Self-organization model on receptive field of neuron with asymmetric time window of synaptic modification

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Abstract The spatial-temporal response properties of some simple neurons in visual pathway arise basically prior to birth. In the absence of visual experience, how do these neurons develop in visual system? Based on Wimbauer network with delay, a four-layer feed-forward network model is proposed, which is characterized by modifying the Hebb learning rule through introducing the asymmetric time window of synaptic modification found recently in neurobiology. The model can not only generate by self-organization more diversified spatial-temporal response characteristics of neuronal receptive field than earlier models but also provide some explanations for the possible mechanism underlying the development of receptive fields of contrast polarity sensitive neurons found in visual system of vertebrate. Thus the proposed model may be more widely applicable than Linsker model and Wimbauer model.

Keywords: neuronal receptive field, self-organization, asymmetric time window of synaptic modification.

A variety of spatial-temporal response characteristics of neurons in visual system of vertebrate have been observed. Experiments show that the formation of basic components in visual system is through prenatal development[1]. A question arises as to the possible mechanism underlying the development of receptive field with certain special spatial-temporal response characteristics in visual system in the absence of visual experience prior to birth. To answer this question, Linsker proposed a linear feed-forward network, in which the connection strengths developed according to a connection-modification rule of Hebbian synapses. If the parameters were chosen in an appropriate regime, the emerging of certain types of receptive fields such as center-surround opponent type and orientation-selective type could be derived from the network by self-organization. Furthermore, if the lateral connections between the cells incorporated to the network, these cells could self-organize into orientation columns[2—4]. A Hebb type multi-layer feed-forward network model constructed by Kammem and Yulli could also generate by self-organization orientation-selective neurons provided that random spontaneous noise was present in the system[5]. These models mentioned above only addressed the spatial characteristics of receptive fields. In order to explore the

development mechanism of neuronal receptive field with dynamic response characteristics, Wimbauer et al. introduced synaptic delay to Linsker model[6]. Thus spatial-temporal dynamic receptive fields such as spatial and temporal differentiator could emerge in the system by self-organization, in this way the receptive field possessed temporal behavior.

The synaptic modification rules adopted in the earlier models are essentially time-symmetric: some neglected synaptic delay, others considered the delay, but only considered the influence of pre- and post-synaptic neuronal states to synaptic potentiation or depression without considering time parameter. But the asymmetry of critical time window for the induction of synaptic potentiation and depression has been discovered in recent studies[7, 8]. The discovery offered an important constrained condition for the development process on the visual neuronal receptive field. Based on Wimbauer network we constructed a four-layer feed-forward network model characterized in modified learning rule by introducing asymmetric time window of synaptic modification. By self-organization, different spatial-temporal separable receptive fields can emerge in the proposed network, which not only exhibited different shapes as those of simple cells observed in Linsker network, but also possessed diversified temporal response properties. Meanwhile our model can provide some explanations for various types of "on/off" response characteristics of visual neurons and for possible forming mechanism of neurons sensitive to contrast polarity found recently. Both results of theoretical analysis and computer simulation indicate that our model may be more widely applicable than Linsker network and Wimbauer network.

1 Self-organization model on receptive field of neuron

As fig. 1 shows, our model is a four-layer feed-forward network with the following properties:

(ⅰ) Synaptic delay time between layers A-B or layers B-C is identical. The probability of synaptic connections is only related to their spatial position; while that between layers C-D exhibits Gaussion distribution and is only related to their delay time, that is, a neuron in layer D only receives inputs of synapses with different delays from layer C's one same neuron.

(ⅱ) Synaptic modification is processed layer by layer. The synaptic modification from layers A-B to layers B-C and between layers C-D is under the influence of random spontaneous electrical activity of layer A and layer C respectively. The activities of layers A and C are uncorrelated in both time and space domains.

