Available online at www.sciencedirect.com

SCIENCE DIRECT

Brain Research 1017 (2004) 13–20

BRAIN RESEARCH

www.elsevier.com/locate/brainres

Research report

Firing rates and dynamic correlated activities of ganglion cells both contribute to retinal information processing

Ai-Hua Chen[a], Yi Zhou[b], Hai-Qing Gong[b], Pei-Ji Liang[b,*]

[a] *Shanghai Institute of Physiology, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Graduate School of the Chinese Academy of Sciences, Shanghai 200031, PR China*

[b] *Department of Biomedical Engineering, Shanghai Jiao Tong University, 1954 Hua-Shan Road, Shanghai 200030, PR China*

Accepted 20 April 2004

Abstract

In the present study, the electrical activities of paired retinal ganglion cells, under full field light stimuli with a variety of chromatic configurations, were recorded from a small functioning piece of retina using multi-electrode array (MEA). Neurons that had increased firings at light-ON and -OFF transients and did not show color-opponent properties were investigated. Single neuronal analysis showed that firing rate of each individual neuron was dependent on the intensity of illumination. Multi-unit analyses revealed that adjacent neurons often fired in synchrony in response to light stimulation. However, in some cases, the strength of correlation between the paired neurons was higher when the retina was exposed to red or green light, and the correlation was attenuated when yellow or white light was given. This seems to suggest that the ensemble activity of non-color-opponent ganglion cells might partly participate in color-information processing, with the red- and green-pathway inputs influencing each other. Such arrangement reflects principle of parsimony: the firing rates of single neuron represent the luminance intensity, and the correlated activities may tell the brain about the color information.

Theme: Sensory system
Topic: Retina and photoreceptors

Keywords: Retina; Ganglion cell; Multi-unit recording; Color-information processing; Correlated activity

1. Introduction

The retina is an important part of the central nervous system where the first stage of visual information processing occurs. In the retina, visual images are first converted into electrical signals by rod- and cone-photoreceptors. These signals are then propagated to bipolar cells, with the latter contacting the retinal output neurons—ganglion cells. The representation of visual stimuli, in patterned activities of the retinal ganglion cells, is then relayed to the central visual system through optic nerves [4,5,12].

One fundamental function of the retina is color-information processing. The ganglion cells respond to colored stimuli in one of two ways: color-opponent responses and luminance responses. In conventional concept, color coding in the ganglion cell layer is characterized by the responses of color-opponent ganglion cells, with these neurons being excited by certain wavelength stimuli and inhibited by other wavelength stimuli [3,12]. For decades, it has been well accepted that there exist two color-opponent processes, loosely termed "red–green" and "blue–yellow". It is believed that the formation of blue–yellow opponency in the ganglion cells is based on combined inputs from OFF-type bipolar cells connecting red- and green-cones and ON-type bipolar cells receiving blue-cone signals [3,5]. The mechanism underlying red–green opponency is not yet clear, and it is assumed that this process involves the activity of a certain type of bipolar cells which respond to red- and green-cone inputs with opposite polarities [10].

On the other hand, one of the characteristic features of the vertebrate retina is that photoreceptors outnumber ganglion cells by a factor of tens or even hundreds, which means that

* Corresponding author. Tel.: +86-21-64070495; fax: +86-21-64070495.
E-mail address: pjliang@sjtu.edu.cn (P.-J. Liang).

0006-8993/$ - see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2004.04.081

information generated from the photoreceptors needs to be greatly compressed into the activity of the ganglion cells, with the latter projecting more divergently to the neurons in the central visual part. This means that the ganglion cells can hardly act as independent channels for visual information processing. Instead, evidence from multi-neuron recordings reveals that retinal ganglion cells fire with significant patterns of concerted activity that cannot be derived from any single-neuron description [14,15,17]. In other words, the population coding in the ganglion cell layer makes the retinal process more efficient for information transmission [22].

Actually, considerably more information can be extracted when temporal correlations between adjacent cells are considered, as compared to single neuronal analysis. Correlated firings of the ganglion cells play a crucial role in forming appropriate, informative retinal output [13,16]. However, although multi-unit neuronal activity patterns has been widely studied, most reports are focused on confirming the notion that the correlation pattern of multi-neuronal firing carries information about visual stimuli, and little has been reported about the contribution that ensemble ganglion cells' activity might made in particular information coding.

The purpose of this work is to compare the firing activities and correlation patterns between nearby retinal ganglion cells in response to various chromatic illuminations. It was found that the correlation pattern between some non-color-opponent ganglion cells might carry chromatic information. For some ON–OFF ganglion cells, the adjacent neurons fired in synchrony in response to red or green light, but the synchronization was broken when yellow or white light was applied. This suggests that these non-color-opponent ganglion cells might participate in color-information coding with the red- and green-pathway inputs influencing each other. This represents an economy arrangement: the firing rates of single neuron represent the luminance intensity, and the correlated firings may tell the brain about the color information.

