Biochemical and Biophysical Research Communications 413 (2011) 5–9

Contents lists available at SciVerse ScienceDirect

Biochemical and Biophysical Research Communications

journal homepage: www.elsevier.com/locate/ybbrc

An information integration model of the primary visual cortex under grating stimulations

Zhizhong Wang, Li Shi *, Hong Wan, Xiaoke Niu

The School of Electrical Engineering, Zhengzhou University, Zhengzhou 450001, China

ARTICLE INFO

Article history:
Received 25 July 2011
Available online 17 August 2011

Keywords:
Primary visual cortex
Integration model
Receptive field
Grating stimulations

ABSTRACT

During the course of information processing, a visual system extracts characteristic information of the visual image and integrates the spatial and temporal visual information simultaneously. In this study, we investigate the integration effect of neurons in the primary visual cortex (V1 area) under the grating stimulation. First, an information integration model was established based on the receptive field properties of the extracted features of the visual images features, the interaction between neurons and the non-linear integration of those neurons. Then the neuropsychological experiments were designed both to provide parameters for the model and to verify its effect. The experimental results with factual visual image were largely consistent with the model's forecast output. This demonstrates that our model can truly reflect the integration effect of the primary visual system when being subjected to grating stimulations with different orientations. Our results indicate the primary visual system integrates the visual information in the following manner: it first extracts visual information through different types of receptive field, and then its neurons interact with each other in a non-linear manner, finally the neurons fire spikes recorded as responses to the visual stimulus.

1. Introduction

The visual system plays an important role in the perception of the natural environment for animals. The information contained in the outside image is accepted by the retina first and then is transferred through the lateral geniculate nucleus (LGN) before arriving at the visual cortex. This is a process of both feature extraction and spatiotemporal integration [1,2]. The information is indicated by different kinds of spiking patterns of neurons in the primary visual cortex. These patterns are the results of the feature extraction made on the natural image integrated with the interaction between neurons. Building a model to describe the integration process of the primary visual system is of great significance to help understand the information transmission process of the visual system as well as its manner to perceive the natural image.

Since Hubel and Weisel found the receptive field property of a simple cell in the primary visual cortex in the 1960s [3,4], many researchers began to study and model the characteristics of visual mechanisms. With respect to the research on integration mechanisms, the work by Hubel and Weisel, Jin et al., and Chen proved that an important way for visual system to deal with natural image is to eliminate redundancy and extract salience through receptive field of different levels [3–6]. Vinje and Tolhurst's research indicated that integration resulted in the sparse property of V1 [7,8]. Yao et al. found some neurons in cats' V1 integrate a large scale complex image through stimulating the area outside the neuron's receptive field [9]. Hirsch discovered that the complex cell integrated the output information of simple cells [10]. On horizontal information integration, Smith et al. and Wang et al. proved that adjacent neurons transmitted information to each other through horizontal connections [11,12]. Berger et al. analyzed spiking activities in cats' V1 under stimulus of different luminance using methods of graph theory. They found that the whole set of correlated multi-unit activity (MUA) is decomposed into a small number of groups of MUAs which have a high degree of overlap of mutually correlated pairs and the spatial scale of this correlation map is in agreement with the scale of orientation tuning maps set up by imaging [13]. Gray et al. calculated the correlation between recorded neurons and found the oscillatory responses in synchrony for cells, which indicates that synchronized oscillation is one of the ways the neurons interacted with each other through horizontal connections [14]. Sharpee et al. demonstrated that the filters computed by directly taking nonlinearity into account have better predictive ability and depend less on the stimulus than those computed under the linear model [15,16]. Victor investigated receptive field properties of single neurons with localized two-dimensional stimuli, the two-dimensional Hermite functions, which implies the presence of nonlinearities that are not local in either space or spatial frequency [17]. The above research on integration indicates

* Corresponding author. Fax: +86 0371 67781407.
E-mail address: shili@zzu.edu.cn (L. Shi).