Assuming layer L (A, B, C) and layer M(B, C, D) are in succession, and M is one layer higher than L. The probability distribution of the synaptic connection between the two layers is $p(j)p(t)$, which is a product of spatial probability distribution $p(j)$ and temporal probabil-

ity distribution $p(\boldsymbol{t})$, $\boldsymbol{t}$ denotes delay time of synapses and j denotes strength of synaptic connections. Let $S_{Mi}(t)$ denote the state of a neuron i in layer M at time t which is a weighted algebraic summation of the input states of the neurons in layer L, and it can be expressed as

$$S_{Mi}(t) = \sum_{j}\sum_{\boldsymbol{t}} p(j)p(\boldsymbol{t})J_{ij}(\boldsymbol{t})S_{Lj}(t-\boldsymbol{t}). \qquad (1)$$
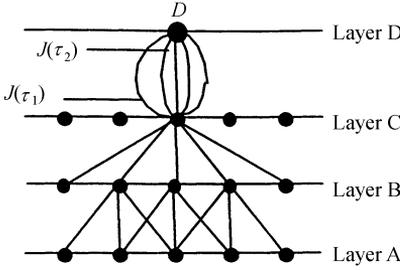

Fig. 1. Architecture of self-organization model for spatial-temporal separable receptive field.

For synaptic modification of the network, two assumptions are made as the following:

(ⅰ) About time parameter, there are two time scales: the change speed of input pattern and the modification speed of synapses, assuming that the former is far greater than the latter, and the change speed of input pattern and the time averaged synaptic delay are in the same order.

(ⅱ) The excitation or inhibition of a post-synaptic neuron is determined by the summation of inputs from plenty of pre-synaptic neurons. Since the synaptic connections, in time domain, follow Gaussian distribution with mean equal $\boldsymbol{t}_0$, from statistics sense, in about time delay $\boldsymbol{t}_0$, the inputs have arrived at the next layer of neurons, activating post-synaptic neurons (excitation or inhibition). Accordingly, the boundary between excitatory region and inhibitory region of the asymmetric time window of synaptic modification should be greater or equal to or a little smaller than $\boldsymbol{t}_0$. Suppose the boundary value is $\boldsymbol{t}^*$.

According to the above assumptions and consulting the properties of the asymmetric time window of synaptic modification, a time window function of synaptic modification is introduced:

$$\text{window }(\boldsymbol{t}) = c \times \text{sign}(\boldsymbol{t}^* - \boldsymbol{t})\exp\left[\frac{-(\boldsymbol{t}-\boldsymbol{t}^*)^2}{2T}\right], \quad (2)$$

where $\text{sign}(\boldsymbol{t}^* - \boldsymbol{t}) = \begin{cases} 1, & \boldsymbol{t}^* - \boldsymbol{t} \geqslant 0 \\ -1, & \boldsymbol{t}^* - \boldsymbol{t} < 0 \end{cases}$, c and T are constants.

Introducing Hebb learning rule with asymmetric time window as

$$\left\langle \Delta J_{ij}(\boldsymbol{t},\, t)\right\rangle = \frac{1}{\Lambda}\int_0^{\Lambda} \text{window }(\boldsymbol{t})\boldsymbol{e}(S_{Mi}(t)-c_1)$$
$$\bullet\, (S_{Lj}(t-\boldsymbol{t})-c_2)\mathrm{d}t$$
$$= \text{window}(\boldsymbol{t})\boldsymbol{e}\left\{\sum_k\sum_{\boldsymbol{t}}J_{ij}(\boldsymbol{t},\, t)p(k)p(\boldsymbol{t}')\right. \qquad (3)$$
$$\left.\bullet[Q(j,k;\boldsymbol{t},\,\boldsymbol{t}')+k_2]+k_1\right\},$$

where

$$Q(j,k;\boldsymbol{t},\boldsymbol{t}') = \frac{1}{\Lambda}\int_0^{\Lambda}\left(S_{Lj}(t-\boldsymbol{t}-s)-\langle S_L\rangle\right)$$
$$\bullet\, S_{Lk}(t-\boldsymbol{t}'-s)-\langle S_L\rangle)\mathrm{d}s,$$

where $\boldsymbol{e}$, c_1, c_2 are all constants, $\langle\;\bullet\;\rangle$ denotes average over time.

It should not lose generality, if assume all weights of synaptic connections between layer A-B-C equal zero, then layer A-B-C network degenerates to Linsker network.

Supposing that all excitatory connections have formed between layers A and B (see refs. [2, 6]), and following property (2), we have

$$\left\langle J_{Bij}(t)\right\rangle = k_1 + \sum_j [Q_B(j,k)+k_2]P_A(k)\langle J_{Bk}(t)\rangle,$$
$$\qquad (4)$$
$$\left|J_{Bij}(t)\right| < J_{\max},$$

where k_1 and k_2 are parameters, by setting the parameters values, layer C would exhibit various types of receptive field, such as all excitatory type or all inhibitory type or center-surround symmetric type or center-surround asymmetric type or the type that boundary shape between excitatory and inhibitory regions is linear or curvilinear[9].

