

Research Report

# Information transmission rate changes of retinal ganglion cells during contrast adaptation

Xin Jin<sup>a</sup>, Ai-Hua Chen<sup>b</sup>, Hai-Qing Gong<sup>a</sup>, Pei-Ji Liang<sup>a,\*</sup>

<sup>a</sup>Department of Biomedical Engineering, Shanghai Jiao Tong University, 1954 Hua-Shan Road, Shanghai 200030, China

<sup>b</sup>Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, 320 Yue-Yang Road, Shanghai 200031, China

Accepted 10 July 2005

Available online 15 August 2005

## Abstract

During adaptation to high-contrast stimulation, retinal ganglion cell's responsiveness change is characterized by decreased firing rate and declined sensitivity. In order to examine the modification of information transmission properties of the ganglion cell during this adaptation process, neural activities were recorded extracellularly from the chicken retina using a multi-electrode recording system, and the information transmission rate of the retinal ganglion cells was estimated. The results show that the response entropy and noise entropy of the ganglion cells both decreased during the adaptation process, which resulted in a modest decline of information transmission rate of ganglion cells after several seconds' adaptation. However, due to the decrease of the neuron's firing rate during the adaptation, it is revealed that the information carried by each spike was increased as compared to pre-adaptation, suggesting that retinal ganglion cells' information processing strategies during contrast adaptation may reflect economical principle by promoting each spike more informative. These results also suggest that contrast adaptation and sensitivity rescaling of the visual neurons provide an efficient manner in information transmission and save the system's metabolic cost in the meantime.

© 2005 Elsevier B.V. All rights reserved.

*Theme:* Sensory systems

*Topic:* Retina and photoreceptors

*Keywords:* Retina; Ganglion cell; Information transmission rate; Contrast adaptation; Metabolic cost

## 1. Introduction

In early psychophysical studies, it was found that exposure to a high-contrast stimulation lead to aftereffects consisting of a decrease of contrast sensitivity as well as a perceived fading of the contrast intensity [5]. This phenomenon was termed "contrast adaptation", the neural bases of which have attracted many investigators for years, and studies were extensively conducted from primary visual cortex [2,7,23,24], to lateral geniculate nucleus (LGN) [28, 30], and recently expanded to retinal ganglion cells [3,6,14,15,29].

Electrophysiological results showed that visual neurons had declined discharge rates during adaptation to high-contrast stimulation, together with an aftereffect of decreased spontaneous activity levels [3,23,24]. However, whether or not such changes in neural activity could exert any influence on information transmission of the visual neurons during contrast adaptation still remains unclear.

"Information theory" approach is a potential tool for quantitative measurement of information transmission rate when neurons are in response to outside stimuli. It provides a new method for quantifying the amount of messages a neuron transmits in response to a specific stimulus by analyzing the probability distribution of the temporal pattern of the neural responses [12,20,31]. This method has also been applied to analyze the information transmission rate of retinal ganglion cell in response to visual stimulation

\* Corresponding author. Fax: +86 21 6407 0495.

E-mail address: [pjliang@sjtu.edu.cn](mailto:pjliang@sjtu.edu.cn) (P.-J. Liang).

[4,18,19]. In the present study, the activities of chick's retinal ganglion cells were recorded using a multi-channel recording system, and the visual stimulus was carefully defined to study the information transmission rate of ganglion cells during contrast adaptation, using the well-developed direct information measure method [20,31]. We aimed to analyze the relationship between quantitative information rate and the neuronal firing behavior during visual contrast adaptation, in the first stage of visual information processing unit—the retina level.

## 2. Materials and methods

### 2.1. Electrophysiology

The preparation of the retina, recording of ganglion cell spike trains, and spike sorting techniques were conducted as previously described [9]. In brief, a small piece of isolated retina from young born chicken (about 7–14 days) was attached with the ganglion cell side onto the surface of a multi-electrode array (MEA, Multi Channel Systems MCS GmbH, German) which consisted of 60 electrodes (10  $\mu\text{m}$  in diameter) arranged in an  $8 \times 8$  matrix with 100  $\mu\text{m}$  tip-to-tip distances. The preparation was kept in standard perfusate containing (in mM): 100.0 NaCl, 5.0 KCl, 3.0  $\text{MgSO}_4$ , 1.8  $\text{CaCl}_2$ , 25.0  $\text{NaHCO}_3$ , 25.0 glucose, and bubbled with a mixed gas of 95%  $\text{O}_2$  and 5%  $\text{CO}_2$  with a pH value of  $7.5 \pm 0.2$ . The perfusion was delivered at a rate of 0.8 ml/min, and the tissue was kept at 37  $^\circ\text{C}$  with a temperature control unit (Thermostat HC-X, Multi Channel Systems MCS GmbH, Germany).

Spikes from ganglion cells were recorded by MEA electrodes using a commercial multiplexed data acquisition system (MCRack, Multi Channel Systems MCS GmbH, German) with a sampling rate of 20 kHz and stored in a Pentium-based computer for off-line analyses. Recorded spikes from individual neurons were sorted based on principal component analysis (PCA) [33] as well as the spike-sorting unit in the commercial software (MCRack, Multi Channel Systems MCS GmbH, Germany). In the present study, in order to get precise data for information estimation, only single-neuron events clarified by manual PCA method, commercial softwares MCRack (Multi Channel Systems MCS GmbH, Germany) and OfflineSorter (Demo version, Plexon Inc. Texas, USA) were used for further analyses.