0006-291X/$ - see front matter
doi:10.1016/j.bbrc.2011.07.120

that V1 integrates information in both latitudinal and horizontal way and in a nonlinear way.

On the basis of the proposed mechanisms of visual information integration, the first step many researchers took was to establish a model to simulate this integration process. Among these integration models, based on the neuronal response property, Field proposed a sparse coding model simulated the receptive field of the simple cell in the primary visual cortex [18]. Hyvarinen introduced the Independent Component Analysis method [19], Independent Subspace Analysis [20], and Topology Independent Component Analysis [21] to simulate the receptive field of the simple cell, the complex cell and the topological relation among the neurons, respectively. Also based on the receptive field property, Yang constructed a computation model to perceive content and direction of the natural images [22]. Eckhom set up a link model about the spiking activity according to the synchropulse phenomenon in the cat visual cortex. The model demonstrates that the visual system integrates the natural image information in a synchronized oscillatory manner [23]. The neurons in the primary visual cortex integrate visual information in a non-linear way. Dan constructed a neuronal network of two layers, which can transform the spatiotemporal visual information to the time-varying activities [24]. Based on the characteristics of the receptive field and the nonlinearity of the neuronal response, Paninski introduced a stochastic Integrate-and-Fire neural encoding model, which can predict neurons' responses [25]. Based on Paninski's work, Butts worked out a neural interaction model, which reveals the mechanism of the primary visual system [26]. Those models were constructed either based on receptive field property or the mechanism of synchronization. As a result, they could not effectually represent the whole property of V1, which integrates the visual information by combining several mechanisms together.

To address the deficiency of the above models, here we report a model to describe the information integration process of the neurons in V1 synthetically utilizing the theories of receptive field, synchropulse and the nonlinearity. The validity of our model is demonstrated by the experimental data recorded in rat V1 under the grating stimulus. Our model is based on the characteristics of the receptive field, interaction among the neurons and nonlinear property of the V1 neurons. The neurophysiological experiments were designed to get some parameters for the model and to further check the model. The results indicate that the integration model can predict the response of the neurons in V1 under the simulation of gratings with different orientations which suggests that when information is being processed, the neural response is the result of many neurons' interacting with each other and integrating the visual information in a nonlinear way.

2. Material and methods

2.1. Building the visual information integration model

There is a projective area on the retina for most neurons in V1, which is called receptive field. The receptive field is considered as the special visual stimulus pattern that can evoke the maximum neural response [3]. The neurons in V1 process the image features in a synchronous and non-linear way after the visual information arrives at V1, and as a result of the neural interaction, the visual cortex shows different kinds of neural firing pattern [27,28].

Based on the information processing principle above, a visual information integration model is built and shown in Fig. 1.

The integration model built in this paper is composed of three parts: Part 1, the preliminary integration; Part 2, the synchronous integration among adjacent neurons; Part 3, the nonlinear global integration among neurons.

2.1.1. Part 1 preliminary integration

This part simulates the neuronal receptive field to extract image features. It is built by applying the method of sparse coding. When the visual information is transmitted through visual system, the receptive field can be considered as a spatiotemporal filter. As a result, the neuronal response in V1 can be obtained by convoluting the receptive field and the visual image, that is

$$A = RF * X \tag{1}$$

where A represents the response of neurons with sparse features, RF denotes the neuronal receptive filed, and X represents the visual image. First the visual image is decentralized and whitened before obtaining the receptive field [29], and then an objective function is defined to measure the sparseness of the response A. Generally, negentropy is used as a criterion to measure the sparseness [19]. It is defined as follows:

$$J(y) \approx \{E[G(y_{\text{gauss}})] - E[G(y)]\}^2 \tag{2}$$

where y_{gauss} has the same variance as y and both satisfy the Gaussian distribution. G is a non-quadratic function. In this paper,