For layer C-D, according to eq. (3), the synaptic modification rule is

$$\left\langle J_c(t)\right\rangle = \boldsymbol{e}\,\text{window}(\boldsymbol{t})\left[J_c(t)P_c(t)\right.$$
$$\left. +k_2\sum_{\boldsymbol{t}'}J_c(t)P_c-(\boldsymbol{t}')+k_1\right]. \qquad (5)$$

Consider a simple case, when $|k_1| > k_2 J_{\max} + J_{\max}$, the symbol of weight increment is determined by the product of $\boldsymbol{t}^*-\boldsymbol{t}$ and k_1, the self-organizing result of the network is

$$k_1 > 0,$$
$$J_c(i,\boldsymbol{t}) = \text{sign}(\boldsymbol{t}^*-\boldsymbol{t})J_{\max},$$
$$k_1 < 0, \qquad (6)$$
$$J_c(i,\,\boldsymbol{t}) = -\text{sign}(\boldsymbol{t}^*-\boldsymbol{t})J_{\max}.$$

Thus, the synaptic connection strengths exhibit the temporal asymmetric structure.

(ⅰ) When $\boldsymbol{t}^*=\boldsymbol{t}_0$, the structure is the same as tempo-

ral differenciator emerged from Wimbauer three-layer network with time delay;

(ⅱ) when $k_1 > 0$, it has on response property;

(ⅲ) when $k_1 < 0$, it has off response property;

(ⅳ) when $t^* \gg t_0$, an approximated spatial symmetrical type of structure is realized by self-organization that means time average to input pattern is conducted. Defining $S_D(t)$ as the output of neuron D at time t, for convenience of analysis, adopting continuum representation (r denotes position of the neuron):

$$S_D(t) = \int dt\, S_c(t-t)(pj)^c(t)$$
$$= \int dt (pj)^c(t) \Big[\int dr(pj)^B(r) \qquad (7)$$
$$\cdot \int dr' P_A(r') S_A(r+r', t-t) \Big],$$

where $(pj)^c(t) = P_c(t)J_c(t)$, $(pj)^B(r) = P_B(r)J_B(r)$.

From eq. (7), we see that the information processing from layer A to layer D follows the spatial-temporal separable function. Because the connections between layer A and layer B are all excitatory type, only do spatial average over input signal, so the receptive field of neuron D is mainly determined by $(pj)^c(t)(pj)^B(r)$. As a result, the receptive field of neuron D has, in spatial domain, the same structure as that of a neuron in layer C, meanwhile the possesses temporal sensitivity, so it is a spatial-temporal separable dynamic receptive field.

2 Computer simulation results and its application

Let layer A be a 25×25 cell matrix, layer B a 17×17 cell matrix and layer C connect with layer D through synapses with 12 kinds of delay time. By properly choosing the parameters and through self-organization the neurons in layer C can form the receptive field with various spatial shapes, and those in layer D with lots of temporal distributions. As a consequence, dynamic spatial-temporal receptive fields of the neurons in layer D are derived. During self-organization, different parameters enable the resultant receptive field to possess diversified temporal response characteristics. In order to illustrate the spatial-temporal distribution about the neuronal receptive fields in layer D, we take two examples: center-surround opponent type and linear edge-detecting type of receptive field. The kernel functions of information processing from layer B to layer D are plotted in figs. 2 and 3.

The spatial-temporal dynamic receptive field can elucidate the principle underlying information processing on various spatial-temporal response characteristics of visual neuron. Different architecture parameters of the network enable the final formed receptive field to have different dynamic response characteristics. In the following, take a center-surround type of receptive field as example to explore how k_1 and t^* influence the

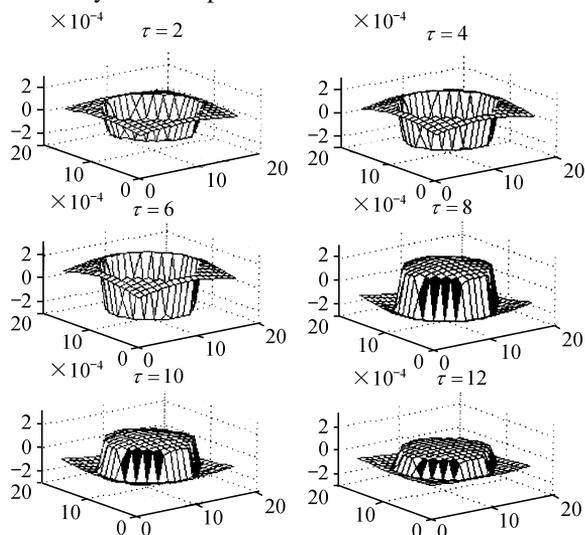"on/off" dynamic response characteristics of neurons.

