Temporal and Spatial Properties of the Retinal Ganglion Cells' Response to Natural Stimuli Described by Treves-Rolls Sparsity

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Abstract — **To investigate the temporal and spatial properties of the retinal ganglion cells' activities in response to natural stimuli, "sparsity" index was applied to analyze the response characteristics of chicken retinal ganglion cells (RGCs) in exposure to checker-board flickering and natural movies (grayscale video-recording) over lifetime and across the population. The statistical results show that the lifetime sparseness of the single cell activity and the population sparseness of the ensemble activities are both more profound for the neuronal responses evoked by natural stimuli as compared to that elicited by checker-board flickering, while the mean firing rates in response to both kinds of stimuli were comparable.**

Keywords -- natural stimuli; lifetime sparseness; population sparseness; Treves-Rolls sparsity

I. INTRODUCTION

In sparse representation, various patterns of the natural stimuli can be encoded by concerted firings of dynamically grouped subsets of activated neurons in sensory system, such phenomenon is termed as "population sparseness" [1]. At the mean time, sparseness can also be defined in terms of the probability distribution of a single sensory neuron's firing activity in response to a set of stimuli. Since in natural environment, single individual neurons rarely fire action potentials with a high rate, they are most of time quiet or only fire with a low rate, the terminology "lifetime sparseness" is given [2].

In the present study, to quantitatively describe the response characteristics of retinal ganglion cells (RGCs), Treves-Rolls sparsity, a measure of the distribution properties of firing activity, was employed [2,3]. The activities of RGC groups in response to grayscale digitized time-varying natural images (movies) were recorded simultaneously from isolated chicken retinas using a multi-electrode array (MEA). Pseudo-random white-noise checker-board stimulation was applied for control experiment [4-6]. The contrast of the checker-board stimulus was adjusted to enable the ganglion cells under investigation to be activated to a level comparable to that evoked by the natural movies. Statistical analyses performed on our experimental data demonstrate that sparsity is more remarkable for the neuronal activities in response to natural stimuli as compared to that elicited by pseudo-random checker-board, in a sense that both the lifetime sparseness and population sparseness are with higher values of index during the natural stimuli.

II. MATERIALS AND METHODS

A. Electrophysiology Recording

Detailed extracellular-recording procedure can be found elsewhere [7, 8]. Spikes from RGCs were recorded by MEA electrodes using a commercial multiplexed data acquisition system (MC_Rack, Multi Channel Systems MCS GmbH, Germany) and stored for off-line analyses. Spikes from individual neurons were sorted using principal component analysis (PCA) [9, 10] and the spike-sorting units provided by the commercial software MC_Rack (Multi Channel Systems MCS GmbH, Germany) and OfflineSorter (Plexon Inc. Texas, USA). In order to get accurate data for further statistical analysis, only single-neuron events consistently clarified by all these methods were used in the present study.

The following stimulation protocols were applied: (1) Pseudo-random binary checker-board flickering consisting of 1920 frames refreshed at a rate of 9.05 Hz and lasted for 221 seconds [11]; (2) Digitized grayscale video recording of natural scenes (downloaded from the website of van Hateren's lab, http://hlab.phys.rug.nl/vidlib/index.html; [12]). Each piece of movie contained 1920 frames and was presented with a refresh rate of 10 Hz (lasted for 192 seconds). Example frames of checker-board flickering and natural scenery movie are shown in Fig. 1.

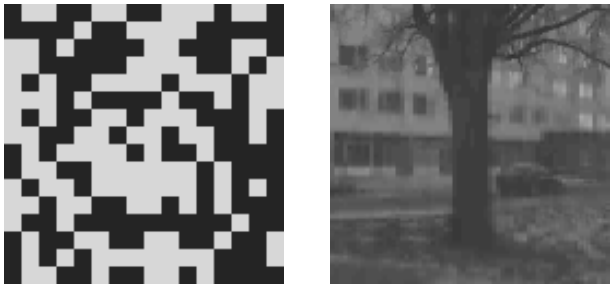

Figure 1. Example frames of pseudo-random white-noise checker-board flickering (left) and grayscale natural scene movie stimuli (right) applied.