2. Methods

2.1. Experimental procedure

Extracellular recordings were made in isolated chicken retina using multi-electrode array (MEA, Multi Channel Systems MCS, Germany) which consisted of a 5×5 cm transparent quartz glass plate with 60 substrate integrated and insulated golden connection lanes running from connector pads at the edge of the plate to the electrode matrix at the center. The tips of these conductors serve as the electrodes (10 μm in diameter) and are arranged in an 8×8 matrix with 100 μm tip-to-tip distances [6,20]. The patterned area of microelectrodes is enclosed in a glass ring forming a tissue perfusion chamber.

Eyes were obtained from newly hatched chicken (about 2–4 days). After decapitation and enucleation of the eye, the eyeball was hemisected with fine scissors or a razor blade. The cornea and lens were separated from the posterior half. The vitreous that adhered to the retinal surface was removed with tweezers. The isolated retina was dissected into 4×4 mm squares. For electrical recording, a small piece of retinal segment was attached with the ganglion cell side to the surface of the multi-electrode array. For improving the adhesion, the MEA was initially covered with 3 μl dissolved cellulose nitrate solution (1.0 cm^2 of Sartorius cellulose nitrate filter in 10.0 ml methanol) and dried in air. The preparation was kept in standard perfusate containing (in mM): 100.0 NaCl, 5.0 KCl, 3.0 $MgSO_4$, 1.8 $CaCl_2$, 25.0 $NaHCO_3$, 25.0 glucose, and bubbled with a mixed gas of 95% O_2 and 5% CO_2 with a pH value of 7.5 ± 0.2. The perfusion was delivered at a rate of 0.8 ml/min and the tissue was kept at 37 °C with a temperature control unit (Thermostat HC-X, Multi Channel Systems MCS). An Ag/AgCl pellet, which was dipped into the bath solution, acted as the reference electrode.

Light stimulus was generated using a computer monitor, and was focused to form a 0.7×0.7 mm image on the isolated retina via a lens system. The stimuli in this experiment consisted of 500 ms full field, uniformly illuminated flashes followed by 1000 ms "light-off" interstimulus intervals. Visual stimuli with various chromatic components (white, red, green, yellow) were obtained by adjusting the output indices of the red, green and blue display guns as given in Table 1. The light intensity of the monitor's output during each chromatic stimulus was measured using a light detection system (IL1400, USA). Each set of stimuli was presented for 40 repeats, with the background being complete darkness.

Multi-unit photo-responses were simultaneously recorded from all 60 electrodes of the MEA, and were amplified with a 60-channel amplifier (single-ended amplifier, bandwidth 10 Hz–3.4 kHz, amplification $1200\times$, amplifier input impedance $>10^{10}$ Ω, output impedance 330 Ω) [6]. The selected channels of recording along with one stimulus signal were digitized with a commercial multiplexed data acquisition system (MCRack) and stored in a Pentium-based computer. The data were sampled at a rate of 20 kHz, plotted on screen instantaneously, and then stored on hard disc for off-line analyses.

2.2. Spike sorting

In extracellular recordings using flat-mounted electrodes such as MEA, the electric signals picked up by a single

Table 1
Composition and intensity of the chromatic stimulations

Stimulation	White	Red	Green	Yellow
Red gun index	255	255	0	255
Green gun index	255	0	255	255
Blue gun index	255	0	0	0
Intensity (μW/cm^2)	0.139	0.048	0.069	0.117

electrode may reflex some combined activities generated by several adjacent neurons. To investigate the coding properties of retinal ganglion cells, the electrode signals should be sorted into the firings of relevant neurons. A basic assumption underlying the spike sorting procedure is that the spike shape of single neuron differs from each other.

In the present study, spikes were sorted using principal component analysis (PCA), the idea behind which is to find an ordered set of orthogonal basis vectors that reflect the directions in the data of largest variation [11]. On comparing the parameters of the first two principal components, the spike data can be classified into a few clusters with each corresponding to a certain neuron's activity. The cluster boundaries was set by calculating the Euclidean distance [9,11,26]:

$$J = \sum_{i=1}^{c} J_i = \sum_{i=1}^{c} \left(\sum_{k, x_k \in G_i} \| x_k - c_i \|^2 \right) \quad (1)$$

The detected action potentials were then taken as identical, only the precise times of firing occurrence were constructed, and discrete series of time events characterizing the spike train of each relevant neurons were obtained.

