# Dynamics of Population Synchrony of Retinal Ganglion Cells During Response to Contrast Stimulus

Li Bing, Liu Xue, Liang Pei-Ji, Zhang Pu-Ming[CA]
School of Life Science and Biotechnology
Shanghai Jiao Tong University
Shanghai, China
pmzhang@sjtu.edu.cn

***Abstract*—The contrast adaptation characterized by retinal ganglion cells when exposed to high density contrast patterns are of important psychophysical significance in visual system. The synchronous discharges exhibit an important way of coding mechanism for information transmission. Our recent study recorded discharges simultaneously from a group of neighbor neurons under contrast stimulus and analyzed the dynamics of population synchrony by employing a measurement of discrepancy, which is based on information theory. The results showed that the population of retinal ganglion cells evolved dynamical synchrony during response to the contrast stimulus. This evolutionary synchrony may contribute to revealing that the coding mechanism was probably embedded in the precise temporal alignment of neuron population.**

***Keywords-dynamics; population; synchrony; retinal ganglion cell; contrast***

## I. INTRODUCTION

When investigating the neuron coding mechanism, the adaptation of a single neuron and the collectively synchronous discharging of neuron population are two important ways. In early studies, it was found that the exposure to a high density contrast stimulus would lead to a response described as an initial burst of intensive discharge followed by an exponential decay afterwards [1], and the decay discharging gradually stabilized to an approximately constant firing rate. After that, this phenomenon was extensively studied from primary visual cortex [2] to lateral geniculate nucleus (LGN) [3] in the visual system. In recent, many interests have been shifted to the retinal ganglion cells [1, 4, 5].

Previous results showed that: (1) By measuring the neurons' information transmission rate, the encoding performance of the retinal ganglion cells after contrast adaptation was proved to be enhanced – with the same information content, though total spike count decreased, the ganglion cell fired more informative spikes after adaptation, with each spike carrying over 10% information content than pre-adaptation in average [6]. (2) Comparing to spontaneous fire rate, the average firing rate increased or decreased after contrast adaptation. However, the Lempel-Ziv complexity of a single neuron after contrast adaptation was much lower [7]. Those facts explored the single-neuron coding mechanism in neuron transmission rate and complexity after adaptation. However, both of them were calculated from whole experimental time after neurons were adapted, and thus lack of temporal precision before they were adapted. One single neuron with a lower complexity but a higher transmission rate after adaptation may not undertake the role of an independent encoder. Thus the neuron population synchrony and their time-varying interaction immediately after the projection of stimulus were under investigation presently.

Neuron synchrony is a way to explore the population coding mechanism [9-12]. Due to the restriction of methods such as cross-correlation, previous investigations had to focus on the pair-wise neurons. The analysis of population synchrony was less conducted and the results were yet unconfirmed partially by lack of methods to deal with the multi-channel spike trains simultaneously recorded. Reference [8] first introduced an analysis method of information discrepancy for multiple spike trains. In the present study, this measurement of discrepancy based on information theory was employed to explore the synchrony of a group of neurons and the temporal variations. Quantitative synchrony indices of weighing the interactions among the neuron group and dynamics of population synchrony were calculated and presented that the neurons under investigation were more synchronous during response to contrast stimulus and the population synchrony was enhanced, which may contribute partly to population coding mechanism.

## II. MATERIALS AND METHOD

### A. Data acquisition

As previously described [13], multi-electrode array (MEA, Multi Channel System, MCS, Germany) was applied to record a group of neuron spikes extracellularly. The eye of a newly hatched chicken (no elder than 2 weeks) was decapitated and enucleated. Then the dissected retina was selected and attached with the ganglion cell side onto the surface of the multi-electrode array.

The spatially uniform white light on the computer screen, which lasts 60 seconds, was refreshed every 12 ms (85Hz), following the rhythm of a two-value pseudo-random sequence generated by m-sequence generator, with the low intensity $I_{min}$ = 2.96 μW/cm$^2$ and high intensity $I_{max}$ = 28.7 μW/cm$^2$, shown in Fig.1(a). The mean intensity was ($I_{max}$ + $I_{min}$) / 2 = 15.83

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$\mu W/cm^2$; and the contrast was $(I_{max} - I_{min}) / (I_{max} + I_{min}) = 81.3\%$. This stimulus was projected via a lens system onto the isolated retina. The ganglion cells' responses was recorded at a sampling rate of 20 KHz and then stored. Spike events recorded from each electrode were detected and classified into neuron activities based on the previously described methods [15, 16] off-line for further analysis.