### 2.2. Visual stimulation

Spatially uniform white light was projected from a computer monitor onto the retina [10]. The stimulus intensity was renewed every 11.8 ms (85 Hz) following a pseudo-random binary sequence (PRBS) with high value of  $I_{\text{max}}$  and low value of  $I_{\text{min}}$ . The mean intensity was  $(I_{\text{max}} + I_{\text{min}}) / 2$ , the contrast was defined as  $(I_{\text{max}} - I_{\text{min}}) / (I_{\text{max}} + I_{\text{min}})$ . In this study, we chose a simple contrast level of 100%

with a medium mean intensity, i.e.,  $I_{\text{max}} = 0.139 \mu\text{W}/\text{cm}^2$ ,  $I_{\text{min}} = 0$ . The resulting stimuli had an entropy value of 1 bit/frame, for a rate of 85 bits/s (Fig. 1a). A PRBS contrast stimulus that lasted for 60 s was firstly applied to investigate the time course of contrast adaptation in retinal ganglion cells (see Fig. 3) [6,10,29].

In order to calculate the information transmission rate of ganglion cells during contrast adaptation, visual stimulation was given as 50 trials with identical statistical properties. Each trial of stimulation consisted of stimulus that lasted for 15 s, with the interval between successive trials being longer than 60 s to allow for adaptation recovery. The stimulus sequences given during the 2nd, 6th, 10th, and 14th seconds were completely identical, which were applied to estimate the noise entropy, while the sequences given during the rest episodes were randomly chosen, used to estimate the total entropy (Fig. 1b).

### 2.3. Information analysis

In the present study, the direct measure method was applied to estimate the information transmission rate of retinal ganglion cells [20,31]. This approach estimates the quantity of the visual information, which is presented in forms of entropy rate, by analyzing the probability distribution of the temporal pattern of the neural response. The idea is to treat the neuron as a communicating unit,

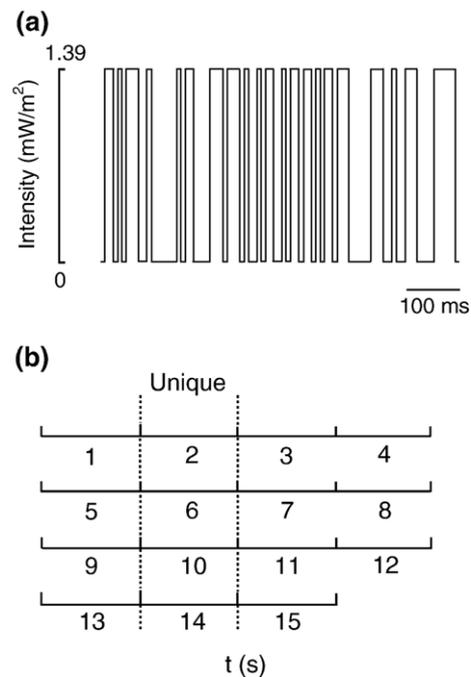


Fig. 1. The stimuli protocol of the experiment. (a) The intensity of the spatially uniform white light was renewed every 11.8 ms (85 Hz) following a random binary sequence, with high value of  $0.139 \mu\text{W}/\text{cm}^2$  and low value of 0. (b) Each repeat of stimuli lasted for 15 s, the stimuli sequence given during the 2nd, 6th, 10th, and 14th seconds was completely identical to measure the noise entropy, and others were randomly chosen to measure the total entropy. A total number of 50 trials were applied.

which sends the information about outside world to the brain through “words” (spike trains) built by “letters” (spike events) [12,31]. The information entropy estimation was based on the statistical results of many repeats of neural response recordings. Following Reinagel and Reid [20], each spike train of length  $T$  in a set of trial is built up by words of  $L$  letters, and the average entropy  $H(L, \theta)$  can be computed as:

$$H(L, \theta) = \frac{1}{T-L} \times \sum_{t=1}^{T-L} \left( -\frac{1}{L\theta} \sum_{w \in W(L, \theta)} P_t(w) \log_2 P_t(w) \right) \quad (1)$$

where  $w$  is a specific “word” constructed according to the temporal pattern of the firings,  $W(L, \theta)$  is the assembly of all

