Available online at www.sciencedirect.com
SCIENCE DIRECT
Brain Research 1059 (2005) 1 – 6
BRAIN RESEARCH
www.elsevier.com/locate/brainres

Research Report

Color information encoded by the spatiotemporal patterns of light response in ganglion cells of chick retina

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

[a]Department of Biomedical Engineering, Shanghai Jiao Tong University, Shanghai 200030, China
[b]Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, Shanghai 200031, China

Accepted 18 July 2005
Available online 23 September 2005

Abstract

In the present study, the light responses of ganglion cells to chromatic stimulus were recorded from isolated retina of neonatal chick. It was found that for some non-color-opponent ganglion cells, the spatiotemporal patterns of the cells' light responses were related to the chromatic information that they received. When stimulus with some chromatic component was applied, some ganglion cells would generate distinguishable temporal patterns of light responses although these cells can be classified as non-color-opponent according to their light responses. The results suggest that in chick retina, the color information might be encoded not only by the color opponent ganglion cells, but also the spatiotemporal patterns of some ganglion cells that are traditionally classified as non-color-opponent subtype.

Theme: Sensory system
Topic: Retina and photoreceptors

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

1. Introduction

It is well known that retinal ganglion cells, the final output neurons of the vertebrate retina, play an important role in visual information processing [6,15]. Various light stimuli are converted into spikes in the retinal ganglion cells and the encoded information is transmitted to the lateral geniculate nucleus (LGN) via optic nerve fibers [3,13]. Among the many features of ganglion cells, one widely accepted concept is that during retinal processing, color information is processed by color-opponent pathways, with relevant neuronal activities changing in opposite directions in response to opponent color stimulations [7,17]. Nevertheless, according to some recent observations made in this laboratory, non-color-opponent ganglion cells might also partly participate in color information processing, with the red–green pathway inputs influencing each other [4]. It was found that not only the firing rates, but also the correlation pattern of firing would contribute to the retinal information processing. For some ON–OFF ganglion cells, the neurons that spatially close to each other would fire in synchrony in response to red or green light, but the synchronization was broken when yellow or white light was applied [4].

Since any changes in synchronization should be originated from the temporal pattern of the relevant spike trains and the cross-correlation analysis could hardly draw the temporal details of the neuronal activity, we tried to use joint peri-stimulus time histogram (JPSTH) [1,11] for a better understanding of the neuronal interrelationship. JPSTH is a widely used method for investigating the dynamics of the interdependence of spike events between pairs of cells. Its results are often taken as an estimate of interaction strength between cells, independent on cells' firing rates [11]. In our experiments, spatially uniform chromatic light stimulus was given repeatedly. Interestingly, it was

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

0006-8993/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2005.07.077

found that for a considerable portion of pair-wise adjacent non-color-opponent ganglion cells, two distinct peaks of synchronization could be identified in JPSTH when chromatic stimulus was given. Furthermore, it was noticed that for some non-color-opponent ganglion cells, there were diversified temporal patterns of responses under various light stimuli, which might be the origination of the temporal pattern found in JPSTH. The occurrence probability of this "double-peak" light response under different wavelength light stimulus was analyzed. Moreover, by analyzing peri-stimulus time histogram (PSTH) of single neurons and JPSTH between pair-wise adjacent neurons, we discussed the possible relationship between spectral configuration of light stimulus and the temporal pattern of neuronal response.

2. Materials and methods

2.1. Experimental procedure

Four retinas from neonatal chicks (3–8 days post hatching) were investigated in this research. Similar experimental operations can be found in previous reports [4,5]. All procedures strictly conformed to the humane treatment and use of animals as prescribed by the Association for Research in Vision and Ophthalmology. After decapitation and enucleation of the eye, the eyeball was hemisected with a fine razor blade. The vitreous body and cornea were removed carefully. To record the spike trains of retinal ganglion cells, a small piece (4 mm × 4 mm square) of the isolated retina was placed on a flat array containing 60 microelectrodes (MEA60, MCS GmbH, Germany) with the ganglion-cell-side facing the electrodes. A small quantity (3 μl) of nitrate cellulose solution (1.0 mg Sartorius cellulose nitrate dissolved in 10.0 ml methanol) was smeared onto the electrode array as electric glue to make a better contact between the array and the retina. The preparation was perfused in oxygenated (95% O_2 and 5% CO_2) Ringer's solution (containing in mM: 100.0 NaCl, 5.0 KCl, 3.0 $MgCl_2$, 1.8 $CaCl_2$, 25.0 $NaHCO_3$, 25.0 glucose) with a pH value of 7.5 ± 0.2. The tissue and perfusate were kept at 38 °C by a temperature control unit (Thermostat HC-X, MCS GmbH, Germany). A small Ag/AgCl pellet with wire was immerged into the bath solution and acted as the reference electrode.

The neuronal photoresponses were recorded simultaneously by the multi-electrode array, and the signals were amplified through a 60-channel amplifier (single-ended amplifier, amplification 1200×, amplifier input impedance $>10^{10}$ Ω, output impedance 330 Ω). Signals from the selected channels along with the stimulus were sampled at a rate of 20 kHz (MCRack) and stored in a Pentium IV-based computer.

After 10–20 min adaptation to the perfusion environment, the light response of the retina would go stable and its stability would last for 7–8 h in our experiments. In this study, all the data analyzed were recorded from the stable period.

2.2. Stimulus

Spatially uniform light (red, green and yellow) was generated from a video monitor and was projected onto the retina via a lens focus system at a certain photonic mean intensity (IL1400, USA) (Table 1). Full-field sustained light with medium intensity was given for 30 s before the repeated stimulus in order to adjust the sensitivity of the ganglion cells to a similar level. Stimulus consisting of light duration of 1000 ms and dark interval of 9000 ms was given repeatedly for 50 times after the adaptation was completed (as shown in Fig. 1). For each individual retina, four color stimulus protocols were applied in random order, and the interval between successive color protocols was 5 min. To assure the stability of retinal responses, any kind of stimulus pattern were repeated at least twice for each retina, in random order. The experimental data were used for further analysis only if the neuron's firing activity was repeatable in response to identical stimulation.

2.3. Spike detection and spike sorting

Before spike detection, the field potentials were wiped off through a band pass filter (100–3000 Hz). Since the extracellular measurement conditions attenuated intracellular potentials by a factor of about 1000 [21], the signal-to-noise ratio (SNR) for extracellular recording was usually not high, and it could hardly set a fixed threshold to select the spike signals. In our study, the threshold for detection of spike events was set to be 4 times the standard deviation (s.d.) of the voltage for each electrode independently [18].

Spike sorting is a necessary and important procedure for the analysis of data from extracellular recording [2,10,12]. Spike events recorded from each electrode were classified into neuronal activities based on principal component analysis (PCA), as described in previous reports [4,22]. In the present study, a total number of 91 electrode signals from 4 individual retinas were analyzed and sorted into 108 neuron activities for further analyses. The interspike

Table 1
Composition and intensity of the chromatic stimulations

Stimulation	White	Red	Green	Yellow
Red gun index	255 (127)	255 (127)	0	255 (127)
Green gun index	255 (127)	0	255 (127)	255 (127)
Blue gun index	255 (127)	0	0	0
Intensity (nW/cm^2)	12.18 (6.09)	4.00 (2.00)	6.52 (3.26)	10.87 (5.44)

Data of the background luminance are presented in parentheses.