$$G(u) = \frac{1}{a}\log\cosh(au) \tag{3}$$

The construction of the receptive field can be treated as an optimization process. In other words, the objective is to find a transition matrix RF to make negative entropy J(A) the largest, where $A = RF * X$. The gradient method is applied to compute RF, as in

$$RF_{n+1} = RF_n + \eta\frac{\partial J(RF_n X)}{\partial RF_n} \tag{4}$$

where X represents the training samples after pretreatment. RF_n and RF_{n+1} are transition matrixes attained at n and $n + 1$, respectively. η is the learning rate. Then the transition matrix is normalized as follows:

$$RF_{n+1} = \frac{RF_n}{\|RF_{n+1}\|} \tag{5}$$

When RFn+1 converges, training is terminated and the receptive field is obtained.

The receptive field of the simple cell can be described by three parameters [30]: location L, orientation O and frequency F. The model distance is defined as follows:

$$D(A_i, A_j) = W_1 * N\left(\sqrt{(L_{ix} - L_{jx})^2 + (L_{iy} - L_{jy})^2}\right) + W_2 * N(|O_i - O_j|) + W_3 * N(|F_i - F_j|) \tag{6}$$

where W_i is the weight. $N(\cdot)$ is the normalizable function. In order to select a proper receptive field, the distance is calculated by using the features of the receptive field of V1 neurons which are obtained experimentally and the features attained by training .The receptive field with the shortest distance is chosen.

2.1.2. Part 2 synchronous integration among adjacent neurons

The neighboring neurons integrate visual information in a synchronous way. The process can be simulated with two components: the modulation section of nonlinear coupling and the reception section. The latter part is composed of a linear input channel and a feedback channel which receive the input information from adjacent neurons and the response from direct external stimuli [23], respectively. The modulation of nonlinear coupling is established by multiplying the weighted inputs from adjacent neurons with the external inputs. Synchronous integration of adjacent neurons is described in the following way:

Weighted sum of inputs from adjacent neurons :

$$L_{ij} = \sum_{i=0}^{M-1}\left(\sum_{j=0}^{M-1} \omega V_{ij}\right) \tag{7}$$

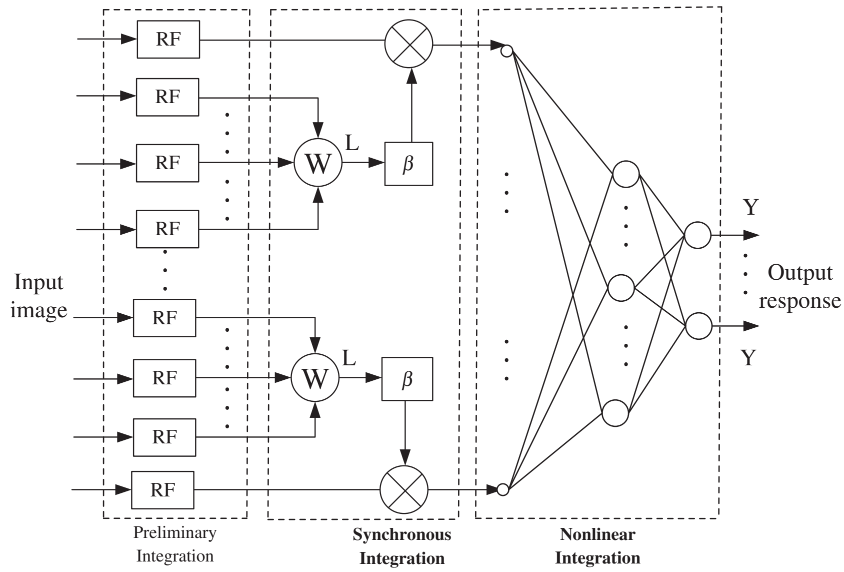

Fig. 1. Visual information integration model.

$$\text{External input}: F_{i,j} = A_{i,j} \tag{8}$$

$$\text{Modulation of nonlinear coupling}: U_{ij} = F_{i,j}[n]\big(1 + \beta L_{ij}[n]\big) \tag{9}$$

In Eq. (7), V_{ij} is a sliding sub-window ($M * M$) of response A. ω is the weight matrix of the response coefficient. In Eq. (8), A_{ij} is the external visual input, corresponding to the center response coefficient in V_{ij}. In Eq. (9), β is the coupling intensity factor.