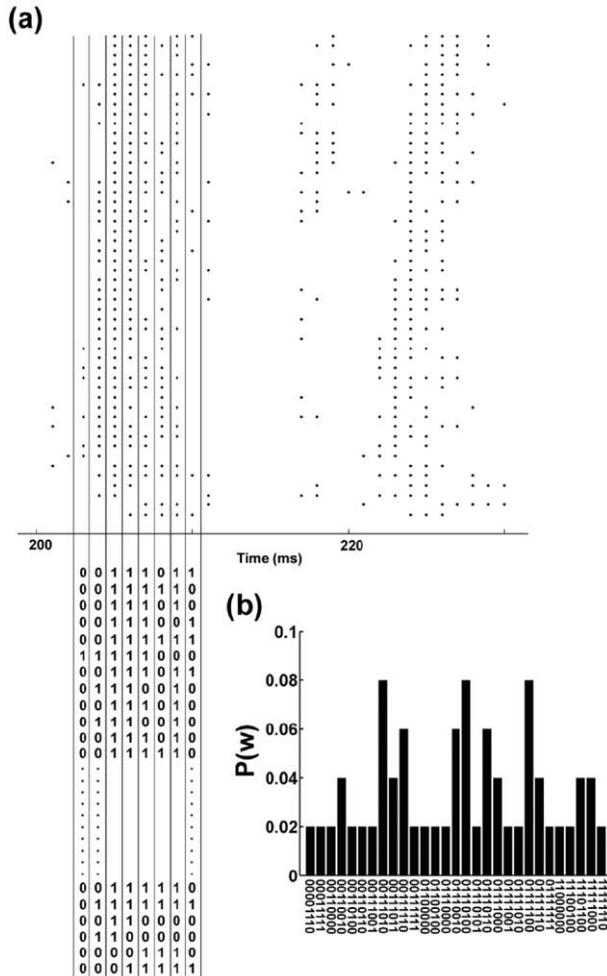


Fig. 2. Estimation of mutual information entropy from a ganglion cell's spike trains. (a) Raster plot for neuron's firing activities in the 50 trials. The spike trains are binned at time size  $\theta = 1$  ms, with each word length  $L = 8$ . The spike count in each bin gives the value of the bin (1 or 0), and the probability distribution of each words is used to calculate the information entropy. (b) The probability distribution of words ( $L = 8$ ,  $\theta = 1$  ms). Although  $2^8$  (256) patterns should be possible, only 29 actually occurred.

possible “words” comprised of  $L$  bins of time scale  $\theta$ , and  $P_t(w)$  is the probability of a specific “word”  $w$  in a group of observations. Detailed illustration of this approach for information entropy calculation is given in Fig. 2.

The mutual information entropy between the neural response and visual stimulus can thus be written as [26]:

$$H(R; S) = H(R) - H(R|S) \quad (2)$$

where  $H(R; S)$  indicates the mutual information between the stimulus  $S$  and response  $R$ ;  $H(R)$  denotes the total information entropy of the neural response, reflecting the variability of neuronal responses to all (non-repeated) possible stimuli in the assembly;  $H(R|S)$  is the response entropy under the stimulus condition of  $S$ , representing the trial-to-trial variability of neuronal responses to a repeated stimulus, giving an estimate of noise entropy  $H_{\text{noise}}$  [20]. A noise-free response should always generate the same output to identical inputs, which yields a zero value for  $H_{\text{noise}}$ .

The visual information  $I$  (which is equivalent to the mutual information  $H(R; S)$ ) can therefore be calculated by subtracting the noise entropy from the total entropy:

$$I = H_{\text{total}} - H_{\text{noise}} \quad (3)$$

In the present study, several particular episodes (the 2nd, 6th, 10th, and 14th seconds) of the firing sequence during the adaptation to high-contrast stimulation were chosen for analysis. Since the stimulation sequences given during these periods were completely identical in our experiment, the total entropy of each episode (the  $n^{\text{th}}$  second,  $n = 2, 6, 10, 14$ ) could only be approximately estimated by averaging the response entropy of the preceding  $(n - 1)^{\text{th}}$  and posterior  $(n + 1)^{\text{th}}$  seconds, while the noise entropy of the  $n^{\text{th}}$  second was measured directly. Consequently, the information entropy  $I$  of the  $n^{\text{th}}$  second was estimated as:

$$I(n) = \frac{H_{\text{total}}(n-1) + H_{\text{total}}(n+1)}{2} - H_{\text{noise}}(n) \quad (4)$$

$(n = 2, 6, 10, 14)$

### 3. Results

#### 3.1. Contrast adaptation in retinal ganglion cells

Visual adaptation to contrast stimulation begins in the retina. Being consistent with previous findings reported by other investigators [6,29], it was observed in this laboratory that the retinal ganglion cells fired actively at the onset of high-contrast stimulation, and the firing rate would be progressively reduced during the following sustained (60 s) contrast stimulus [10]. In the present study, only those cells showed good stability and high sensitivity that lasted until the experimental protocol finished were further investigated, these ganglion cells consisted of ON transient and

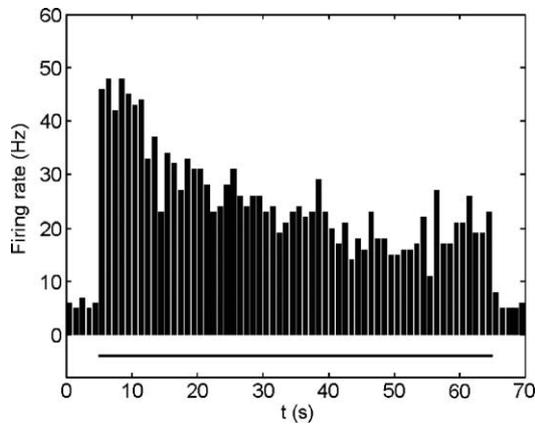


Fig. 3. A typical ON–OFF transient ganglion cell's response to 60-s contrast stimuli, which shows a decay time constant of  $\tau = 10.0$  s. The firing rate is presented with 1-s time bins, and the black line below indicated the stimulus onset.

ON–OFF transient subtypes. A typical response of an ON–OFF transient ganglion cell to contrast stimulus is shown in Fig. 3, which has a decay time constant of  $\tau = 10$  s. Significant adaptation occurred during the time course of about 15 s, after the onset of the stimulus (Fig. 3), therefore all the analyses were focus on this period to investigate the information transmission behavior changes in the adaptive process.