### B. *Information discrepancy analysis*

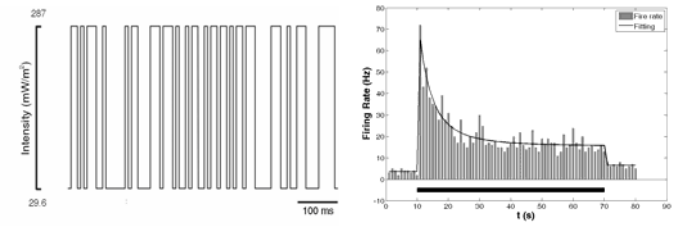
Multiple sequence comparison refers to the search for similarity among more than two sequences. The discrepancy measurement based on information theory has been brought into this area most recently, which studies the probability distribution of the temporal pattern of the neural discharges in response to a specific stimulus and gives a way to process more than two spike trains at the same time [8, 14]. It largely reduces the computational time-consumption and meanwhile keeps objectivity. As the algorithm is detailed previously [8, 14], the measurement $B$ and $R$ are representing the discrepancy among the $s$ sequences being investigated; and $B_k$ is a weighing of "relative distance" between the $k$-th sequence and the average of all $s$ sequences in the group.

Calculating as per the formula, it can be noticed that for different sequences with identical subsequence distribution, there will be the same information discrepancy value; however, this may coincide on a certain word length $l$ and never happens to all different $l$s in the Complete Information Set (CIS) [14]. To avoid this possible misjudgment, more than 3 different combinations of parameters in the real data set were selected for discrepancy measurement, as to be illustrated in the next part.

## III. RESULTS

### A. *Contrast adaptation in ganglion cells*

The contrast adaptation of retinal ganglion cells was significant in our experiment, which was consistent with the previous reports [5]. In front of high contrast stimulus, the retinal ganglion cells exhibited a fierce activity initially; and then calm down to a sustained stage. In the present study, the type of retinal ganglion cells recorded covered ON and ON-OFF transient subtypes. Fig.1 (b) gives a typical ON-type response, in which the horizontal solid line represents the time of the contrast stimulus, which lasts 60 second.




(a) (b)

Figure 1. The stimulus protocol of the experiment. (a) The spatially uniform white light on the computer screen at a refresh rate of 12 ms (85Hz), following a two-value pseudo-random sequence, with low value of 2.96 $\mu W/cm^2$ and high value of 28.7 $\mu W/cm^2$. (b) A typical ON type ganglion cell's fire rate under the prescribed stimulus protocol, fitted by an exponential curve. The horizontal solid line in the bottom represents the 60s contrast stimulus.

### B. *Dynamics of Population Synchrony*

The algorithm of discrepancy measurement is used to analyze the interactive behavior of a group of neurons. Following the experimental protocol previously described in II, section (A), we selected 10 channels of responses on the MEA map (shown in Fig.2). The 10 channels of signals were then sorted into 10 neuron spike trains and their synchronization after adaptation was tested pair-wisely by cross-correlation. Four examples are plotted in Fig.3, which gives the correlations from distant couples S1 vs. S9 and S2 vs. S10, to neighbors S4 vs. S5 and S5 vs. S10. It shows that arbitrary neuron couples in this group present a correlated relation.

To explore the time-varying interactions among the 10 neurons, the 60-second experiment time was split up into 6 periods, each of which represented 10-second time length. The algorithm was then performed in each of the period. The discrepancy value $B_k$, representing the original spike train $S_k$ , was calculated one by one across all periods and illustrated in

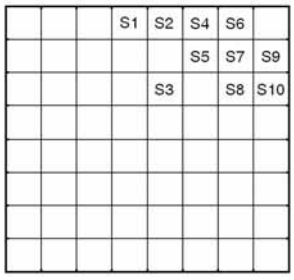
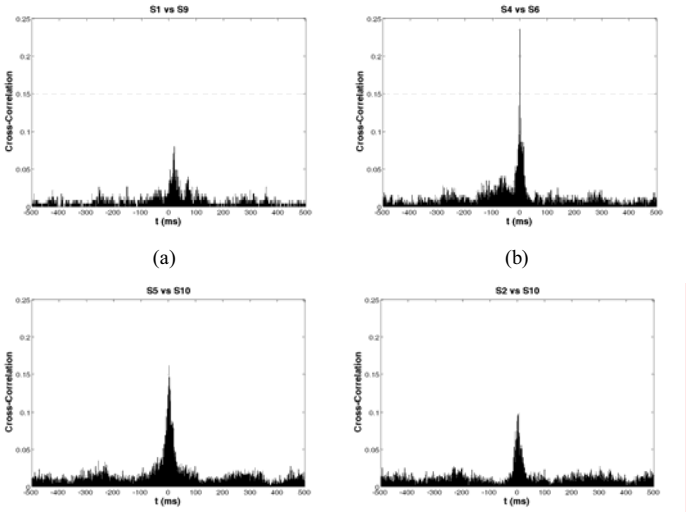



Figure 2. Geography of the selected neurons S1-S10.