2.1.3. Part 3 the nonlinear global integration among neurons

The neurons in V1 integrate visual information through connections between different kinds of synapses. The global integration among neurons was established using Backpropagation neural network (BPNN), which is generally composed of three layers, namely the input layer, output layer and hidden layer. The output of the modulation of nonlinear coupling is treated as the input to the BPNN and the firing rate of different channels is chosen as the output of the network. The neural inspiring function is 'sigmoid' and the BPNN is trained by error-reverse-transmitting algorithm.

2.2. Neurophysiological experiments

The experiments were designed both to determine the parameters of the established model and to prove the model's validity. The sinusoidal drifting grating with different orientations (in step of 30°, spatial frequency, 0.2 cycles/°) was chosen as visual stimulus. The data were obtained through microelectrode array (MEA) implanted in Long Evans rat's V1 and recorded through cerebus 128-channel acquisition system (provided by Blackrock Company).

Offline analysis was performed using Matlab's programmes. The single unit activity was obtained using band-pass filtering between 0.25 and 7.5 kHz, threshold detecting and spike sorting in preprocessing. Then the spiking activity was further analyzed as follows:

2.2.1. Examining the orientation selectivity of each unit

The average firing rate under each orientation was computed and the orientation tuning curve of each neuron was drawn. To determine the preference intensity, an index was defined as $ORI = (R_{pref} - R_{org})/(R_{pref} + R_{org})$, in which R_{pref} was the average firing rate to the optimal orientation and $org = pref + \pi/2$. Only those with $ORI > 0.7$ were considered to be orientation-selective and the optimal orientation was recorded simultaneously.

2.2.2. Measuring the synchronization between each pair of neurons

Cross-covariance is used to describe the relationship between two neurons. A large value of cross-covariance means there is a close connection between the spike trains of the two neurons, which also implies there is a certain relationship between the two neurons. Otherwise, they are independent and there is no interaction between them.

The cross-covariance between every two neurons is calculated as follows:

$$\mathrm{cov}_{XY}(mT) = \begin{cases} \displaystyle\sum_{n=0}^{N-|m|-1} \begin{array}{l} \left(X(nT) - \frac{1}{N}\sum_{i=0}^{N-1} X_i(T)\right) \\ \times\left(Y[(n+m)T] - \frac{1}{N}\sum_{i=0}^{N-1} Y_i(T)\right) \end{array} & m \geqslant 0 \\ \mathrm{cov}_{YX}(-mT) \quad m < 0 \end{cases} \tag{10}$$

where T is the time period, which can be calculated by Pre-stimulus Time Histogram (PSTH). $X(nT)$ is the firing rate of neuron X at time nT. $Y(n+m)T$ is the firing rate of neuron Y at time $(n+m)T$. The degree of connection between X and Y is described by $\mathrm{cov}_{XY}(mT)$ after mT delay.The covariance coefficient between any two neurons with $m = 0$ was calculated to determine the connection extent of the neurons in the paper. After all model neurons are selected and cross-covariance matrix between each two of them was calculated separately, the parameter ω in the second part of the model was constructed in following way,

$$\omega = \begin{bmatrix} P_{r_1r_1} & \cdots & P_{r_1r_n} \\ \vdots & \ddots & \vdots \\ P_{r_nr_1} & \cdots & P_{r_nr_n} \end{bmatrix} \tag{11}$$

where $P_{r_1r_n}$ is the cross-covariance of neuron r_1 and neuron r_n.