### 3.2. Variability and reproducibility of ganglion cells' spike trains

Neural system is full of noise and highly variable [12,17]. A typical neuron's response to the step-in of high-contrast stimulation is shown in Fig. 4a. In this experiment, the stimuli given during the 2nd, 6th, 10th, and 14th seconds were identical for each episode and each repeat, the rest were given randomly. Fig. 4b shows the per-stimulus time histogram (PSTH) of the neuron given in Fig. 4a during the 5th (left panel) and 6th (right panel) seconds of the contrast stimuli, with time bins of 10 ms. Averaged responses were calculated across the 50 repeats. It is clearly shown that, during the episode of the 5th second, the ganglion cell's PSTH presents some modest fluctuation due to the trial-to-trial variation in the cell's responses. However, during the 6th second, since the identical stimulation sequence was applied, the neuron's activity had a repeatable pattern, the PSTH presents some consistent peaks. The relationship between mean spike rate and its variance is usually used to investigate the distribution pattern of firing activities [12,32]. Fig. 4c shows the variance of the spike count of the ganglion cell as a function of the mean count for all 50 random (left panel) and unique (right panel) repeats in 5th and 6th seconds using a 10-ms-wide sliding window, respectively. In these plots, each data point represents a variance–mean combination for counts across all 50 trials in a fixed time window. Successive windows shift in 1-ms step, and the

dotted lines in both plots indicate the variance of Poisson distribution for comparison. As the figure illustrates, the neural activity elicited by random stimuli approximately followed the Poisson behavior, while the repeated stimuli induced more reproducible trial-to-trial responses. This result ensures that the responses of the ganglion cell recorded in our experiment should be stable and reliable enough for information estimation.

### 3.3. Estimating the information transmission rate of ganglion cells during contrast adaptation

The estimate of the information transmission rate of a retinal ganglion cell during the adaptation process to contrast stimuli is plotted in Fig. 5. Following the experimental protocol designed as given in Fig. 1, the total response entropy and the noise entropy estimated during the first 15 s (time bin  $\theta = 1$  ms, word length  $L = 8$ ) are illustrated in Fig. 5a (triangles and squares respectively), the dotted lines are fitted to guide eyes. During the contrast adaptation, the neuron's total response entropy decreased continuously as well as the neuronal intrinsic noise entropy did. The information transmission rate of the ganglion cell in the 2nd, 6th, 10th, and 14th seconds in response to the contrast stimuli was computed using Eqs. (3) and (4), as shown in Fig. 5b (the dotted line is fitted to guide eyes). The ganglion cell's firing rates in the 2nd, 6th, 10th, and 14th seconds are given in Fig. 5c. The average amount of information carried by each spike was measured by dividing the information transmission rate over the neuron's discharge rate, as illustrated in Fig. 5d. Since the firing rate of the ganglion cell decreased more dramatically than the information transmission rate did during the adaptation process, the result was such that the information content that each spike provided was increasing during the process of adaptation (Fig. 5d).

Since the estimate of the information transmission rate was dependent on the parameters [20,31], we therefore did the calculation using various combinations of time bin and word length, which expanded the time scale related to behavior from 4 ms, 8 ms, 16 ms, to 32 ms. Fig. 6a showed the information transmission rate (the same ganglion cell as given in Fig. 5) calculated using time bin = 1 ms and  $L = 4$  (square), bin = 1 ms and  $L = 8$  (triangle, same as Fig. 5b), bin = 2 ms and  $L = 8$  (diamond), and bin = 4 ms and  $L = 8$  (circle). It is shown that, with the use of increased time bin size, the calculated information rate decreased dramatically [20]. Fig. 6b illustrates the average amount of information carried by each spike under different combinations of time bin and word length. The result is that the comparison of information transmission between the 14th and the 2nd seconds gave qualitative consistency. For information transmission rate, the ratio values were 91.0%, 88.1%, 85.3%, and 83.4% under above four combinations and for information content per spike, the ratio values were 128.2%, 124.1%, 120.1%, and 117.5%, respectively.