Fig. 2. Spatial-temporal response characteristics of the off-center receptive field: for different time delay t, the spatial distribution of receptive field of neurons in layer D. Abscissas and ordinates represent r, the position of neurons in layer B, z axis represents the value of $(pj)^C(t)(pj)^B(r)$. Synapses with different delay process input signal appeared in the receptive field in different ways. Cooperative effects of both fast-delay synapses and slow-delay synapses make the neuron sensitive to the illumination change in the center of receptive field from light to dark.
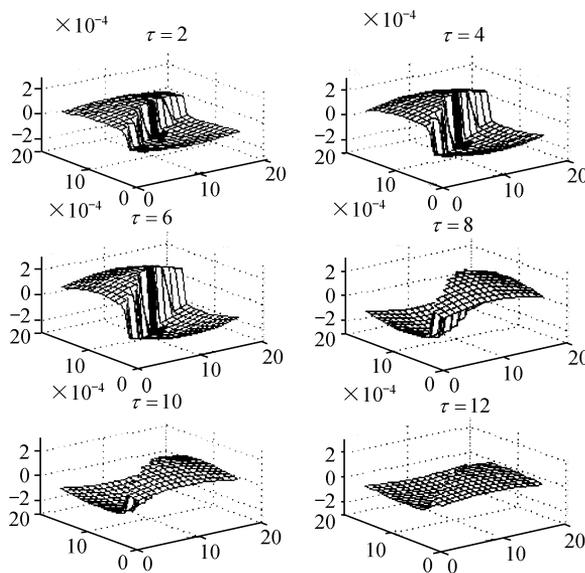

Fig. 3. Spatial-temporal response characteristics of edge-detecting type of receptive fields: sensitive to the moving edge along the border between excitatory and exbibitory regions.

Stimulating central region of receptive field using a round light point, for different k_1 and t^*, the response of the network can be illustrated in fig. 4.

(ⅰ) When $k_1 > 0, t^* \leqslant t_0$ (fig. 4 (a), (b)), it exhibits

a transient ON type of response. (ⅱ) When $k_1 > 0$ $t^* > t_0$ (fig. 4(c)) it exhibits a sustained type of ON response. (ⅲ) When $k_1 < 0, t^* \geqslant t_0$ (fig. 4(d), (e)) it exhibits a transient OFF type of response. (ⅳ) When $k_1 < 0, t^* < t_0$ (fig. 4(f)) it exhibits a sustained OFF type of response. The lower curves in the figure represent the variation of light stimulus strength in time. As a result, the proposed model can give some explanations of different "on/off" response characteristics of neurons and their forming mechanism.
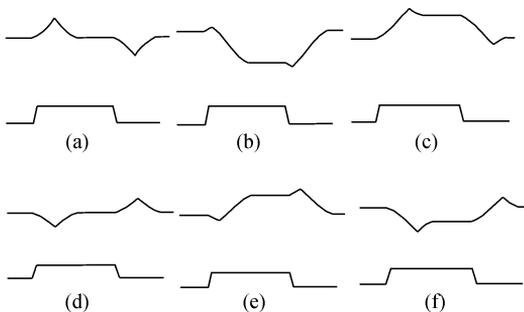

Fig. 4. For different k_1 and τ^*, the variation of "on/off" response characteristics of neurons. (a) $k_1 > 0$, $t^* = 6$; (b) $k_1 > 0$, $t^* = 3$; (c) $k_1 > 0$, $t^* = 10$; (d) $k_1 < 0$, $t^* = 6$; (e) $k_1 < 0$, $t^* = 10$; (f) $k_1 < 0$, $t^* = 4$. The upper curves represent response of neurons, while the lower ones represent the variation of light stimulus strength in time. (a) and (b) showing transient "on" response ; (c) showing sustained "on" response; (d) and (e) showing transient "off" response; (f) showing sustained "off" response.