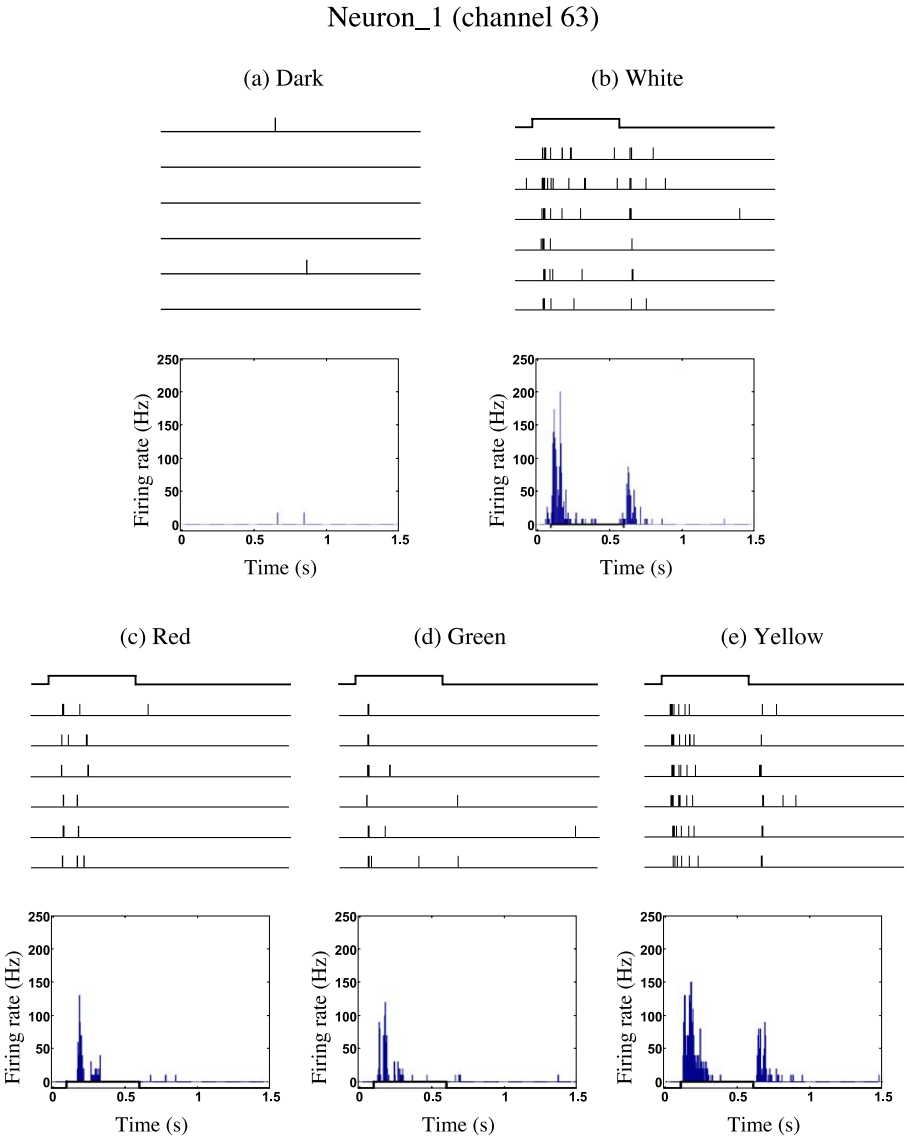

Fig. 1. The firing patterns of a neuron (neuron #1) during various stimulation conditions. The cell fired spontaneously and sparsely during dark (a), and responded to light stimuli with increased firings at ON- and OFF-transients. The firing rate was higher when the retina was exposed to intense light stimuli. In panels b–e, the top traces in each panel represent the raster plot of the cell's firing sequences during each condition to 6 consecutive test trials (500 ms light-on period followed by 1000 ms light-off interval). The bottoms of each panel are the PSTH calculated for each condition (bin 5ms, 40 repeats).

2.3. Cross-correlations analysis

The patterns of interaction between pairs of neurons in chicken retinal ganglion cells were studied by examining their cross-correlation function, which reflected the mean firing rate of one cell as a result of the activity of another. Generally, the cross-correlation function is defined as:

$$c_{xy}(m) = \begin{cases} \sum_{n=0}^{N-|m|-1} x_n y_{n+m} & m \geq 0; \\ c_{yx}(-m) & m < 0 \end{cases} \quad (2)$$

where x_n denotes the value of sequence x at moment n; y_{n+m} is the value of sequence y at moment $n+m$; $c_{xy}(m)$, by definition, represents the correlation between sequences x and y with a lag of m, which reflects the effect of signal x exerts on signal y with a time delay m.

