Neural Coding Analysis in Retinal Ganglion Cells using Information Theory

Ferrández J.M.[1,2], Bongard M.[1,3], García de Quirós F. [1], Bolea J.A[1], Fernández E.[1]

[1]Instituto de Bioingeniería, U. Miguel Hernández, Alicante,
[2]Dept. Electrónica y Tecnología de Computadores, Univ. Politécnica de Cartagena,
[3]Dept. Neurobiologie, Univ. Oldenburg, Germany

Corresponding Author: jm.ferrandez@upct.es

Abstract. Information Theory is used for analyzing the neural code of retinal ganglion cells. This approximation may quantify the amount of information transmitted by the whole population, versus single cells. The redundancy inherent in the code may be determined by obtaining the information bits of increasing cells datasets and by analyzing the relation between the joint information compared with the addition the information achieved by aisle cells. The results support the view that redundancy may play a crucial feature in visual information processing.

1. Introduction

Information transmission and information coding in neural systems is one of the most interesting topics in neuroscience, nowadays. As technology grows new neural acquisition tools become available. They permit recording simultaneously tens, even hundreds of cells stimulated under different conditions. This process produces enormous data files, which need new tools for extracting the underlying organization of the neural principles, captured in the recordings.

First of all, it is necessary to determine if there exists an aisle cell coding, or a population coding. An aisle cell fires with limited action potentials, in a restricted interval, so it is difficult to code, numerically speaking, a broad spectrum of stimuli on its parameters. On the other hand a population of cells have more coding capabilities, and it can provide robustness to the representation of the stimuli by using redundancy on the population firing patterns. Adding more cells for coding the same stimuli will produce a fault tolerance system.

There have been published studies about auditory [1] and olfactory coding [2], however understanding visual coding is a more complex task due to and number and characteristics of the visual stimulation parameters, and the difficulty of achieving a filtered population ganglion cells firing pattern database with a considerable number of cells recorded simultaneously. New tools are also required for understanding this vast database. Initially it has been applied statistical analysis, [3][4][5] for obtaining insights about the parameters used in the visual system for coding and transmitting the information to higher centers in the visual hierarchy. Artificial neural networks are also another tool, which can provide, supervised or autoorganizative, new insights about the way visual parameters are encoded and the inherent organization principles. [5][6]

Recent approaches use Information Theory for quantifying the code transmission. It can be used for comparing, also, the aisle cells coding capability versus the population code. It looks at the disorder, entropy, of a system, assuming that a system with more variability (disorder) will be able to transmit more symbols that a system with zero variance. Some studies [8] replace symbols with a list of action potential firing times for analyzing the neural data.

This paper uses information theory for quantifying the information transmitted by single retinal ganglion cells compared with the information conveyed by the whole population. The number of neurons in the datasets is also changed for determining if information grows linearly with number of neurons involved in the coding or it saturates, producing a redundancy phenomenon. Finally the redundancy effect will be observed for assuming if it is consequence of the saturation limit on the information, or if it exists for lower number of cells, aspect that will produce the desired robustness in the code. The results show that information is transmitted by the population code mainly, there exist some saturation on the information provided, determined by the stimuli dataset, and redundancy appears for all numbers of cells involved in the coding.

2. Methods

Registers were obtained on isolated turtle (Trachemy scripta elegans) retinas. The turtle was dark adapted for a few hours, before it was sacrificed and decapitated. Then the head was stored half an hour under 4º Celsius in order to ease the removing of the vitreous. The eye was enucleated and hemisected under dim illumination, and the retina was removed using bubbled Ringer solution taking care to keep intact the outer segment when removing the pigment epithelium. The retina was flatted in an agar plate, and fixed using a Millipore filter with a squared window where the electrodes will be placed. The agar plated with the retina was placed in a beam splitter with the ganglion cell on the upper side and bubbling Ringer solution flowed through the filter.

Light stimulation was applied using a halogen light lamp, selecting the wavelength by means of narrow band pass interference filters. Intensity was fixed by using neutral density filters, and a shutter provides flashes of the stimuli to the preparation. For each stimuli (the wavelength, the intensity, and the spot was varied) seven consecutive flashes, with 250 msec. length, were applied, using a lens to focus the stimulus on the photoreceptor layer of the whole retina.

The Utah microelectrode array was used for obtaining the extracellular recordings (Figure 1). It consists in an array of 100 (10x10); 1.5 mm long niddles with a platinized tip 50 microns long. The distance between each niddle is 400 mm, and the rest of the array is insulated with polyamide for providing biocompatibility. It was mounted on a micromanipulator, and each electrode was connected to a 25000 gain band pass (filtered from 250 to 7500 Hz) differential amplifier. The analog signal was digitized using a multiplexer and an A/D converter and stored in a computer.