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The images were of same size while being presented on the screen and projected onto the retinal piece via an optical lens system. The projected images covered the whole area of the multi-electrode array.

B. Calculation of the sparsity

In the present study, we employed Treves-Rolls sparsity to measure the sparseness of the neuronal activities in exposure to time-varying pseudo-random white-noise checker-board flickering and natural stimuli.

Treves-Rolls sparsity was proposed and applied to study how the primary visual cortex encodes the natural scenes, this index is related to the response distribution [2, 3, 13]:

$$a = \frac{\left(\frac{1}{n}\sum_{i=1}^{n} r_i\right)^2}{\frac{1}{n}\sum_{i=1}^{n} r_i^2} \qquad (1)$$

based on which a sparseness index S can be calculated (Vinje and Gallant, 2000):

$$S = \frac{1-a}{1-\frac{1}{n}} \qquad (2)$$

where r_i (i = 1, 2, ..., n) denotes one neuron's firing counts in response to the ith segment of the whole stimulation (in this case, lifetime sparseness S_L can be obtained) or the firing counts of the ith neuron out of the group during a given period of the stimulation (in this case, population sparseness S_P can be calculated). This value of S is ranged from 0 to 1, higher value is related to higher level of sparseness.

In the present study, all the calculations were performed on the binned spike trains of the RGCs' firing activities in response to the stimulation.

III. RESULTS

Experimental results from one example retina are presented in Fig. 2. During the experiment, neuronal responses were recorded from a total number of 44 ganglion cells from this retina. A histogram comparing the overall mean firing rates (across the whole recording period and across all recorded neurons) in response to the 221-s checker-board flickering and three different pieces of movie (each lasted for 192 seconds) is plotted in Fig. 2. In this set of experiments, the intensities of the checker-board flickering were adjusted such that the mean rate of the firing responses evoked by the checker-board flickering was comparable to that elicited by the natural movies (t-test, p values > 0.05, checker-board against movies #1, #2 and #3 respectively).

A. Lifetime sparseness of individual neurons

Response probability distributions of an example cell (channel #40) evoked by the 221-s checker-board flickering and the 192-s natural movie (#1) are shown in Fig. 3 (bin size = 200 ms). The firing probability distribution of the neuronal response in exposure to the natural movie (#1) is with a sharper peak and a longer tail than that to the checker-board flickering. The sparsity is larger for the neuronal response to the natural movie (S_L = 0.7864) than that to the checker-board flickering (S_L = 0.6890).

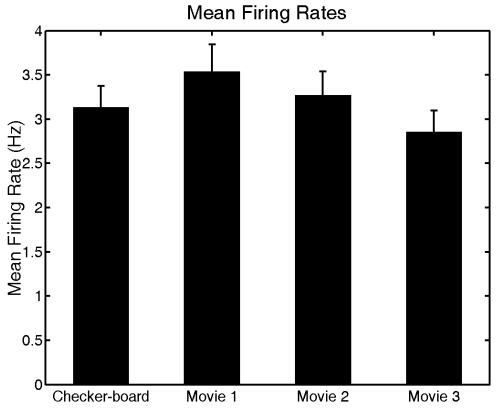

Figure 2. A histogram of the mean firing rates of the 44 neurons in response to the 221-s pseudorandom white-noise checker-board flickering and three different pieces of natural movie (#1, #2 and #3, each lasted for 192 s).