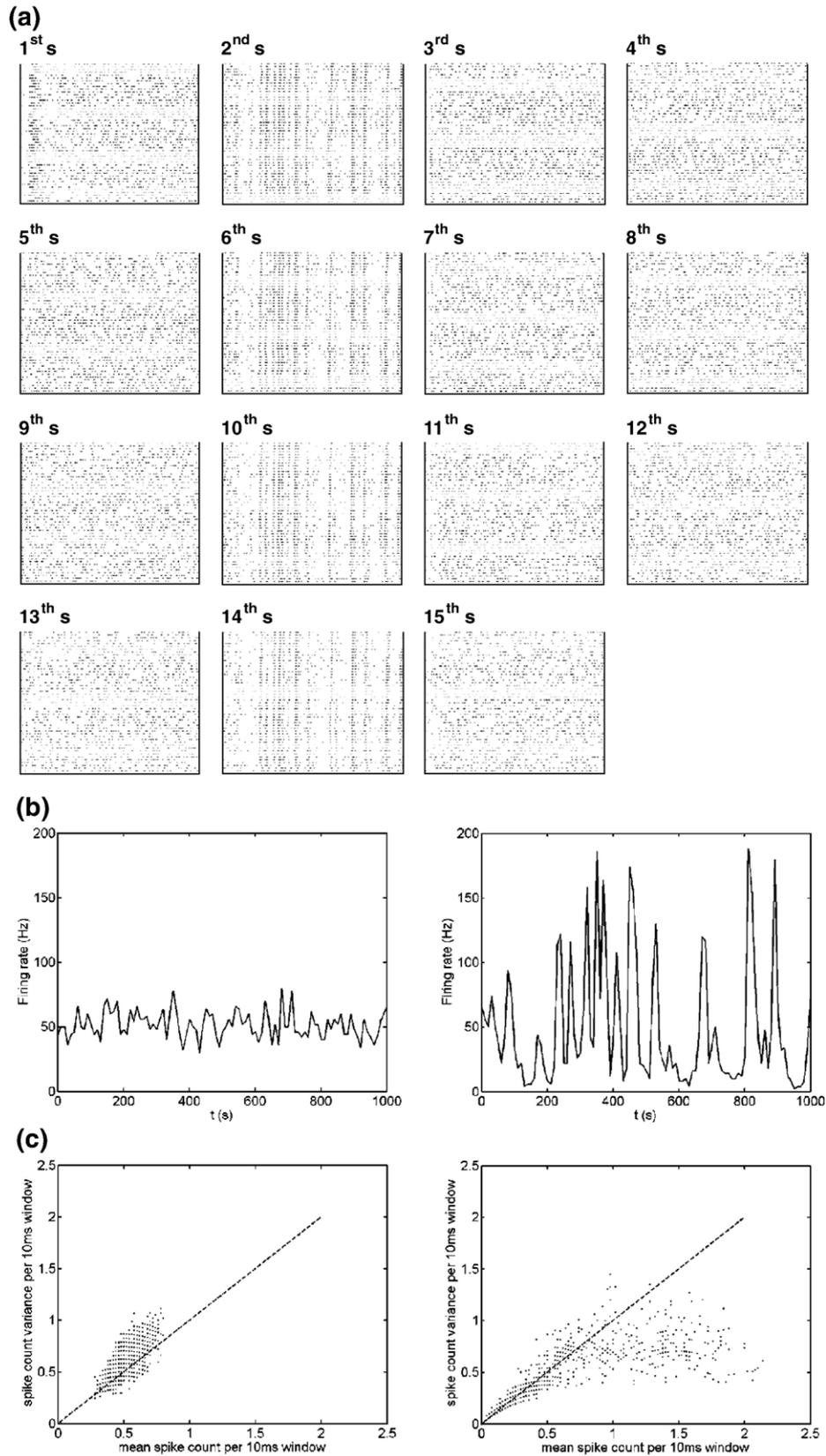


Fig. 4. A ganglion cell's response to 50 repeated trials of 15-s contrast stimulus. (a) Raster plot of spike trains from 1st to 15th seconds (50 repeats). (b) Averaged PSTH for the neuron's activities during the 5th (left panel) and 6th seconds (right panel), with time bin of 10 ms. (c) Mean–variance relationship of the neuron's activity during the 5th (left panel) and 6th seconds (right panel), with time bin of 10 ms. The dotted lines in both plots show the mean–variance relationship of Poisson distribution for comparison.

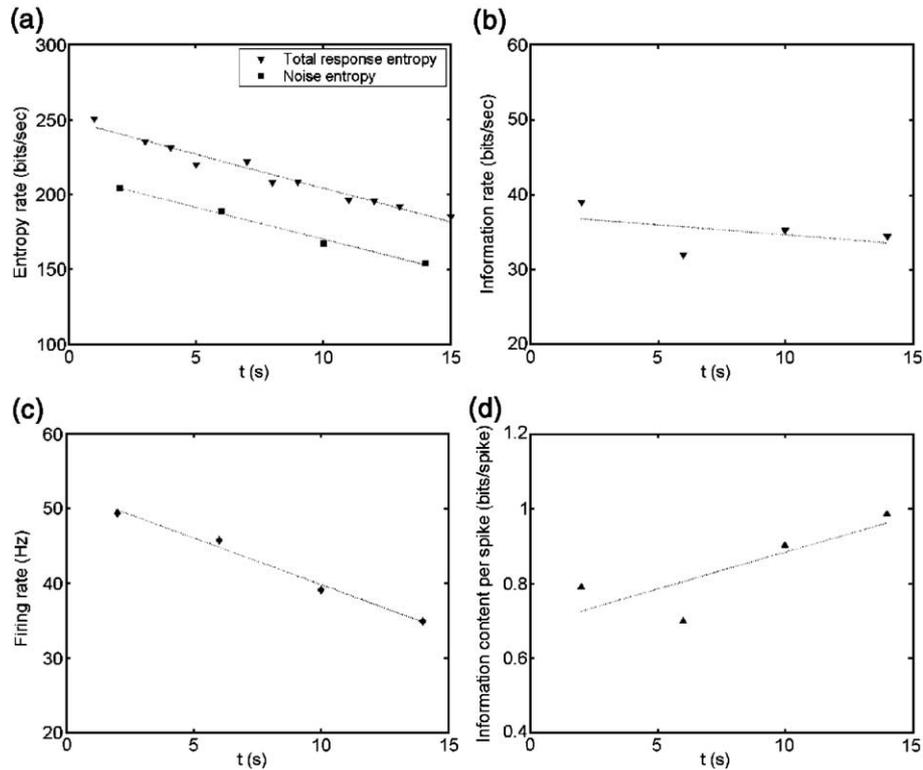


Fig. 5. Estimate of information transmission rate of a ganglion cell during adaptation. (a) The total entropy value calculated for the 1st, 3rd, 4th, 5th, 7th, 8th, 9th, 11th, 12th, 13th, and 15th seconds (triangles), and the noise entropy calculated for the 2nd, 6th, 10th, and 14th seconds (squares). (b) The mutual information estimated for the 2nd, 6th, 10th, and 14th seconds using Eq. (4) in the Materials and methods session. (c) The neuron’s firing rate during the 2nd, 6th, 10th, and 14th seconds. (d) The average information content carried by each spike during the 2nd, 6th, 10th, and 14th seconds. The dotted lines are fitted to show the tendency of changes.

