\Delta t = t_{post} - t_{pre}$ is the interval between pre- and postsynaptic spikes. A_+ and τ_+ respectively determine maximum amount and the time constant of LTP and A_- and τ_- respectively determine those of LTD.

Let Δt_1 and Δt_2 are intervals of pre- and postsynaptic spikes and $\Delta t_1 > \Delta t_2$. The difference of modification,

$$\begin{aligned} |\Delta w_1 - \Delta w_2| &= \\ \begin{cases} A_+ \left(\exp\left(-\frac{\Delta t_2}{\tau_+}\right) - \exp\left(-\frac{\Delta t_1}{\tau_+}\right) \right) & (\Delta t_2 > 0) \\ A_- \left(\exp\left(-\frac{\Delta t_1}{\tau_-}\right) - \exp\left(-\frac{\Delta t_2}{\tau_-}\right) \right) & (0 > \Delta t_1) \end{cases} \end{aligned}$$

is small when τ_+ and τ_- are large. The synaptic modification by STDP is less sensitive to fine difference of the interval between pre- and postsynaptic spikes with large time constants τ_+ and τ_- . There are correlations between neurons in the same and between different eye-specific layers in large time scale. Eyespecific Layers are not distinguished by STDP with the large time constants. Therefore STDP with large τ_+ and τ_- may lead to formation of orientation selective map, and small τ_+ and τ_- may lead to formation of ocular dominance map.

2.2 Primary visual cortex model

The model network consists of 225 cortical neurons and 225 LGN neurons in each sublaminae. We used Izhikevich neuron model [9] for cortical neurons, that is,

$$\frac{\mathrm{d}v}{\mathrm{d}t} = 0.04v^2 + 5v + 140 - u + I,$$

$$\frac{\mathrm{d}u}{\mathrm{d}t} = a(bv - u),$$
if $v \ge 30 \,\mathrm{mV}$ then, $v \leftarrow c, u \leftarrow u + d.$
(3)

Here, a, b, c, and d are dimensionless parameters, and the variable I represents synaptic currents. In this simulation, we set parameters, a = 0.02, b = 0.2, c = -65, and d = 8. The variable v is the membrane potential. The variable u represents the recovery variable providing negative feedback to v. The cortical neuron i receives synaptic currents I_i :

$$I_{i} = \sum_{E \in \{con, ips\}} \sum_{C \in \{on, off\}} \sum_{j} w_{ij}^{E,C} s_{j}^{E,C} + \sum_{j} w_{ij}^{cor} s_{j}^{cor}, \qquad (4)$$
$$ds_{j}^{cor} = -\frac{1}{2} e^{cor} + \delta(t - t_{j})$$

$$\frac{\mathrm{d}t}{\mathrm{d}t} = -\frac{1}{\tau_s}s_j + \delta(t-t_j),$$

$$\frac{\mathrm{d}s_j^{E,C}}{\mathrm{d}t} = -\frac{1}{\tau_s}s_j^{E,C} + \delta(t-t_j).$$

Here, w_{ij} is the synaptic strength from neuron j to neuron i, and δ is the delta function. Synaptic current from cortical neuron j is represented by s_j^{cor} , and synaptic current from LGN neuron j in eye-specific layer E whose center type is C is represented by $s_{ij}^{E,C}$. The presynaptic neuron j generates a spike at t_j .

2.3 LGN model

The LGN neuron j at location (x, y), location of the center of LGN is (0, 0), generates spikes through Poisson process with the following firing rate:

$$\lambda_{j}^{on} = 0.015 + 0.015 \exp\left(-\frac{x_{\theta}^{2} + y_{\theta}^{2}}{\sigma^{2}}\right) \cos\left(\frac{2\pi x_{\theta}}{\lambda^{sp}}\right),$$

$$\lambda_{j}^{off} = 0.015 - 0.015 \exp\left(-\frac{x_{\theta}^{2} + y_{\theta}^{2}}{\sigma^{2}}\right) \cos\left(\frac{2\pi x_{\theta}}{\lambda^{sp}}\right),$$

$$x_{\theta} = x \cos\theta + y \sin(\theta), \qquad (5)$$

$$y_{\theta} = 0.3 \times (-x \sin(\theta) + y \cos(\theta)).$$

Here, $\theta \in \{0, \pi/6, \pi/3, \pi/2, 2\pi/3, 5\pi/6\}$ is the orientation of the input, and σ and λ^{sp} are parameters determining the spatial variance of the input. The firing rate of the neuron j in the on-center sublamina is λ_j^{on} , and the firing rate of neuron j in the off-center sublamina is λ_j^{off} . In addition, spikes of LGN neurons in the same and different sublaminae are correlated in different time scale as previously indicated (Figure 1).