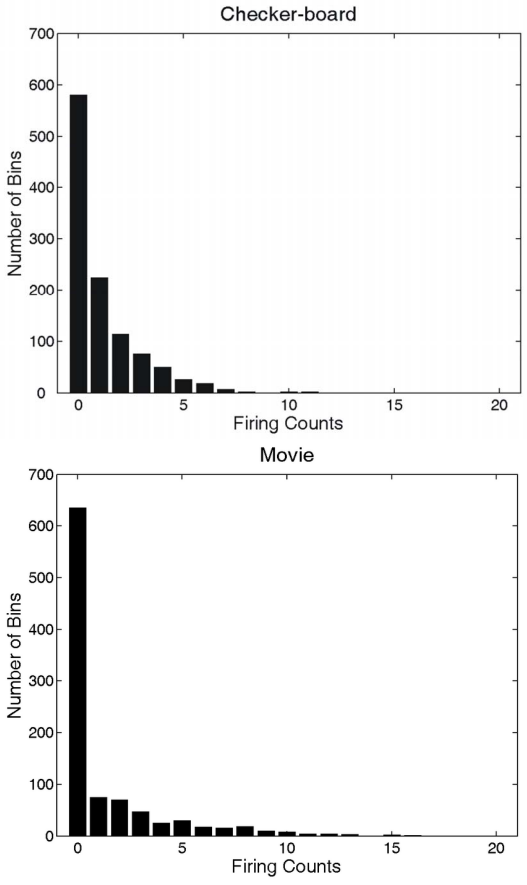

Figure 3. The distribution of the neuronal activity in response to checker-board flickering (top panel) and the natural movie #1 (bottom panel).

The overall results of the lifetime sparseness (S_L) calculated for these 44 RGCs' neuronal activities evoked by the checker-board flickering and movie #1 are shown in Fig. 4 (bin size =

200 ms). Among all the 44 neurons being investigated, each firing sequence (in response to the checker-board flickering and movie #1) has a S_L value greater than 0.5. Furthermore, the statistical results show that the overall S_L values of the group neurons' activities in response to the movie are significantly larger than that to checker-board flickering (paired t-test, p values < 0.05, n = 44).

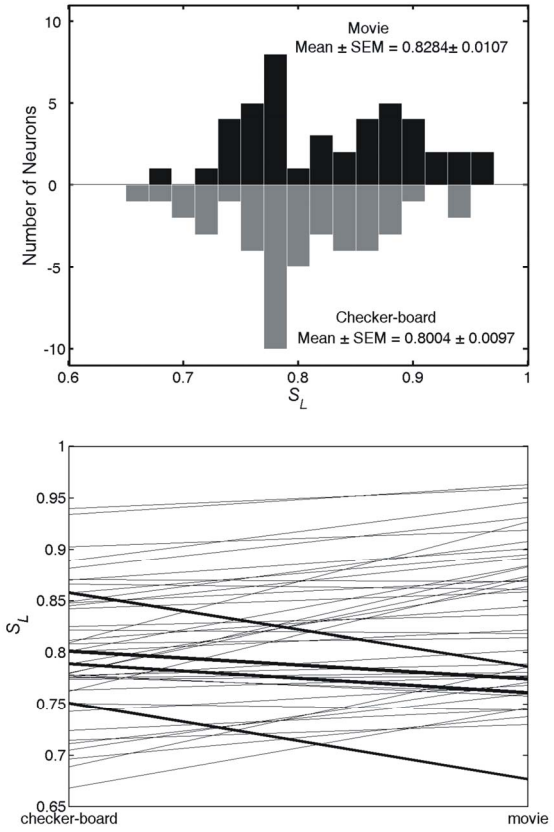

Figure 4. Statistical results for the lifetime sparseness of 44 RGCs' responses elicited by the checker-board flickering and natural movie (#1). The top panel shows the histogram of the 44 RGCs' S_L values in response to the checker-board flickering (gray bars) and the movie (black bars). The bottom panel gives the S_L value changes of each RGC from the checker-board flickering to the movie, with only 4 RGCs' S_L values going downward obviously (thick lines).

B. Population sparseness of the group neuron

Distributions of firing counts of the group of 44 neurons recorded in the example retina during an example 200-ms segment (the 250th time bin, bin size = 200 ms) of the checker-board stimulation and the natural movie (#1) are shown in Fig. 5 (time bin = 200 ms). When the natural movie was applied, the response distribution of the group neurons activities has a longer tail than that during the checker-board flickering. Thus the S_P value of the former (0.8109) is larger than the latter (0.7105).