The pre-processing consisted of fixing a threshold (based on an estimate of the noise of the electrode) in order to extract the kinetics of electrical activity above this threshold. Spike waveform prototypes were separated by template matching. For each stimulus and for each electrode, the time of the first and second spike, the number of spikes, and the interspike interval during the flash interval was also computed.

3. Information Theory

Information theory had its origins in 1929, Shannon published “The Mathematical Theory of Communication” [10] where thermodynamic entropy was used for computing different aspects about information transmission. Later it was applied for computing the capacity of channels for encoding, transmitting and decoding different messages, regardless of the associated meaning.

Information theory may be used as a tool for quantifying the reliability of the neural code just by analyzing the relationship between stimuli and responses. This approach allows one to answer questions about the relevant parameters that transmit information as well as addressing related issues such as the redundancy, the minimum number of neurons need for coding certain group of stimuli, the efficiency of the code, the maximum information that a given code is able to transmit, and the redundancy degree that exists in the population firing pattern.

In the present work, the population responses of the retina under several repetitions of flashes were discretized into bins where the firing rates from the cells of the population implement a vector **n** of spikes counts, with an observed probability P(**n**). The probability of the occurrence of different stimuli has a known probability P(s). Finally the joint probability distribution is the probability of a global response **n** and a stimulus s, P(s,**n**).

The information provided by the population of neurons about the stimulus is given by:

$$I(t) = \sum_{s \in S} \sum_{n} P(s,n) \log_2 \frac{P(s,n)}{P(s)P(n)} \qquad (1)$$

This information is a function of the length of the bin, *t*, used for digitizing the neuronal ensembles and the number of the stimuli in the dataset P(s).

To study redundancy, first the information transmitted for aisle each cell is calculated. Also the information conveyed by a group if cells, that is, jointly. If neuron were independent the relation between the joint information, and the sum of the information of the aisle cells, which form the group, should be equal to unity. If the joint information related to the sum of aisle cells is greater that one there exists a synergistic code, and finally if the joint information related to the summatory of individual cell information is lower than one, that is the sum of the aisle cells carry more information than the joint population, denotes redundancy.

In this paper, equation (1) was computed to determine the information contained in the firing trains of isolated retinal ganglion cells for 7 different stimuli and this data was compared to the information carried out by the whole population. The information contained in an increasing set of ganglion cells was also computed in order to determine if the information grows linearly with the number of cells or if it saturates at a given value. And finally the relation between the aisle cells information is compared with the joint information for determining the characteristic, independent, synergistic, or redundant of the coding.

4. Results

For both experiments shown on this results, neural activity was recorded in most of the electrodes. The cells were selected by pattern matching algorithms for separating different signal sources. The firing rate vectors were computed and finally the stimulus-response table was constructed for the task of discriminating between seven different light intensities. In Figure 1, the information, in bits, is plotted for single cells in the population versus the whole population. Cells with more variability in their response show a higher information capability. The average information for single cells (dotted line), is much lower than the whole population transmitted information in both cases.

The analysis of the saturation limit is plotted in Figure 2. The information for an increasing cell population is show for increasing cell datasets. If initially, for small groups, information rises linearly with the number of cells, it saturates with groups bigger than certain number of cells for both experiments. This means that adding more new cells to the analysis does not provide more information. The degree to which the rise of information with the number of cells deviates from linearity is related to the redundancy of the code. A redundant representation will provide robustness, or fault tolerance to the system.

Finally Figure 3, shows the relation between the joint information transmitted and the sum of the information for each aisle cell in increasing size groups. It can be seen in booth experiments that the values are below unity, that is the behavior of the coding is not synergistic, neither independent but redundant, providing robustness to the code, and fault tolerance to the system.

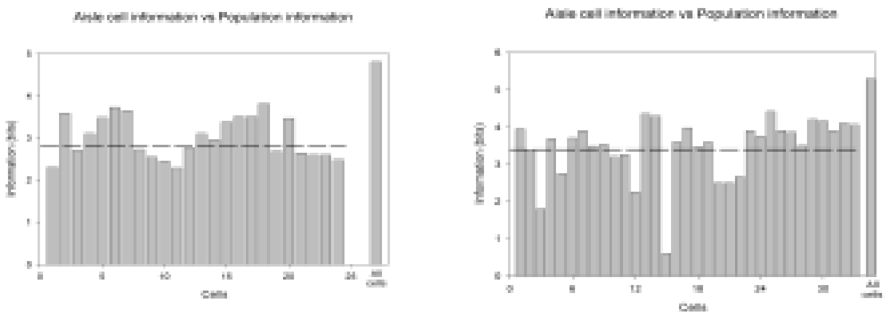

Fig. 1. Single cell coding versus population coding

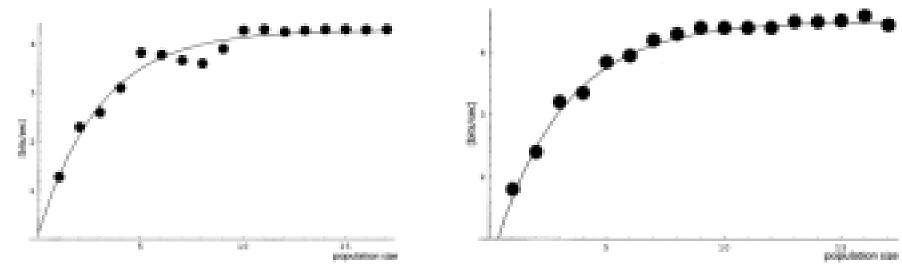

Fig. 2. Information transmitted for an increasing population of retinal ganglion cells in discriminating intensities.