Edge-detecting neurons, which are sensitive to special contrast polarity (brighten or darken), have been observed in visual pathways of some amphibians, birds and mammals, showing "head/tail preference"[10—14]. The proposed model can explain both the principles underlying information processing and the development mechanism of these special neurons. Take an example of toad's R3 ganglion cell. Its receptive field, which is sensitive to contrast polarity, could be constructed as follows: By setting suitable parameters, the center-surround type of receptive field and the temporal distribution with transient "off" response characteristic could emerge in layer C and layer D, respectively. When a stripe stimulus is traversing the receptive field, the response of the neuron is shown in fig. 5.

When the contrast polarity of object/background is reversed, there is time difference in neuronal response. For a black stripe moving against a white background, when its leading edge arrives at the excitatory region of the receptive field, the neuron's response gradually increases to the maximum, whereas for a white stripe moving against a black background, until its trail edge arrives at the exciting region of the receptive field, the neuron's response begins to increase gradually and then reaches its maximum. Hence both cases exhibit "head/tail prefer-
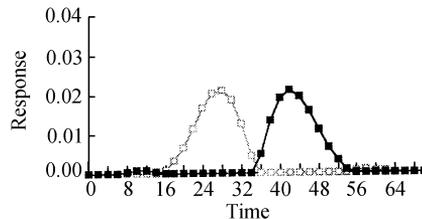
ence".

Fig. 5. Computer simulation results on "head/tail preference" response of a toad's R3 neuron. —□—, b/w; —■—, w/b.

3 Conclusion and discussion

We explore the possible mechanism underlying the receptive field development of visual neurons by self-organization, to answer how the spatial-temporal response characteristics of some simple-feature analysis neuron form through prenatal development in the absence of visual experience. According to recent results of neurobiology on synaptic modification, i.e. there is an asymmetric time window, we modified Hebb learning rule and constructed a new model for self-organization of neuronal receptive field. By setting suitable parameters, this four-layer feed-forward network model could form by self-organization various spatial-temporal separable receptive fields, which possessed, in spatial domain, a variety of shapes as those of simple cell's receptive field, and in temporal domain, diversified "on/off" dynamic response characteristics. Our model could fairly explain the special visual information processing principle underlying the contrast polarity sensitive neurons observed recently in the visual system of vertebrate, meanwhile searched for the possible mechanism underlying the formation of neuronal receptive field. During the embryo developing process, the connections between neurons undergo a precise adjusting and modifying process[1]. The effect of architecture parameters of the network on its final structure may elucidate that the formation of receptive field is the result of interaction of genetic factors and self-organization.

The proposed model is more widely applicable than Linsker model and Winmbauer model, therefore it can provide new possibility to show how the diversified spatial-temporal receptive field of various types of visual neuron form. Both Linsker network and Winmbauer network become special examples of our network: if layer C is all excitatory receptive field and if $t^* = t_0$, that is t^*, the boundary value between excitatory and inhibitory regions in an asymmetrical time window in layer D is equal to t_0, then the self-organizing results of our model is just as temporal differentiator emerged in Wimbauer network; if layer C is a linear boundary-detecting type of receptive field, and excitatory and inhibitory regions are equal in area, meanwhile if in layer D the temporal distribution is uniform, then the self-organizing result of our model is

just as spatial differentiator emerged in Wimbauer network. If the synaptic connections between layers C and D with no time-delay property, our network would degenerate into three-layer Linsker network.

There are various possibly connective manners between different layer's neurons in visual system. A certain neuron may receive inputs with the same delay time from different regions, but also may receive inputs with different delay time from the same region. Therefore, it is of biological basis that assuming different connective manners exist between layers A-B, B-C and C-D. Because we attempt to explore theoretically the basic developing mechanism of neuronal spatial-temporal receptive fields in different kinds of animal with different types of visual pathway, only a simplified and abstract model was studied. The cell's connections from layers A to D can be regarded as an approximation to the neuronal connections between different layers in visual system, just as Linsker network, in which the cell's connection between different layers was regarded as an abstract representation for the neuronal connections from retina to visual cortex. Nevertheless, many neurons from retina to visual cortex may all have the possibility possessing the properties of abstract neurons in the proposed network, such as convergent type of inputs, feed-forward connections, etc. The feedback between layers and nonlinear property in neuronal response were neglected in our model. At present, among all possible connective manners we only conducted research on one manner, yet the model with this type of neuronal connection has already made explanations to the possible mechanism underlying the formation of some important spatial-temporal separable type of receptive fields. For other connective manners, we will deal with them later, for the derivation of mathematics is more complicated.

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