2.4. Shift-predictor

When light stimulus is projected onto the retina, it often causes increased spike firings from some neurons. Such increased activities may result in increased synchronized firings between the neurons under investigation. So, when we look into the activity patterns between paired neurons, the correlation between the two spike sequences may include two components, with one corresponding to real correlated activities due to the functional wiring, and another due to the increased-firing-related synchronization. The latter part can be corrected via a shift predictor, which is computed similarly as for the cross-correlation function, except that the spike trains correlated corresponding to two successive trials [21].

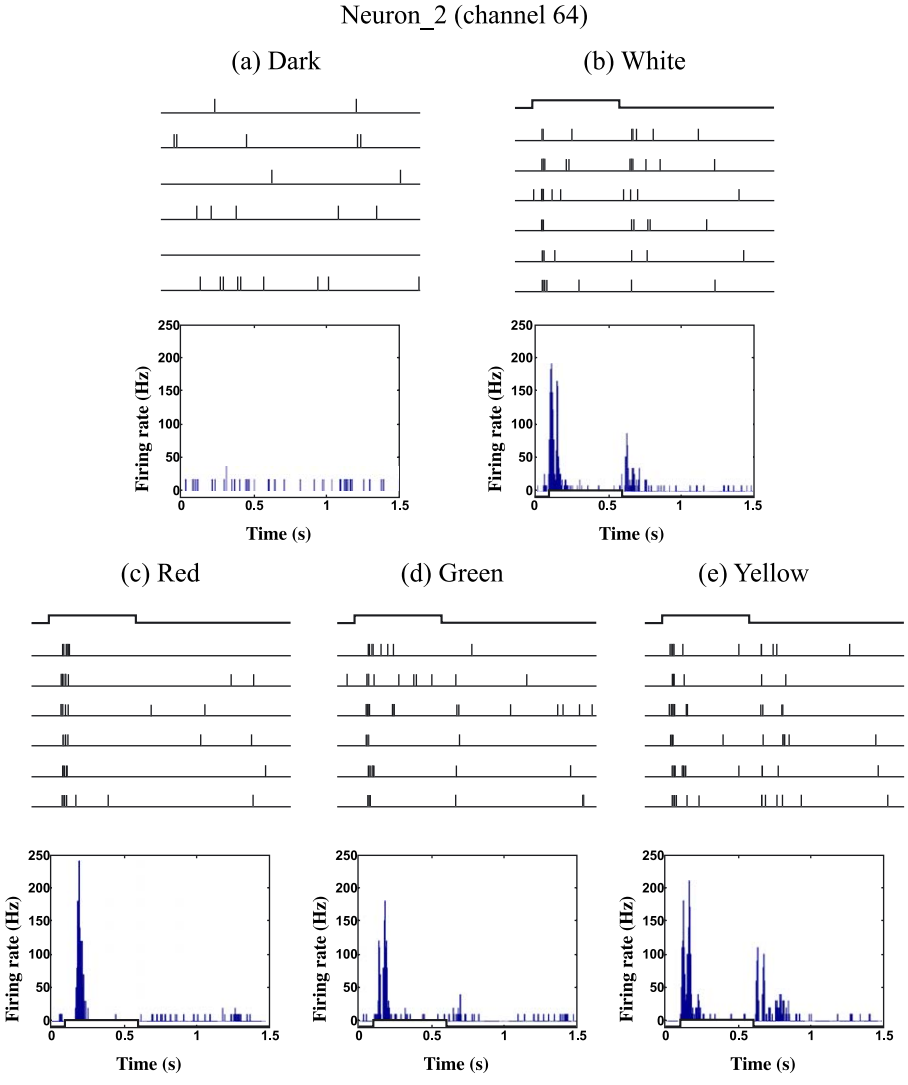

Fig. 2. The activity changes of another neuron (#2,) in response to various stimuli. Details are as Fig. 1.

3. Results

In this study, ganglion cells responded to white light flash at both light-ON and -OFF transients were investigated. Experiments were performed on 12 retinas. Among a total number of 555 ON–OFF ganglion cells recorded, correlated firings were detected from 60 pairs of adjacent neurons.

Fig. 1 is an example of activity changes of an ON–OFF ganglion cell (neuron #1) in response to various light stimulations. It is shown that the neuron had spontaneous and sparse firings in the dark, and revealed typical ON–OFF transient responses to white (0.139 μW/cm^2) or yellow (0.117 μW/cm^2) flashes. It fired more frequently in response to light-ON transient than to light-OFF transient. This neuron fired with a reduced rate when red (0.048 μW/cm^2) or green (0.069 μW/cm^2) illumination was given, and response could only be observed during light-ON transient in these cases. Such response difference might be related to the intensity of the stimulation, since in our experiment, the intensity of red and green flashes was weaker as compared to that of white and yellow stimulation.