3.4. Statistical results

The analysis was performed on a total number of 17 ganglion cells recorded in our experiment, following that explained in Fig. 5. Statistical results are given in Fig. 7. The information transmission rate of the 14th second vs. that of the 2nd second is illustrated in Fig. 7a. The results show that this value is  $77.8 \pm 14.4\%$  ( $n = 8, P < 0.05, t$  test) for

the ON type ganglion cells and is  $81.3 \pm 7.2\%$  ( $n = 9, P < 0.05, t$  test) for the ON–OFF type ganglion cells, which indicates that the information transmission rate for per second is decreased during the adaptation process. However, the information transmission rate for per spike is increased (Fig. 7b), with relevant ratio being  $110.8 \pm 19.7\%$  ( $n = 8, P < 0.05, t$  test) and  $114.8 \pm 17.5\%$  ( $n = 8, P < 0.05, t$  test) for ON and ON–OFF cells, respectively. No significant differ-

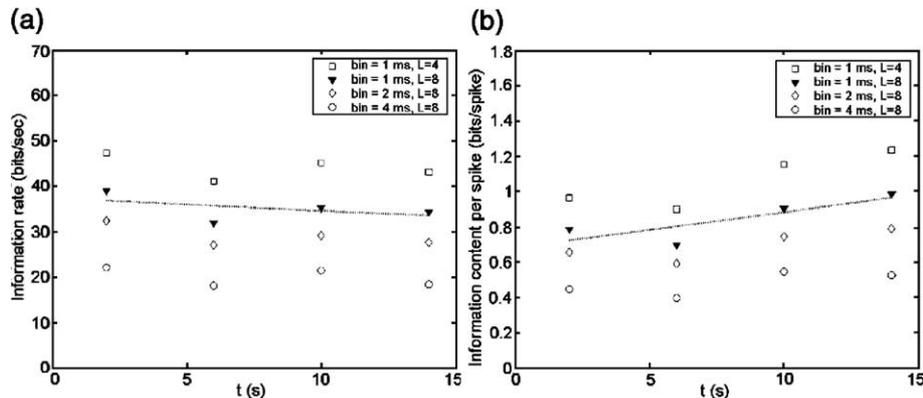


Fig. 6. Information transmission rate under different combinations of time bin and word length. (a) The information transmission rate of the ganglion cell same as presented in Fig. 5 using time bin = 1 ms and  $L = 4$  (square), bin = 1 ms and  $L = 8$  (triangle, same as Fig. 5b), bin = 2 ms and  $L = 8$  (diamond), and bin = 4 ms and  $L = 8$  (circle). The information rate sharply decreased with increasing time bin size. (b) The average amount of information carried by each spike under different combinations of time bin and word length. These estimations showed qualitatively similar tendency of change under various combinations of time bin and word length. The dotted lines in panels (a) and (b) were both fitted from the result of bin = 1 ms and  $L = 8$ , same as Fig. 5 to guide the eye.

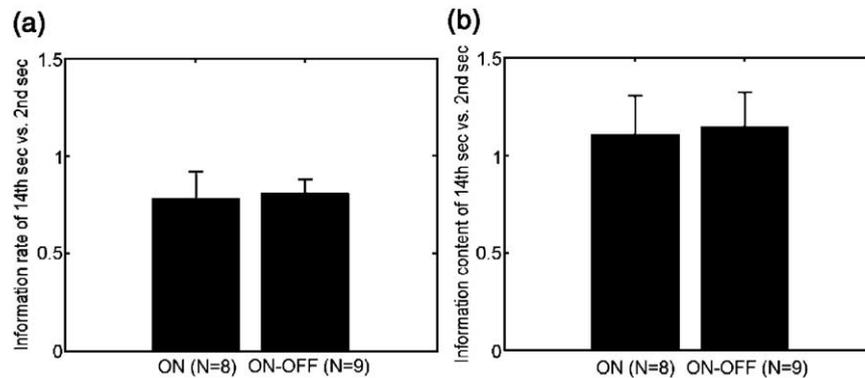


Fig. 7. Statistical results of information rate changes of the ganglion cells during contrast adaptation. (a) The modification of the cells information transmission during contrast adaptation, presented by comparing the transmission rates during the 14th second vs. that of the 2nd second. (b) The modification of the cells information transmission, presented by comparing the information contents carried by each spike in the 14th second vs. that in the 2nd second.

ence between ON and ON–OFF type ganglion cells in information transmission behavior changes during the adaptation processes is found ( $P > 0.05$ ,  $t$  test).

#### 4. Discussion

In the present study, the encoding performance of the retinal ganglion cells during contrast adaptation was investigated by measuring the neurons' information transmission rate. For practical consideration, the information entropy of the  $n^{\text{th}}$  second was estimated by averaging that of the  $(n - 1)^{\text{th}}$  and  $(n + 1)^{\text{th}}$  seconds episodes, for approximation. It is revealed that the information transmission rate of ganglion cells was slightly decreased during the contrast adaptation. However, the information content that each spike carried was significantly increased after adaptation.