3. Results

3.1. The obtained parameters

(1) Orientation tuning curve

We recorded a total of 120 neurons from 10 rats. For each neuron the orientation tuning curve was drawn and the preference intensity was calculated according to the method referred to in Section 2.2.

(2) The constructed receptive field

Thirteen natural images (512 × 256 pixels) were selected from http://www.cis.hut.fi/projects/ica/data/images to construct the receptive field. From each image we randomly sampled 5000 image blocks (16 × 16 pixels) to construct the receptive fields (shown in Fig. 2), each image block represents a basic function (BF) shown in Fig. 2 by applying the method referred to in 2.1(1). The results indicate that the features of the BFs are consistent with that of the neuronal receptive field. In this article, the grating was chosen as the stimulus in the experiments. Only the orientation of the images was changed while all other parameters were set at optimal values. As a result, the orientation is considered as the primary feature when selecting the receptive field for Part 1. The method of receptive field selection is described as follows. First, each gray image was transformed into binary image by using Otsu's method. Then for each image the shape of the excited area was fit by using the ellipse with the same second order statistic quantity as the excited area. Finally the angle of the long and short axes of the fitting ellipse is computed as the orientation of the BF. The BFs and the selected receptive field are shown in Fig. 2.

Each image block in Fig. 2 represents the receptive field of a single neuron. The marked ones are the receptive fields selected from the experiment. These receptive fields supplied the parameters in Part 1 of the model, which extracted the features of the image.

3.2. The predicted result

The model built in this paper was tested through the comparison of the orientation tuning curves obtained from the neurophysiological experiments with the firing rate predicted by the model under the same stimulation of grating ($16 * 16$) having different orientations. The result for one of the recorded neurons is shown in Fig. 3.

The blue dashed line in Fig. 3 is the result predicted by the model and the red solid line is the result obtained from the experiments. It can be concluded that the response predicted by the model is consistent with the recorded data under different grating stimulations. Furthermore, we separately compared the response of all recorded neurons with the predicted ones. Those results are shown in Table 1.

Nine experiments were performed by using the method given above. The matching frequency is shown in Fig. 4.

It can be seen from Fig. 4 that the responses predicted by the model are largely consistent with those recorded in experiments for most neurons. In other words, the model reflected the mechanism of information integration of the rat's primary visual cortex to some extent. From the above comparison, it is concluded that the visual system processes information in a nonlinear way, and

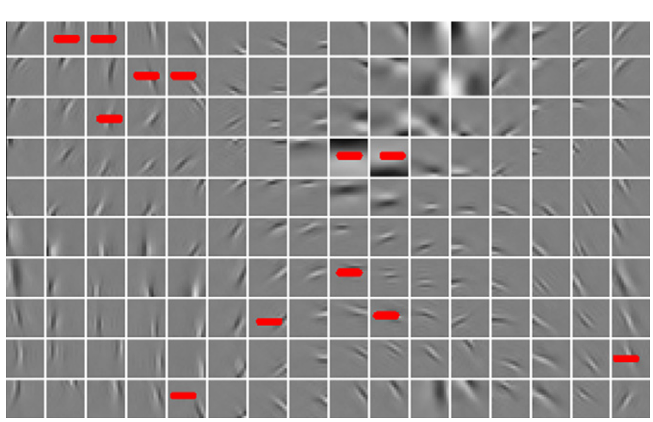

Fig. 2. Receptive field in the integration model.