The activity of this neuron did not show red–green color-opponent property since the neuron was activated when either red or green light was performed. Besides, the firing rate was modulated by the intensity of light flash, as shown by the peri-stimulus time histogram (PSTH). Both peak level and duration time of PSTH were increased in exposure to intense illumination.

Fig. 2 presents the recordings obtained from another ON–OFF ganglion cell (neuron #2) adjacent to the one given in Fig. 1. Similar to the results illustrated in Fig. 1, this neuron fired spontaneously and sparsely when no light was given. It responded to white or yellow illumination with increased spikes at the light-ON and -OFF transients. The cell's firing rate was very much decreased in exposure to red or green flashes, and its OFF-response was even diminished when red light was applied.

On comparing the firing patterns in response to red and green light flashes, it is clear that the neurons given in Figs. 1 and 2 are not color-coding neurons, since the activity of these neurons failed to show any color-opponent property.

On the other hand, since the two neurons were next to each other, it is highly probable that these neurons responded to light stimulation with particular correlation patterns. Fig. 3 gives the results of cross-correlation analyses calculated based on the data obtained during various light stimulations as presented in Figs. 1 and 2. The results were such that when no light was applied, neurons #1 and #2 both showed some spontaneous firings as illustrated in Figs. 1 and 2, but each neuron fired independently, the cross-correlation function between the two firing sequences was flat and close to zero (Fig. 3a); light flashes effectively elicited some synchronized firings in the two cells, as shown in Fig. 3, panels b–e.

One thing worth mentioning is that in both neurons, the cells' firing rate increased when the intensity of light stimulus was increased, as shown in Figs. 1 and 2. However, the results plotted in Fig. 3 revealed that when red or green light was performed, the neurons' activities were highly correlated, with the correlation coefficient being 0.1687 and 0.1302, respectively, although the intensity for red or green flashes was comparatively weak. On the contrary, when white or yellow flashes were applied, the correlation between the investigated neurons was modest, with the correlation coefficient being 0.0650 and 0.0632, respectively, despite the fact that the neurons fired with higher frequen-

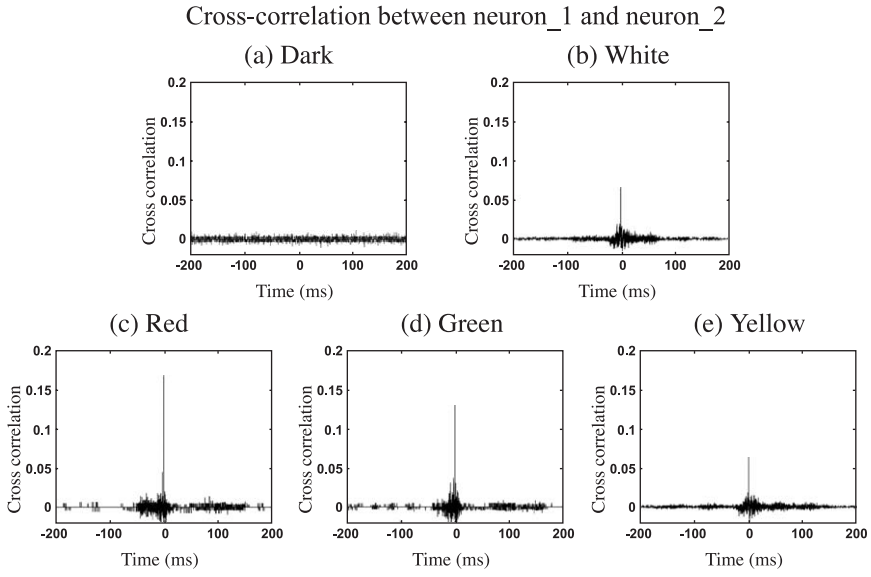

Fig. 3. Correlated firings of neurons #1 and #2 during various stimulation conditions. No correlation was detected when the two neurons fired spontaneously in the dark (a). The strength of correlation was comparatively high when red or green stimulus was presented (b–c), although both neurons fired with lower firing rate during these conditions as compare to that during white or yellow stimulation (d–e).