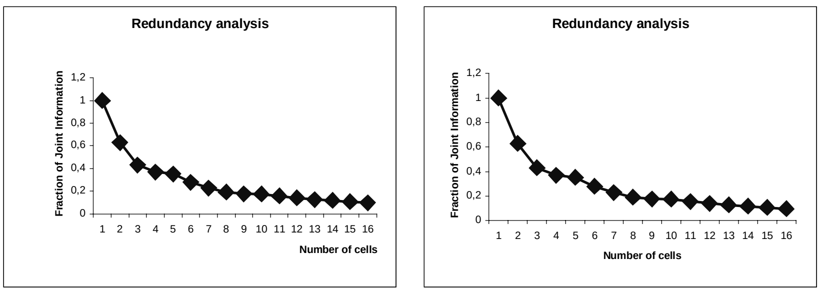

Fig. 3. Redundancy analysis for an increasing population of retinal ganglion cells.

5. Conclusions

Information Theory has been applied for analyzing the neural code of retinal ganglion cells. The information transmitted by the population of cells is always higher than the information contained in the responses of aisle cell, suggesting a population code instead of a single cell code. The overall information registered may vary, it depends on the experiment, number of cells recorded, discriminative character of this cells, location of the multielectrode array, size of the bins, etc., however the overall behavior does not change significantly.

The information on the population grows linearly with number of cells until certain limit, where information saturates. Adding more cells to the set does not provide more information. The redundant characteristic of this scenario has been proved by relating the joint transmitted information versus the addition of the singles cell transmitting rate. Redundancy could be useful to achieve the robustness required for the retina to maintain its performance under adverse environments.

This analysis may be also applied to color coding as well as coding of natural scenarios, where synergistic behaviors may appear. The cooperation between new multichannel acquisition system and innovative analysis tools will provide new insights in neural coding.

Acknowledgements
This research is being funded by E.C. QLK-CT-2001-00279, Fundación Séneca PI-26/00852/FS/01, a grant from the National Organization of the Spanish Blind (ONCE), and Fellowship from the Spanish Ministerio de Educacion to M.B.

References

1 Secker H. and Searle C.: “Time Domain Analysis of Auditory-Nerve Fibers Firing Rates”. J. Acoust. Soc. Am. 88 (3) pp. 1427-1436, 1990.

2 Buck L.B..: “Information Coding in the vertebrate olfactory system”. Ann. Rev. Neurosci. 19, pp. 517-544, 1996.

3 Fitzhugh, R. A.: “A Statistical Analyzer for Optic Nerve Messages”. J. Gen. Physiology 41, pp. 675-692, 1958.

4 Warland D., Reinagel P., Meister M.: “ Decoding Visual Information from a Population of Retinal Ganglion Cells”. J. Neurophysiology 78, pp. 2336-2350, 1997.

5 Fernández E., Ferrández J.M., Ammermüller J., Normann R.A.: “Population Coding in spike trains of simultaneously recorded retinal ganglion cells Information”. Brain Research, 887, pp. 222-229, 2000.

6 Ferrández J.M., Bolea J.A., Ammermüller J. , Normann R.A. , Fernández E.: “A Neural Network Approach for the Analysis of Multineural Recordings in Retinal Ganglion Cells: Towards Population Encoding”. Lecture Notes on Computer Science 1607, pp. 289-298, 1999.

7 Shoham S., Osan R., Ammermuller J. Branner A., Fernández E., Normann R..: “The Classification of the Chromatic, and Intensity Features of Simply Visual Stimuli by a Network of Retinal Ganglion Cells”. Lecture Notes on Computer Science 1607, pp. 44-53, 1999.

8 Rieke F., Warland D., van Steveninck R., Bialek W.: “Spikes: Exploring the Neural Code”. MIT Press. Cambridge, MA, 1997.

9 Jones, K.E., Campbell, P.K. and Normann, R.A.:”A glass/silicon composite intracortical electrode array”. Annals of Biomedical Engineering 20, 423-437 (1992).

10 Shannon C.E..: “A Mathematical Theory of Communication”. Bell Sys Tech J. 27. pp. 379-423 , 1948.