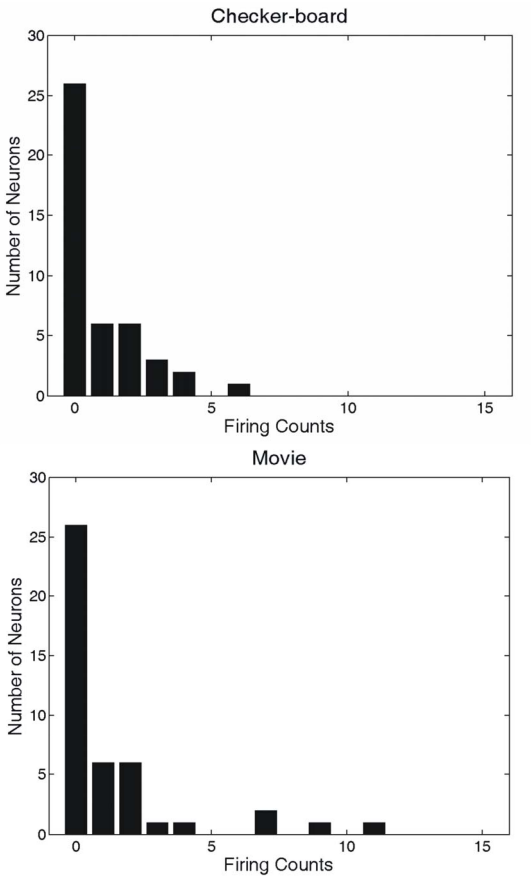

Figure 5. Distributions of the 44 neurons' activities in response to the 200-ms segment checker-board flickering (top panel) and the natural movie (bottom panel).

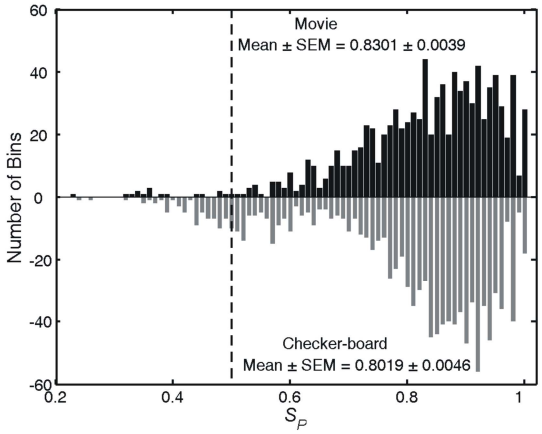

Figure 6. Statistical results for the population sparseness of the population neurons responses elicited by the checker-board flickering and natural movie stimuli. Histogram of the S_P of the group neurons' activities in response to every 200-ms segment of the checker-board flickering (gray bars) and natural movie (black bars).

The overall results of the population sparseness indices calculated for the population neurons (44 neurons) in this piece of chicken retina in response to all stimulation segments (221-s checker-board flickering and 192-s natural movie #1) are

shown in Fig. 6. The results show that 93.3% of the checker-board-response segments and 98.4% of the movie-response segments have S_P values over 0.5. However the intensity of the population sparseness of the neurons' activities during the movie is greater than that during the checker-board flickering (t-test, p values < 0.05).

The temporal and spatial properties of population neurons' responses (S_L and S_P) in exposure to the other two pieces of movie (#2 and #3) are also analyzed and compared to the checker-board evoked activities, similar results are obtained (data not shown).

IV. Discussion

In the present study, the lifetime sparseness and population sparseness of the chicken RGCs' activities in response to natural stimuli and checker-board flickering (control) were quantified using Treves-Rolls sparsity. The results are consistent with our previous work applying the index of kurtosis [14], and suggest that chicken RGCs also use sparse code to represent the natural stimuli and checker-board flickering. However the degree of sparseness during movie-responses is stronger than that during flickering-response while the firing intensities of the RGCs remain comparable in response to both kinds of stimulation.

According to the calculation of the Treves-Rolls sparsity, the tail of the distribution contributes greatly to the value of the index. In the lifetime sparseness, the single neuron's firing distribution with a longer tail gets larger value of S_L, as shown in Fig. 3. While in the population sparseness, when a few neurons within the group fire intensely making a long tail of the response distribution of the group neurons, the index turns out to be more close to 1 like that in Fig. 5. So one possible explanation of the sparse representation of RGCs in response to the natural stimuli is that most of the neurons keep silence most of the time, but once they fire, they tend to fire synchronously to make the information transmission efficient. However, the possible coding details need further research.

Acknowledgment

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