(a) (b)

(c) (d)

Figure 3. Four Examples of cross-correlogram of the 10 neuron responses from distant couples S1 vs. S9 and S2 vs. S10, to neighbors S4 vs. S5 and S5 vs. S10, respectively.

Fig.4. As the contrast stimulus was projected on to the retina, the 10 neurons discharged fiercely at the beginning; the $B_k$ values of all the individuals in the same period are of large diversity, representing asynchrony among the neurons, shown in Fig.4 (a) and (b). As the cells were adapted, their fire rate declined gradually to a sustained stage, and the difference of their respective $B_k$ became smaller in each of the remaining periods (Fig.4 (c)-(f)), which were referred to as synchronization, as pointed out by Wang [8]. The result gave the temporal variance of relationship among those neurons in the population before and after contrast adaptation – the neurons were firing more synchronously. Although the peak in Fig.4 (e) represents a larger discrepancy of S5 against the others, comparing to its smooth predecessor in Fig.4 (d), the average of $B_k$s in (e) are smaller than in (d), which implies that the other neurons are more "tight" in (e) than in (d).

On the other side, instead of investigating the interactions inside the neuron group, these neurons were taken as one group to measure the dynamics of population synchrony. The discrepancy ratio, *R*, was employed as the measuring index.

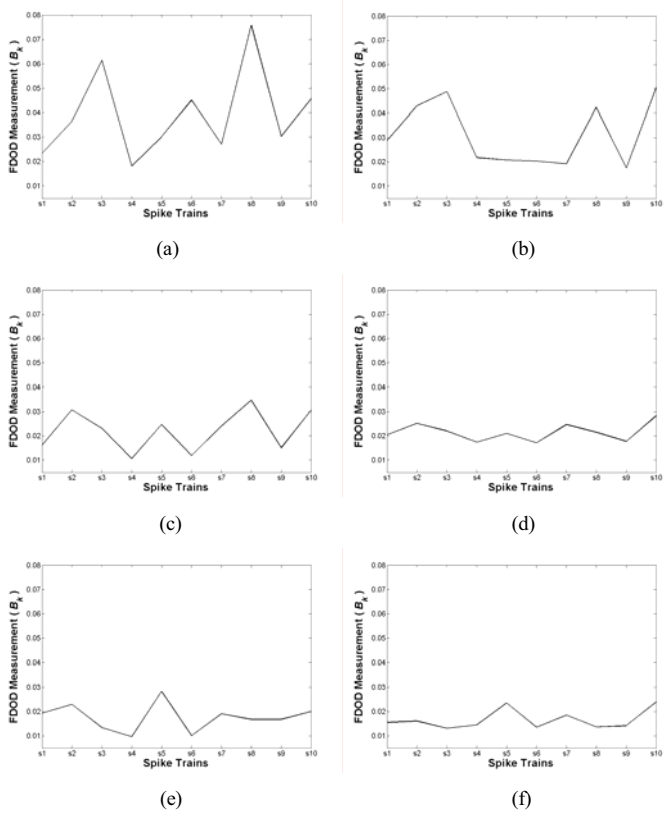



Figure 4. Dynamics of synchrony inside a given group of retinal ganglion cells during response to a high contrast stimulus. The bin size across the 6 plots was chosen to be 2 ms; and the word length is $l = 8$. (a) Different values $B_k$ of each spike train Sk calculated in the first 10s after the stimulus began. (b) Different values $B_k$ of each spike train $S_k$ calculated during 10s – 20s after the stimulus began. (c) Different values $B_k$ of each spike train $S_k$ calculated during 20s – 30s after the stimulus began. (d) Different values $B_k$ of each spike train $S_k$ calculated during 30s – 40s after the stimulus began. (e) Different values $B_k$ of each spike train $S_k$ calculated during 40s – 50s after the stimulus began. (f) Different values $B_k$ of each spike train $S_k$ calculated during 50s – 60s after the stimulus began.

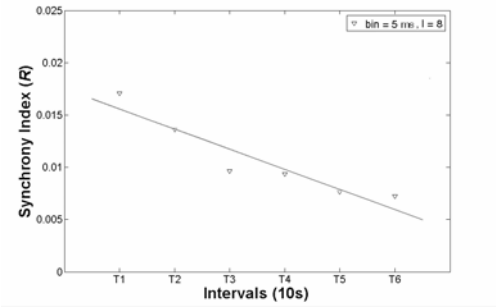



Figure 5. Dynamics of synchrony of a group of ganglion cells during the 60s contrast adaptation. The combinations of parameters are bin = 2 ms and word length $l = 8$. Larger *R* implies a disorder while smaller *R* represents synchrony. The ticks T1-T6 in x-scale represent 10-seconds time length, respectively. The solid line is the linear fitting curve using Least Square Method.