##### 4.1. Estimation of ganglion cell's information transmission rate

Information theory approaches for investigating visual neurons' encoding behavior have been extensively applied during the past years. Applications were performed to analyze the reproducibility and variability of the motion-sensitive H1 neurons in fly [12] and the temporal structure of retinal ganglion cells' spike trains in salamander and rabbit [4]. Passaglia and Troy [19] have recently investigated the information transmission rate of cat retinal ganglion cells under binary contrast stimuli of various spot sizes. However, it still remains unclear about how is the neuron's information transmission behavior quantitatively modulated during the adaptation to visual stimuli. In the present study, the analysis results show that the response entropy and noise entropy of the ganglion cells were both decreased during adaptation to the contrast stimuli, with the total entropy having a more profound decrease, which resulted in a reduction in the information transmission rate, measured for per unit time. This result was similar to the findings reported by Juusola and

de Polavieja [13] that the rate of information transfer in *Calliphora* photoreceptor was reduced during adaptation to a prolonged dim environmental light.

It has also been reported that the direct information estimation method can be biased because it requires reproducibility and reliability of the neuron's activity over a prolonged period for repeated testing trials, which is very difficult to achieve in real experimental recordings [19,20,31]. In the present study, to avoid the neuron's response property changes due to long-lasting experiment, we chose to shorten the experimental protocol by particular design. Therefore, the entropy values of the examined episodes (i.e., the 2nd, 6th, 10th, and 14th seconds) were approximated. Although this will also introduce in some bias in estimation, it still allows us to make comparison between pre- and post-adaptation time periods to make reasonable inference.

##### 4.2. Information transmission in retinal coding

Traditionally, firing rate was assigned as an acceptable language for neural coding [1,25]. Although it has been recently realized that the temporal pattern of firing activities may also be important to information coding [4,21], little has been known about the modulation of the coding behavior during adaptation in exposure to changing stimuli. Contrast adaptation begins in retinal bipolar cells [22]. In addition to the changes of bipolar cells' signals input to ganglion cells during contrast adaptation, the firing threshold of ganglion cells is also increased due to the reduction of the cation channels' excitability [14,15], which results in a lowered firing rate in the ganglion cells. On the other hand, the computational result of this study reveals that, as a compensation, the ganglion cells fire more informative spikes after adaptation, with each spike carrying over 10% ( $n = 17$ ) more information content than pre-adaptation in average, even though the total information rate for per unit time is decreased. This ensures that the information transmission can be reasonably maintained during the reduced firing activity due to adaptation and is also compatible to the

notion that the stimulus information could be stored in retinal network [10], when the retinal ganglion cells can regulate their coding efficiency by neuronal and circuitry modification during adaptation.

#### 4.3. Adaptation, metabolic cost, and information transmission

The functional roles of contrast adaptation in retinal neurons have been extensively studied. Its physiological significance is, not only to adjust the visual sensitivity to match the temporal structure of the light input [14,27], but also to regulate the light response kinetics of the ganglion cells [27,29]. Since the adaptation is characterized by decrease in firing activity, it would be reasonable to ask if the reduced activity should reflect a reduction in information transmission. The computation results obtained in the present study reveal that there is indeed a slight decline of information transmission rate (per unit time) of the ganglion cells during contrast adaptation. However, because the neurons' firing rate has more profound decrease during the adaptation process, the information carried by each spike is actually increased. This suggests that the retinal ganglion cells' information processing strategies may advance economical transmission of information during contrast adaptation by promoting each spike more informative. Physiologically, the increased information content carried by each spike was ensured by more precise spike events for signaling contrast stimulation during contrast adaptation. Retina will inform the brain with the environmental light intensity changes in a more economical and assured manner, once it has adapted to a new environment.

Since the spikes fired by the same neuron should have approximately equal metabolic cost ( $\sim 9 \cdot 10^6$  ATP per spike, see [16]), therefore in our case, the ganglion cells could save  $\sim 29.2 \pm 4.8\%$  ( $1 - R_{14}/R_2$ ,  $R_n$  represents the firing rate during the  $n^{\text{th}}$  second,  $n = 17$ ) energy after adaptation. At the mean time, most ganglion cells under investigation reduced the metabolic cost for each bit of information to  $\sim 90.9 \pm 15.4\%$  ( $I_{\text{Spi-2}}/I_{\text{Spi-14}}$ ,  $I_{\text{Spi-n}}$  indicates the information content carried by each spike during the  $n^{\text{th}}$  second,  $n = 17$ ). It is noticeable that no significant difference in the behavior changes in information processing is tested between the ON and ON-OFF ganglion cells, which may suggest that their adaptation strategies for information coding are generally similar in spite of the widely acknowledged asymmetry in ON and OFF pathways [8,11].

#### Acknowledgments

This work was supported by grants from National Basic Research Program of China (2005CB724301), National Foundation of Natural Science of China (60375039), and the Ministry of Education (20040248062).

#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.brainres.2005.07.006](https://doi.org/10.1016/j.brainres.2005.07.006).