Figure 1: Cross-correlation functions calculated between neurons within the same sublamina (top), between the on-center sublamina and the off-center sublamina within the same eye-specific layer (middle), and between different eye-specific layers (bottom). Spikes were binned into 10 ms (left) and 100 ms (right).

3 Results

We simulated in three conditions, small, medium, and large time constants. We determined A_{-} in equation (2) to keep the value of $A_{-}\tau_{-}$ constant and modified A_{+} to balance LTP with LTD (table 1).

Table 1: Parameters of STDP.

τ_+	10	50	100
τ_{-}	50	250	500
$ A_+ $	0.3	0.026	0.008
A_{-}	0.13	0.026	0.013



Figure 2: The orientation selective map with $\tau_{+} = 50$ and $\tau_{-} = 250$. One black square represents one cortical neuron. Values of $w_{ij}^{on} - w_{ij}^{off}$ are represented by colors. Here, w_{ij}^{on} and w_{ij}^{off} are same as in equation (6).



Figure 3: The ocular dominance map with $\tau_+ = 50$ and $\tau_- = 250$.

Figure (2) and figure (3) are the orientation selective map and the ocular dominance map obtained with $\tau_{+} = 50$ and $\tau_{-} = 250$. Though many neurons are selective to certain orientation, few neurons are selective to contralateral or ipsilateral eye.

To evaluate differences of orientation selectivity and ocular dominance, we defined degrees of orientation selectivity S_i^{OR} and ocular dominance S_i^{OC} of the cortical neuron i below.

$$O_{i}^{\theta} = \frac{\sum_{j} \left(\lambda_{j}^{on} w_{ij}^{on} + \lambda_{j}^{off} w_{ij}^{off}\right)}{\sum_{j} \left(\lambda_{j}^{on} + \lambda_{j}^{off}\right)},$$

$$\left(S_{i}^{OR} e^{i\psi}\right)^{2} = \frac{\sum_{\theta} \left(e^{i\theta} O_{i}^{\theta}\right)^{2}}{\sum_{\theta} \left(O_{i}^{\theta}\right)^{2}},$$

$$S_{i}^{OC} = \frac{\left(\sum_{j} w_{ij}^{con}\right)^{2} - \left(\sum_{j} w_{ij}^{ips}\right)^{2}}{\left(\sum_{j} w_{ij}^{con}\right)^{2} + \left(\sum_{j} w_{ij}^{ips}\right)^{2}}.$$
(6)

Here, θ is the orientation of the input and λ_j^{on} and λ_j^{off} are frequencies of the LGN neuron j. These are defined in equation (5). Synaptic strengths from the oncenter and the off-center neurons j are represented by $w_j^{on} = w_j^{con,on} + w_j^{ips,on}$ and $x_j^{off} = w_j^{con,off} + w_j^{ips,off}$. Those from LGN neurons j in eye-specific layers selective to the contralateral eye and the ipsilateral eye are represented by $w_j^{ips} = w_j^{ips,off} + w_j^{ips,off}$.

Table 2: Selectivity in three conditions of time constants.

τ_+/τ	S^{OR}	S^{OC}
10/50	0.2799 ± 0.0919	0.2721 ± 0.2002
50/250	$0.3425 {\pm} 0.0779$	$0.1129 {\pm} 0.0886$
100/500	$0.3273 {\pm} 0.0715$	$0.0779 {\pm} 0.0605$

The difference between degrees of orientation selectivity $\tau_{+} = 10$ and $\tau_{+} = 50$ is significant (P < 0.05, t-test). The difference between $\tau_{+} = 50$ and $\tau_{+} = 100$ is not significant (P < 0.05, t-test). About ocular selectivity, though it is significant between $\tau_{+} = 50$ and $\tau_{+} = 100$, not significant between $\tau_{+} = 10$ and $\tau_{+} = 50 (P < 0.05, \text{ t-test})$.

4 Conclusion

We showed that STDP with different time constants result different topographic maps. If cortical neurons could modulate time constants by any way, STDP could explain the negative correlation between the orientation selective and ocular dominance map without implausible constraints. Such modification, however, has not found either in vitro or in vivo.

In our model, we explained formation of orientation selectivity and ocular dominance by differences of correlations of inputs in different time scales. Hence, we can yield other "multiple maps" representing multiple informations, only if inputs have different correlations in different time scales.

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