Table 2
Comparison of correlation indices between red-response vs yellow-response and green-response vs yellow response

	$Coeff_R > Coeff_Y$ $Coeff_G > Coeff_Y$	$Coeff_R > Coeff_Y$ $Coeff_G < Coeff_Y$	$Coeff_R < Coeff_Y$ $Coeff_G > Coeff_Y$	$Coeff_R < Coeff_Y$ $Coeff_G < Coeff_Y$
Data pairs	9	1	8	42

cies under these conditions. It is interesting to notice that when the retina was exposed to red or green light flashes, one of the two signal pathways was activated; in this case, the firings of the two neurons showed significant synchronization, the firing sequences were closely correlated. On the other hand, when yellow flashes were performed, under which circumstance both red- and green-signal pathways were activated, the neurons fired more frequently, but the synchronization between the two neurons was attenuated, as compared to that during red or green stimulation. Such attenuation in synchronization was even more significant when white flashes were applied.

In our experiments, the yellow light was given as a combination of red and green lights, and white light consisted of red, green and blue lights. For simplicity, further comparisons were made between data collected during red, green and yellow stimulations. In 18 neuron pairs out of the total number of 60 pairs of cells that had correlated activities, correlation coefficients were estimated higher from the firing sequences in response to red and/or green lights, as compared to that obtained during exposure to yellow light. This constitutes 30% of the data examined, while in the rest 70% data sets, correlation coefficients were estimated higher for the firing sequences in response to yellow light as compared to red and green lights (Table 2).

One argument might be raised that the correlated behavior is influenced by the firing activity. Comparisons were thus made between neuron activities in response to various chromatic stimulations with different intensities. Table 3 gives an example. It is shown that when white light was given, the firing rate of one of the neurons (#3) was measured 52.4 Hz when light intensity was 0.106 μW/cm^2, and the firing rate was reduced to 39.3 Hz when the light intensity was decreased to 0.053 μW/cm^2. Similar results were observed when red, green or yellow flashes were performed. This was also true for neuron #4. At the mean time, for each chromatic composition, a stronger stimulation also elicited more synchronized firings between the paired neurons, the correlation coefficients between these two neurons were estimated 0.016 and 0.012, when the intensity of white light was 0.106 and 0.053 μW/cm^2, respectively. Such intensity-dependent correlation was consistent for all the chromatic configurations. However, the cross-correlation indices estimated from the neurons responses to red and green lights were consistently higher than that in response to yellow and white lights, although the intensity for red and green light was comparatively weaker (Table 3).

Taken together, these results seem to suggest that the neurons' firing rate is increased when the intensity of light stimulation is increased. However, synchronization is sometimes dependent on the complexity of chromatic composition, and not necessarily related to the neurons' firing rate and the intensity of stimulation.

4. Discussions

Concerted firings of neurons play important roles during information processing in visual system. Some previous studies revealed that synchronized activities could occur between those neurons with similar response properties. In retinal ganglion cell layer, nearby neurons with similar receptive field properties often fired in concerted manner, and the correlation pattern actually carried information about some particular properties of the receptive fields. Cross-correlation function between two firing sequences had a peak near zero lag when both neurons were with same center sign (i.e., both ON-center or both OFF-center); on the other hand, a trough would be observed in case two cells were with opposite receptive field centers (i.e., one ON- and one OFF-center). Furthermore, the strength of correlation between two cells was dependent on the overlapping degree of their receptive field centers [13,14,18]. Similar findings were also made in the central visual parts. For orientation selective neurons, the correlation was determined by the orientation selectivity of the neurons and their cortical distance. Correlation of neurons with similar orientation preferences was higher than those of neurons with different orientation preferences [2].

Some other works further indicated that the correlation pattern between the neurons could be dynamically changed in response to various stimulus patterns, even without any obvious changes in single neuron activities. It was reported

Table 3
Correlation indices of a pair of neurons (#3 and #4) estimated during responses to various stimulus conditions

		White		Red		Green		Yellow	
Intensity (μW/cm^2)		0.106	0.053	0.027	0.014	0.044	0.022	0.068	0.034
Correlation Index		0.016	0.012	0.018	0.015	0.030	0.011	0.018	0.014
Mean firing rate (Hz)	Neuron#3	52.4	39.3	23.9	15.8	27.8	22.4	44.1	37.0
	Neuron#4	59.2	47.7	24.7	19.2	34.1	29.0	49.0	43.2