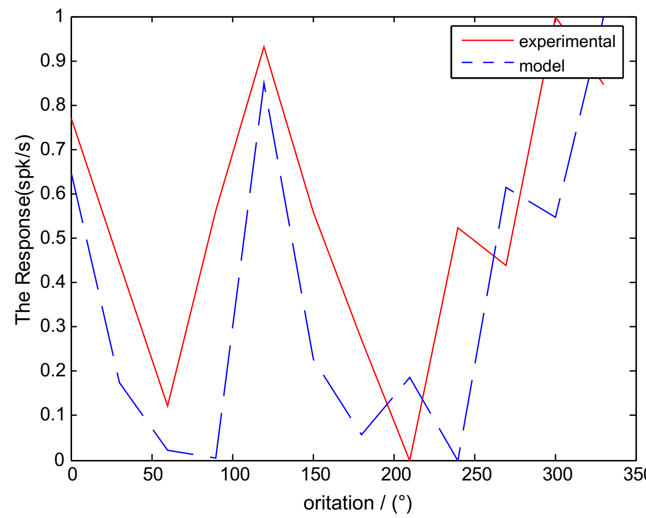

Fig. 3. A neuron's response to different grating stimulations.

the recorded neuronal response is a result of the interaction between many adjacent neurons. However, there are still some inconsistencies, which may be resulted from the noise during the experiment or due to the influence of flash frequency.

4. Discussion

Based on the neuronal receptive field property in V1, synchrony among neurons and the nonlinear integration characteristics, we constructed an integration model of V1 to describe the information integration mechanism in a global way. This model reflected not only the preliminary integration made on visual information and the synchronization between adjacent neurons but also the global integration in a highly nonlinear manner.

Li et al. pointed out that V1 not only integrated the visual information within the receptive field but also would respond to the

Table 1
Orientation selectivity of different neurons.

Channel number	Item	Experimental result	Model result
1	Optimal ori	180	180
	ORI	0.82	0.90
2	Optimal ori	300	330
	ORI	0.72	0.77
3	Optimal ori	150	60
	ORI	0.56	0.20
4	Optimal ori	90	300
	ORI	0.45	0.15
5	Optimal ori	0	0
	ORI	0.96	0.84
6	Optimal ori	300	300
	ORI	0.88	0.85
7	Optimal ori	180	180
	ORI	0.63	0.95
8	Optimal ori	270	180
	ORI	0.10	0.17
9	Optimal ori	30	30
	ORI	0.80	0.78
10	Optimal ori	180	150
	ORI	0.27	0.23
11	Optimal ori	300	300
	ORI	0.73	1.00
12	Optimal ori	60	60
	ORI	0.71	0.77

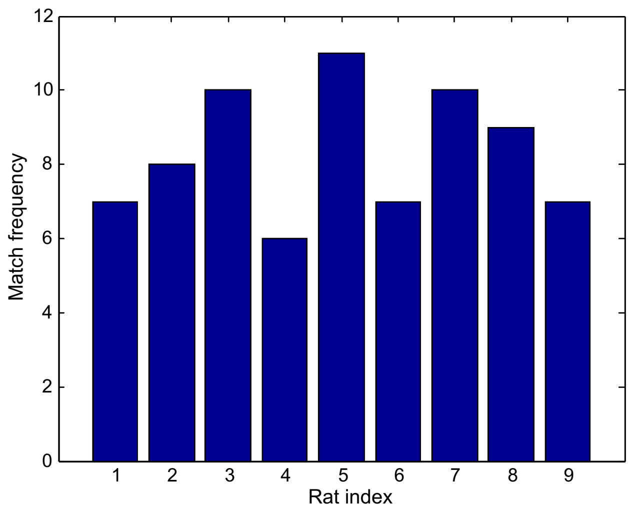

Fig. 4. Statistical results of nine experiments.

information beyond the receptive field [31]. The model constructed in this paper is reasonable considering that the visual system extracts the visual information through different types of receptive fields and the neuronal response is the results of interaction of a large number of neurons in V1, where they integrate visual information in nonlinear way. The experimental results show that the integration model can truly reflect the response characteristics of neurons in V1 under grating stimulations.