A smaller value of *R* represented synchronous discharges, while a larger one signified a disorder. The 60-second time was also divided into 6 periods equally, each of which represented 10-second time length. Each R of the 6 periods was traversed and the result was shown in Fig.5. The solid line was drawn using the Least Square Method to give a direct viewing of the decreasing trend, which implied an increasing synchrony of the ganglion cell population. This decreasing trend along the ordinal time periods denotes that after stimulus was projected on to the retina, those neurons did come "closer in distance", i.e., they were evolving dynamical synchronization.

Since the discrepancy calculation was dependent on the parameters [8], different parameters combinations of time bin and word length were also applied; and the results were shown in Fig.6. Fig.6 (a) shows the inter-neuron relationship (the same period as Fig.4 (a)) during the first 10s after stimulus is projected, using the combinations of (bin = 2 ms, $l = 4$), (bin = 5 ms, $l = 4$) and (bin = 5 ms, $l = 8$), respectively, reflecting the consistency across different parameter combinations. Fig.6 (b) shows the dynamics of synchrony through 60-second experiment, using the combinations of (bin = 2 ms, $l = 4$), (bin = 5 ms, $l = 4$) and (bin = 5 ms, $l = 8$), respectively, in which the decline trend can all be noticed.

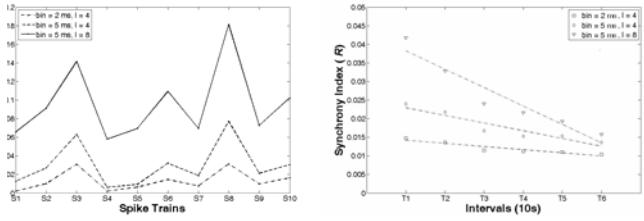



Figure 6. Dynamics of synchrony under different combinations of bin size and word length. (a) Dynamics inside a group of retinal ganglion cells during 60 seconds the same as shown in Fig.4 (a). The dash-dotted, dash and solid line denotes the (bin, word length) combinations of (2 ms, 4, dash-dotted), (5 ms, 4, dash) and (5 ms, 8, solid), respectively. (b) Dynamics of synchrony of the group the same as shown in Fig.5, the triangle, square and diamond symbols represent data sets of 3 combinations of bin and word length, which are (2 ms, 4, square), (5 ms, 4, diamond) and (5 ms, 8, triangle), respectively.

## IV. DISCUSSIONS

In the present study, the dynamics of population synchrony of a group of ganglion cells during response to high contrast stimulus was under investigation. To investigate the differences over a number of neurons at the same time, a discrepancy measurement based on information theory was employed. This measurement revealed the dynamics of population synchrony and quantitated a decreasing index trend, which represented an increasing rhythm from disorder to synchronization. This dynamically evolved synchrony of neuron population implied that the mechanism for information transmission is probably embedded in the temporal structure of the synchronous population.

The discrepancy measurement is an effective method for investigating the synchronization pattern of a large number of neurons, not only because it largely reduces the calculation effort comparing to those pair-wise measurements, but also keeps a strong objectivity to yield the correct judgment. However, this measurement still has its requirements for pre-processing the raw data recorded so that it won't affect the eventual result. The detailed discussion was presented previously [8] and in the current study, the combinations in which the number of symbols, *m*, was fixed to 2, the bin width was 5 ms and the word length *l* was assigned to 2, 4 and 8, were applied after being examined. Fig.6 proves that different combinations of parameters are consistently following a similar trend.

After the neurons evolved synchronization, they are signaling in response to the stimulus with a precision in the millisecond range, which is in accordance with previous results [12]. The reason for this precision is that synchronized EPSPs are more likely to trigger postsynaptic spikes at next processing stage than temporally dispersed inputs. These synchronous discharges could elicit postsynaptic spikes with minimal latency and thus transmit the information contained in the stimulus with high precision over different synaptic stages [12]. Another experiment [6] practiced in our lab also supported this point, in which a 15-second contrast stimulus with identical content in the $2^{nd}$, $6^{th}$, $10^{th}$ and $14^{th}$ second was designed, and then the information transmission rate (bits/spike) was calculated second by second. Results showed that though less spikes was fired after adaptation, the transmission rate in bits/spike was continuously increasing in the four specific second mentioned above, which implies that the precise temporal structure in the spike trains can account for this improving efficiency in transmission. This temporally aligned discharging pattern, i.e., synchrony, is a more economical strategy employed by retinal ganglion cells to encode the stimulus once they adapts themselves to the new environment, which consumes less energy, brings more efficiency and presents a metabolic significance.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