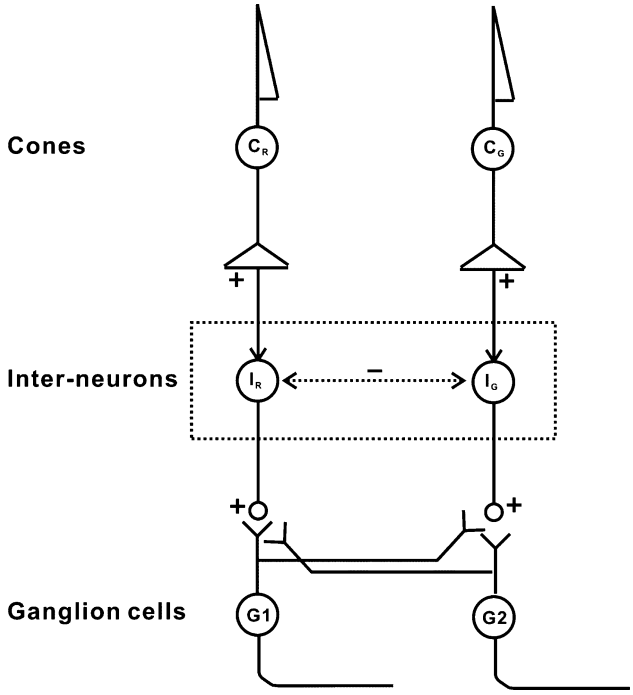

Fig. 4. Diagrammatic scheme of the information processed by non-color-opponent ganglion cells. In the ganglion cell layer, some neurons may be wired to both red-and green-signal pathways. When one pathway is activated, these neurons will receive signal input simultaneously, and synchronized firing occurs. On the other hand, when both pathways are activated at the same time, they may have negative influence on each other, this may result in some attenuation in the synchronization.

that for two retinal ganglion neurons with separated receptive fields, the responses were independent to each other when the area between the receptive fields was not illuminated, but if the stimuli continuously covered the area between the receptive fields, the responses in the neurons became highly correlated [19]. Similarly, in area 17 of cat visual cortex, two neurons with same orientation preference responded to a long continuous moving bar in highly correlated manner, and the synchronization was apparently attenuated when the moving bar was discontinued, although the change in stimulus configuration did not affect the response behavior in single neurons perspective [7,8].

Our results were, to some extent, analogous to these observations. The retinal ganglion cells responded to light stimulation in a stimulation-dependent manner. The firing rate of each individual neuron was highly related to the intensity, but not the chromatic component, of light illumination. According to conventional concepts, these neurons could be classified as non-color-opponent ganglion cells. Meanwhile, the neuron pairs with similar response properties fired in synchrony in response to light stimulation. However, what might be interesting was that the strength of correlation between the paired neuron activities was sometimes dependent on the complexity of the chromatic configuration, which suggested that the concerted activities might also be able to convey color information about the stimulation.

One widely accepted idea is that during retinal processing, color information is processed by color-opponent pathways, with relevant neurons' activity changes in opposite directions in response to opponent color stimulations. The results obtained in the present study revealed that, in part of non-color-opponent neurons which had increased firings in light-ON and -OFF transients, each single neuron had increased activities in response to light stimulation with higher intensity; however, higher firing frequency did not necessarily lead to higher correlation. In some cases, the paired neuron activities could be highly correlated when either red- or green-signal pathway was activated, and the correlation was very much attenuated when both signal pathways were activated simultaneously in exposure to yellow or white stimulation. It was previously suggested that the correlation pattern between retinal ganglion neurons might be resulted from a few factors including the functional wiring of the signal pathways [1] and the functional status of relevant neurons such as bipolar and amacrine cells [23–25]. So it might suggest that these paired neurons were wired to both red- and green-signal pathways, but the two pathways may interact with each other in a negative manner (as shown in Fig. 4).

One thing imperfect in this study was that the light stimulations were given via a computer monitor. Therefore, light projected onto the retina consisted a certain range of wavelengths. This results in some difficulties in calculating the precise intensity in terms of quanta/sec/m^2, given the measured intensity in $\mu W/cm^2$. However, the differences among the intensities for various wavelengths are significant, the intensity for yellow light roughly doubled that of red or green light, as listed in Table 4.

In general, these results might suggest that both firing rates and dynamic correlated firing contribute to retinal information processing. Although the cells investigated in the present study can be grossly classified as non-color-opponent neurons, they also partly participate in color-information processing. This represents an economy of coding: the firing rate indicates some information about

Table 4
Composition and estimated intensity of the chromatic stimulations

Stimulation	White	Red	Green	Yellow
Intensity ($\mu W/cm^2$)	0.139	0.048	0.069	0.117
Wavelength (nm)		600–680	500–530	540–560
Quanta/s cm^2		1.533×10^{11}–1.738×10^{11}	1.837×10^{11}–1.947×10^{11}	3.364×10^{11}–3.489×10^{11}

the intensities of the stimulus, while the correlation between some nearby ganglion cells indicates chromatic information.

Acknowledgements

This work was supported by grants from Shanghai Science and Technology Development Funding (02JC14008), National Foundation of Natural Science of China (60375039) and the National Basic Research Program of China (G1999054000).