The model was obtained by combining mechanism deduction with neurophysiological experiments. In the section of mechanism deduction the model was described mathematically and was of hierarchy based on neurobiological fact. The neurophysiological experiments involved obtaining data through vivo-recording both to provide parameters for the model and to verify its result useful. The two parts provide mutual supports for each other.

The model results, however, do not completely agree with those obtained from the experiments. The following factors can contribute to the discrepancy: (1) The parameters of the integration model are determined by the responses of the oriented neurons. However, 20% of all recorded neurons are insensitive to orientation [32], which may affect the results. (2) The number of recorded neurons is finite and the integration between the neurons is simulated using these finite number of neurons. It is in fact impossible to estimate how each neuron interacts with adjacent neurons [33,34], this can also cause deviation.

The integration model is constructed with the data under grating stimulation and the information integration process is described based on the response of finite neurons and the basic mechanism, which provides a good basis for modeling stimulated complex images. With respect to the stimulation of complex images, many more neurons would involve in the integration process which would be more complicated and the structure would be more complex. In addition, the data was recorded with microelectrode array of finite number of electrodes. Therefore, it could not reflect the whole response situation of V1. Some imaging equipment, such as the Functional Magnetic Resonance Imaging and Optical Imaging [35], would alleviate the limitations of the microelectrode array. This will be one of the goals in our future research.

