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Research Report

Transmission efficiency in ring, brain inspired neuronal networks. Information and energetic aspects

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A B S T R A C T

Organisms often evolve as compromises, and many of these compromises can be expressed in terms of energy efficiency. Thus, many authors analyze energetic costs processes during information transmission in the brain. In this paper we study information transmission rate per energy used in a class of ring, brain inspired neural networks, which we assume to involve components like excitatory and inhibitory neurons or long-range connections. Choosing model of neuron we followed a probabilistic approach proposed by Levy and Baxter (2002), which contains all essential qualitative mechanisms participating in the transmission process and provides results consistent with physiologically observed values.

Our research shows that all network components, in broad range of conditions, significantly improve the information-energetic efficiency. It turned out that inhibitory neurons can improve the information-energetic transmission efficiency by 50%, while long-range connections can improve the efficiency even by 70%. We also found that the most effective is the network with the smallest size: we observed that two times increase of the size can cause even three times decrease of the information-energetic efficiency.

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1. Introduction

Huge effort has been undertaken recently to understand the nature of neuronal coding, its high efficiency and mechanisms governing it (van Hemmen and Sejnowski, 2006; de Ruyter van Steveninck and Laughlin, 1996; Levin and Miller, 1996; Juusola and French, 1997; Rieke et al., 1997; Salinas and Bentley, 2007; Lánský and Greenwood, 2007; London et al., 2008). To quantify information transmission many authors have concentrated on treating neuronal communication process in the spirit of information theory (Borst and Theunissen, 1999; Levy and Baxter, 2002; Paprocki and Szczepanski, 2011). Important question in this theory is the existence of efficient decoding schemes and this problem constitutes the essence of the fundamental Shannon theorem (1948). This theorem states that it is possible to transmit information through a noisy channel at any rate less than so-called channel capacity with an arbitrarily small

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probability of error. Completely reliable transmission is not possible if the processed information is greater than the channel capacity. Therefore much work is done to analyze capacity of neurons and neuronal networks (Wiener and Richmond, 1999; Kish et al., 2001; Ikeda and Manton, 2009; Kostal, 2010; Paprocki and Szczepanski, 2011, 2012).

On the other hand, in case of biological systems it is known that organisms often evolve as compromises, and many of these compromises can be expressed in terms of energy efficiency (Levy and Baxter, 1996; Berger and Levy, 2010; Sengupta et al., 2010; Cruz-Albrecht et al., 2012; Hu et al., 2012). Thus, many authors analyze energetic costs processes during information transmission in the brain (Tyrcha and Levy, 2004; Hasenstaub et al., 2010; Moujahid et al., 2011; Kostal, 2012).

In this paper we study information transmission rate per energy used in a class of specific ring, brain inspired networks. We assume that these networks are comprised of main brain components, for instance *excitatory* and *inhibitory* neurons or *long-range connections*. Single neurons are the fundamental constituents of all nervous systems. Electrophysiologists, familiar with the notion of ion channels that open and close depending on environmental conditions, generally prefer biophysical models (Jolivet et al., 2008; Gerstner and Naud, 2009). In this paper we consider the neuron model based on the information-theoretical concepts proposed by Levy and Baxter (2002) rather than Hodgkin–Huxley type neuron models. This model contains all essential qualitative mechanisms participating in the transmission process and it provides results consistent with physiologically observed values. Using the high quality entropy estimators (Strong et al., 1998) we determine optimal values of the mutual information between input signals and neurons' responses in terms of energy used for these *brain-like* neuronal architectures.

2. Theoretical concepts

Information theory is concerned with the analysis of an entity called a *communication system*. In general, such system is represented by a source of messages, a communication channel and messages representations expressed in an output alphabet (Shannon, 1948; Ash, 1965; Cover and Thomas, 1991). Recent attempts to quantify information transmission have concentrated on treating neurons already as communication channels (Rieke et al., 1997). From mathematical point of view messages can be understood as trajectories of stochastic processes being in fact sequences of symbols. It is assumed that the set of symbols (alphabet) is finite and the stochastic processes under consideration have stationary distributions (Ash, 1965; Cover and Thomas, 1991).

First we recall basic concepts of information theory that we apply to analyze transmission efficiency (Ash, 1965; Golberg et al., 2009; Paprocki and Szczepanski, 2011). Let Z^L be a set of all blocks (or words) $z^L = z_1 z_2 \cdots z_L \in Z^L$ of length L, built of symbols (letters) from some finite alphabet Z. If $\{Z\}$ is a stationary stochastic process, then each word z^L can be treated as a message sent by this information source. If $P(z^L)$ denotes the probability of generating the word $z^L \in Z^L$, then the Shannon *information* carried by this word is defined as

$$I(z^L) := -\log P(z^L), \tag{1}$$

and since in this paper logarithms to the base 2 are used, this quantity is measured in units of bits. In this sense, less probable events (words to be generated) carry more information. Expected or average information of Z^L, called Shannon *block entropy*, is defined as

$$H(Z^L) := \mathbb{E}(I(Z^L)) = -\sum_{z^L \in Z^L} P(z^L) \log P(z^L), \tag{2}$$

and is also measured in units of bits. The word length L can be chosen arbitrary, so the block entropy does not perfectly describe the process $\{Z\}$. The *entropy rate* (or source entropy) is an invariant quantity characterizing $\{Z\}$

$$H(Z) := \lim_{L\to\infty} \frac{H(Z^L)}{L} \tag{3}$$

and this limit exists if and only if the process is stationary (Cover and Thomas, 1991). We see that entropy rate can be understood as the average information transmitted by source per symbol.

2.1. Mutual information and its estimation

The fundamental concept of Shannon theory is *mutual information*, which quantifies the information dependence of random variables or stochastic processes. If $\{X\}$ and $\{Z\}$ are input (e.g. stimuli) and output (e.g. observed reaction) discrete stochastic processes, then mutual information between them is given as

$$I(X;Z) := H(X) - H(X|Z) = H(X) + H(Z) - H(X,Z), \tag{4}$$

where $H(X|Z)$ is entropy of X conditional on Z and $H(X,Z)$ is joint entropy of X and Z. Mutual information should be understood as a measure of how much information of one process is reflected in the realization of the other one. This quantity shows its importance especially if one process, say Z, is an outcome of some transformation of known process X, i.e. $X \to f(X) = Z$, for example evolution of signal transmitted through neuron. Therefore, in other words, $I(X;Z)$ measures the reduction of uncertainty concerning realization of X having knowledge about the realization of Z. This concept can be complementary (Christen et al., 2006; Haslinger et al., 2010) to cross-correlations analysis since it includes also higher correlations (DeWeese, 1996; Panzeri et al., 1999; Onken et al., 2009). Maximal mutual information, called channel capacity, $C = \sup_{p_X} I(X;Y)$, reflects the upper bound on amount of information that can be communicated over the channel.

Quantitative analysis of mutual information between different input sources and their outcome transformations by neurons is the essence of this paper. However, if the distribution of a stochastic process, say Z, is unknown, no entropy dependent on Z can be determined analytically, hence these component entropies in (4) have to be estimated numerically. Entropy rate estimation is broadly discussed in the literature (Kontoyiannis et al., 1998; Paninski, 2003; Amigo et al., 2004; Kennel et al., 2005; Lesne et al., 2009). In this paper we use the estimator described by Strong et al. (1998) because of its high accuracy and low computational complexity. The method is based on calculating block entropies using observed frequencies of words z^L for some few consecutive