References

[1] I.H. Brivanlou, D.K. Warland, M. Meister, Mechanisms of concerted firing among retinal ganglion cells, Neuron 20 (1998) 527–539.
[2] M. Brosch, R. Bauer, R. Eckhorn, Synchronous high-frequency oscillations in cat area 18, Eur. J. Neurol. 7 (1995) 86–95.
[3] D.J. Calkins, P. Sterling, Evidence that circuits for spatial and color vision segregate at the first retinal synapse, Neuron 24 (1999) 313–321.
[4] D.M. Dacey, Circuitry for color coding in the primate retina, Proc. Natl. Acad. Sci. 93 (1996) 582–588.
[5] D.M. Dacey, Primate retina: cell types, circuits and color opponency, Prog. Retin. Eye Res. 18 (1999) 737–763.
[6] U. Egert, B. Schlosshauer, S. Fennrich, W. Nisch, M. Fejtl, T. Knott, T. Müller, H. Hämmerle, A novel organotypic long-term culture of the rat hippocampus on substrate-integrate multi-electrode arrays, Brain Res. Protoc. 2 (1998) 229–242.
[7] A.K. Engel, P. König, C.M. Gray, W. Singer, Stimulus-dependent neuronal oscillations in cat visual cortex: inter-columnar interaction as determined by cross-correlation analysis, Eur. J. Neurosci. 2 (1990) 588–606.
[8] A.K. Engel, P. König, A.K. Kreiter, T.B. Schillen, W. Singer, Temporal coding in the visual cortex: new vistas on integration in the nervous system, TINS 15 (1992) 218–226.
[9] V. Faber, Clustering and the continuous *k*-means algorithm, Los Alamos Sci. 22 (1994) 138–144.
[10] S. Haverkamp, W.D. Eldred, O.P. Ottersen, D. Pow, J. Ammermuller, Synaptic inputs to identified color-coded amacrine and ganglion cells in the turtle retina, J. Comp. Neurol. 389 (1997) 235–248.
[11] M.S. Lewicki, A review of methods for spike sorting: the detection and classification of neural action potentials, Network 9 (1998) R53–R78.
[12] R.H. Masland, The fundamental plan of the retina, Nat. Neurosci. 4 (2001) 877–886.
[13] D.N. Mastronarde, Correlated firing of retinal ganglion cells, TINS 12 (1989) 75–80.
[14] M. Meister, Multineuronal codes in retinal signaling, Proc. Natl. Acad. Sci. U. S. A. 93 (1996) 609–614.
[15] M. Meister, M.J. Berry, The neural code of the retina, Neuron 22 (1999) 435–450.
[16] M. Meister, R.O. Wong, D.A. Baylor, C.J. Shatz, Synchronous bursts of action potentials in ganglion cells of the developing mammalian retina, Science 252 (1991) 939–943.
[17] M. Meister, J. Pine, D.A. Baylor, Multi-neuronal signals from the retina: acquisition and analysis, J. Neurosci. Methods 51 (1994) 95–106.
[18] M. Meister, L. Lagnado, D.A. Baylor, Concerted signaling by retinal ganglion cells, Science 270 (1995) 1207–1210.
[19] S. Neuenschwander, W. Singer, Long-range synchronization of oscillatory light responses in the cat retina and lateral geniculate nucleus, Nature 379 (1996) 728–732.
[20] W. Nisch, J. Böck, U. Egert, A thin film microelectrode array for monitoring extracellular neuronal activity in vitro, Biosens. Bioelectron. 9 (1994) 737–741.
[21] Q. Pauluis, S.N. Baker, E. Olivier, Precise burst synchrony in the superior colliculus of the awake cat during moving stimulus presentation, J. Neurosci. 21 (2001) 615–627.
[22] S. Thorpe, A. Delorme, R. Van Rullen, Spike-based strategies for rapid processing, Neural Netw. 14 (2001) 715–725.
[23] N. Vardi, R.G. Smith, The AII amacrine network: coupling can increase correlated activity, Vis. Res. 36 (1996) 3743–3757.
[24] W.T. Wong, J.R. Sanes, R.O. Wong, Developmentally regulated spontaneous activity in the embryonic chick retina, J. Neurosci. 18 (1998) 8839–8852.
[25] W.T. Wong, K.L. Myhr, E.D. Miller, R.O. Wong, Developmental changes in the neurotransmitter regulation of correlated spontaneous retinal activity, J. Neurosci. 20 (2000) 351–360.
[26] P.M. Zhang, J.Y. Wu, Y. Zhou, P.J. Liang, J.Q. Yuan, Spike sorting based on automatic template reconstruction with a partial solution to the overlapping problem, Neurosci. Methods 135 (2004) 55–65.