References

[1] Bruno A. Olshausen, David J. Field, How close are we understanding V1?, Neural Computation 17 (2005) 1665–1699.
[2] Dwight J. Kravitz, Kadharbatcha S. Saleem, Chris I. Baker, et al., A new neural framework for visuospatial processing, Nature Reviews 4 (2011) 217–230.
[3] David H. Hubel, T.N. Wiesel, Receptive fields, binocular interaction, and functional architecture in cat's visual cortex, Physiology 160 (1962) 106–154.
[4] David H. Hubel, T.N. Wiesel, Receptive fields and functional architecture of monkey striate cortex, Physiology 195 (1968) 215–243.
[5] Jianzhong Jin, Yushi Wang, Harvey A. Swadlow, et al., Population receptive fields of ON and OFF thalamic inputs to an orientation column in visual cortex, Nature Neuroscience 14 (2) (2011) 232–238.
[6] Xiaodong Chen, Excitatory and suppressive receptive field subunits in awake monkey primary visual cortex (V1), PNAS 104 (48) (2007) 19120–19125.
[7] William E. Vinje, Jack L. Gallant, Sparse coding and decorrelation in primary visual cortex during natural vision, Science 287 (2000) 1273–1276.
[8] David J. Tolhurst, Darragh Smyth, Ian D. Thompson, The sparseness of neuronal responses in ferret primary visual cortex, The Journal of Neuroscience 29 (8) (2009) 2355–2370.
[9] H.S. Yao, C.Y. Li, Clustered organization of neurons with similar extra-receptive field properties in the primary visual cortex, Neuron 35 (2002) 547–553.
[10] Judith A. Hirsch, José-Manuel Alonso, R. Clay Reid, et al., Martinez synaptic integration in striate cortical simple cells, The Journal of Neuroscience 18 (22) (1998) 9517–9528.
[11] Matthew A. Smith, Adam Kohn, Spatial and temporal scales of neuronal correlation in primary visual cortex, The Journal of Neuroscience 28 (48) (2008) 12591–12603.
[12] Hsi-Ping Wang, Donald Spencer, Jean-Marc Fellous, et al., Synchrony of thalamocortical inputs maximizes cortical reliability, Science 328 (2010) 106–109.
[13] Denise Berger, David Warren, et al., Spatially organized spike correlation in cat visual cortex, Neurocomputing 70 (2007) 2112–2116.
[14] C.M. Gray, W. Singer, Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex, Proceedings of the National Academy of Sciences of the United States of America (86) (1989) 1698–1702.
[15] Tatyana O. Sharpee, Adaptive filtering enhances information transmission in visual cortex, Nature 439 (2007) 936–942.
[16] Tatyana O. Sharpee, Kenneth D. Miller, Michael P. Stryker, On the importance of static nonlinearity in estimating spatiotemporal neural filters with natural stimuli, Neurophysiology 99 (2008) 2496–2509.
[17] Jonathan D. Victor, Ferenc Mechler, Michael A. Repucci, et al., Responses of V1 neurons to two-dimensional hermite functions, Journal of Neurophysiology 95 (2006) 379–400.
[18] Bruno A. Olshausen, David J. Field, Emergence of simple-cell receptive field properties by learning a sparse code for natural images, Nature 381 (1996) 607–609.
[19] J.H. vanHateren, Aapo Hyvärinen, Independent component filters of natural images compared with simple cells in primary visual cortex, Proc of Royal Society London, Series B 265 (1998) 359–366.
[20] Aapo Hyvärinen, Patrik O. Hoyer, Emergence of phase and shift invariant features by decomposition of natural images into independent feature subspaces, Neural Computation 12 (7) (2000) 1705–1720.
[21] Aapo Hyvärinen, Patrik O. Hoyer, M. Inki, Topographic independent component analysis, Neural Computation 13 (7) (2001) 1527–1558.
[22] Wenlu Yang, Liqing Zhang, Libo Ma, The computation model for perceiving content and direction, Science in China 38 (4) (2008) 386–397.
[23] R. Eckhorn, H.J. Reitboeck, M. Arndt, et al., Feature linking via synchronization among distributed assemblies: simulation of results from cat cortex, Neural Computation 2 (3) (1990) 293–307.
[24] Brian Lau, Garrett B. Stanley, Yang Dan, Computational subunits of visual cortical neurons revealed by artificial neural networks, PNAS 99 (13) (2002) 8974–8979.
[25] Liam Paninski, Maximum likelihood estimation of a stochastic integrate-and-fire neural encoding mode, Neural Computation 16 (2004) 2533–2561.
[26] Daniel A. Butts, Chong Weng, Jianzhong Jin, et al., Temporal precision in the neural code and the timescales of natural vision, Nature 449 (2007) 92–95.
[27] Rodrigo Quian Quiroga, Stefano Panzeri, Extracting information from neuronal populations: information theory and decoding approaches, Nature Reviews 10 (2009) 173–185.
[28] Andrea Benucci, Dario L Ringach, Matteo Carandini, Coding of stimulus sequences by population responses in visual cortex, Nature Neuroscience 12 (10) (2009) 1317–1324.
[29] Daniel J. Graham, Damon M. Chandler, David J. Field, Can the theory of "whitening" explain the center-surround properties of retinal, Vision Research 46 (2006) 2901–2913.
[30] Matteo Carandini, Jonathan B. Demb, Valerio Mante, et al., Do we know what the early visual system does?, The Journal of Neuroscience 25 (46) (2005) 10577–10597.
[31] G. Chen, Y. Dan, C.Y. Li, Stimulation of non-classical receptive field enhances orientation selectivity, Journal of Physiology 564 (1) (2005) 233–243.
[32] Spencer L. Smith, Michael Häusser, Parallel processing of visual space by neighboring neurons in mouse visual cortex, Nature Neuroscience 13 (9) (2010) 1144–1149.
[33] Alfonso Renart, Jaime de la Rocha, Peter Bartho, et al., The asynchronous state in cortical circuits, Science 1 (327) (2010) 587–590.
[34] Y. Wen, Q. Zhang, Ensemble cortical responses to rival visual stimuli: effect of monocular transient, Biochem. Biophys. Res. Commun. 380 (1) (2009) 105–110.
[35] Sean P. MacEvoy, Thomas R. Tucker, David Fitzpatrick, A precise form of divisive suppression supports population coding in the primary visual cortex, Nature Neuroscience 12 (6) (2009) 637–645.