#### References

- [1] E.D. Adrian, The Basis of Sensation, W. W. Norton, New York, 1928.
- [2] D.G. Albrecht, S.B. Farrar, D.B. Hamilton, Spatial contrast adaptation characteristics of neurones recorded in cat's visual cortex, *J. Physiol. (London)* 347 (1984) 713–739.
- [3] S.A. Baccus, M. Meister, Fast and slow contrast adaptation in retinal circuitry, *Neuron* 36 (2002) 909–919.
- [4] M.J. Berry, D.K. Warland, M. Meister, The structure and precision of retinal spike trains, *Proc. Natl. Acad. Sci. U. S. A.* 94 (1997) 5411–5416.
- [5] C.B. Blakemore, F.W. Campbell, On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images, *J. Physiol. (London)* 203 (1969) 237–260.
- [6] S.P. Brown, R.H. Masland, Spatial scale and cellular substrate of contrast adaptation by retinal ganglion cells, *Nat. Neurosci.* 4 (2001) 44–51.
- [7] M. Carandini, D. Ferster, A tonic hyperpolarization underlying contrast adaptation in cat visual cortex, *Science* 276 (1997) 949–952.
- [8] D. Chander, E.J. Chichilnisky, Adaptation to temporal contrast in primate and salamander retina, *J. Neurosci.* 21 (2001) 9904–9916.
- [9] A.H. Chen, Y. Zhou, H.Q. Gong, P.J. Liang, Firing rates and dynamic correlated activities of ganglion cells both contribute to retinal information processing, *Brain Res.* 1017 (2004) 13–20.
- [10] A.H. Chen, Y. Zhou, H.Q. Gong, P.J. Liang, Luminance adaptation increased the contrast sensitivity of retinal ganglion cells, *Neuro-Report* 16 (2005) 371–375.
- [11] E.J. Chichilnisky, R.S. Kalmer, Functional asymmetries in ON and OFF ganglion cells of primate retina, *J. Neurosci.* 22 (2002) 2737–2747.
- [12] R.R. de Ruyter van Steveninck, G.D. Lewen, S.P. Strong, R. Koberle, W. Bialek, Reproducibility and variability in neural spike trains, *Science* 275 (1997) 1805–1808.
- [13] M. Juusola, G.G. de Polavieja, The rate of information transfer of naturalistic stimulation by graded potentials, *J. Gen. Physiol.* 122 (2003) 191–206.
- [14] K.J. Kim, F. Rieke, Temporal contrast adaptation in the input and output signals of salamander retinal ganglion cells, *J. Neurosci.* 21 (2001) 287–299.
- [15] K.J. Kim, F. Rieke, Slow  $\text{Na}^+$  inactivation and variance adaptation in salamander retinal ganglion cells, *J. Neurosci.* 23 (2003) 1506–1516.
- [16] S.B. Laughlin, R.R. de Ruyter van Steveninck, J.C. Anderson, The metabolic cost of neural information, *Nat. Neurosci.* 1 (1998) 36–41.
- [17] Z.F. Mainen, T.J. Sejnowski, Reliability of spike timing in neocortical neurons, *Science* 268 (1995) 1503–1506.
- [18] S. Nirenberg, S.M. Carcieri, A.L. Jacobs, P.E. Latham, Retinal ganglion cells act largely as independent encoders, *Nature* 411 (2001) 698–701.
- [19] C.L. Passaglia, J.B. Troy, Information transmission rates of cat retinal ganglion cells, *J. Neurophysiol.* 91 (2004) 1217–1229.
- [20] P. Reinagel, R.C. Reid, Temporal coding of visual information in the thalamus, *J. Neurosci.* 20 (2000) 5392–5400.
- [21] B.J. Richmond, Information coding, *Science* 294 (2001) 2493–2494.
- [22] F. Rieke, Temporal contrast adaptation in salamander bipolar cells, *J. Neurosci.* 21 (2001) 9445–9454.

- [23] M.V. Sanchez-Vives, L.G. Nowak, D.A. McCormick, Membrane mechanisms underlying contrast adaptation in cat area 17 in vivo, *J. Neurosci.* 20 (2000) 4267–4285.
- [24] M.V. Sanchez-Vives, L.G. Nowak, D.A. McCormick, Cellular mechanisms of long-lasting adaptation in visual cortical neurons in vitro, *J. Neurosci.* 20 (2000) 4286–4299.
- [25] M.N. Shadlen, W.T. Newsome, Noise, neural codes and cortical organization, *Curr. Opin. Neurobiol.* 4 (1994) 569–579.
- [26] C.E. Shannon, A mathematical theory of communication, *Bell Sys. Tech. J.* 27 (1948) 379–423, 623–656.
- [27] R. Shapley, J.D. Victor, The effect of contrast on the transfer properties of cat retinal ganglion cells, *J. Physiol. (London)* 285 (1978) 275–298.
- [28] T. Shou, X. Li, Y. Zhou, B. Hu, Adaptation of visually evoked responses of relay cells in the dorsal lateral geniculate nucleus of the cat following prolonged exposure to drifting gratings, *Vis. Neurosci.* 13 (1996) 605–613.
- [29] S.M. Smirnakis, M.J. Berry, D.K. Warland, W. Bialek, M. Meister, Adaptation of retinal processing to image contrast and spatial scale, *Nature* 386 (1997) 69–73.
- [30] S.G. Solomon, J.W. Peirce, N.T. Dhruv, P. Lennie, Profound contrast adaptation early in the visual pathway, *Neuron* 42 (2004) 5–7.
- [31] S.P. Strong, R. Koberle, R.R. de Ruyter van Steveninck, W. Bialek, Entropy and information in neural spike trains, *Phys. Rev. Lett.* 80 (1998) 197–200.
- [32] A.K. Warzecha, M. Egelhaaf, Variability in spike trains during constant and dynamic stimulation, *Science* 283 (1999) 1927–1930.
- [33] 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, *J. Neurosci. Methods* 135 (2004) 55–65.