Optimizing information processing in brain-inspired neural networks

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Abstract. The way brain networks maintain high transmission efficiency is believed to be fundamental in understanding brain activity. Brains consisting of more cells render information transmission more reliable and robust to noise. On the other hand, processing information in larger networks requires additional energy. Recent studies suggest that it is complexity, connectivity, and function diversity, rather than just size and the number of neurons, that could favour the evolution of memory, learning, and higher cognition. In this paper, we use Shannon information theory to address transmission efficiency quantitatively. We describe neural networks as communication channels, and then we measure information as mutual information between stimuli and network responses. We employ a probabilistic neuron model based on the approach proposed by Levy and Baxter, which comprises essential qualitative information transfer mechanisms. In this paper, we overview and discuss our previous quantitative results regarding brain-inspired networks, addressing their qualitative consequences in the context of broader literature. It is shown that mutual information is often maximized in a very noisy environment e.g., where only one-third of all input spikes are allowed to pass through noisy synapses and farther into the network. Moreover, we show that inhibitory connections as well as properly displaced long-range connections often significantly improve transmission efficiency. A deep understanding of brain processes in terms of advanced mathematical science plays an important role in the explanation of the nature of brain efficiency. Our results confirm that basic brain components that appear during the evolution process arise to optimise transmission performance.

Key words: neural network, entropy, mutual information, noise, inhibitory neuron.

1. Introduction

Understanding the mechanisms of brain activity remains one of the most elusive but also most important frontiers in science. The brain can solve complex tasks, such as pattern recognition, within milliseconds – much more rapidly than any contemporary computer vision system. Therefore, a huge effort has been undertaken lately to analyse neural coding. Recent attempts to quantify information transmission have concentrated on treating neural communication processes in the spirit of Shannon information theory [1]. The basic concept of this theory is mutual information (MI) between input and output signals [2]. Mutual information plays an essential role in the Shannon fundamental theorem. This theorem states that it is possible to transmit information through a noisy channel at any rate less than the so-called channel capacity (maximal MI) with an arbitrarily small probability of error. Recent interesting analytical results concerning channel capacity in the context of stochastic resonance for noisy threshold devices were presented in [3]. In this paper, the sufficient conditions for the optimality of a parallel array of independently noisy identical threshold nonlinearities – including model neurons in the limit of large array size (i.e., channel capacity) – were derived analytically.

The crucial part in mathematical or computer analysis of brain processes, or more generally neural network learning and information processing, is to develop appropriate models: one for a single neuron, next for a biologically-inspired network

[4–6]. In general, these models should preferably reproduce all of the mechanisms found in biological nerve cells and provide results consistent with experimental physiological data. Several trends in neuron modelling are being developed [7], of which the following two are most common. The first is detailed biophysical modelling, best exemplified by the Hodgkin-Huxley model [8], which describes ion channels on the tree-like spatial structure of a neural cell. The second is a family of so-called integrate-and-fire models, based on treating electrical activity as threshold process. In this paper, we explore yet another approach–namely treating the Levy-Baxter model as a Shannon communication channel [9–11]. This model has an information-theoretical character, and it can be seen as an attempt to grasp biophysical qualitative mechanisms participating in the transmission process in a mathematically rigorous, probabilistic way. The relevance of the presented quantitative results yields an interesting perspective on the future considerations of other models of neurons, such as the biophysical Hodgkin-Huxley model [8], the Izhikevich model [12], and integrate-and-fire models [13].

The human brain consists of more than 10^{11} neurons, in comparison, the Internet – the largest computer network in the world – has only millions of processing units. Artificial neural networks, starting with perceptrons, are designed as general-purpose architectures, whereas natural neural systems show high levels of specialisation according to different tasks and functions. Recently, authors have been looking at the high-level organisation of the brain and biological systems [14–19], including parts for different tasks and different sensory modalities (e.g. sound, vision, touch). Nonetheless, similar organisation and processing [20] has been found at the very local level of connectivity within modules. Moreover, in Ferraz et al. [21],

it was shown that information processing can be optimised in neuronal networks even beyond critical states.

A lot of attention has recently been drawn to the relation between classical thermodynamics and modern information theory. Although the two areas have always been somewhat connected due to the common concept of entropy as their obvious similar figure, it is only now that contemporary research has opened new promising perspectives for them to link up. Interesting examples of thermodynamics and information theory joint uses are more often seen in the field of brain science. For instance, Sengupta et al. [22] derive a relation between minimizing variational free energy and the tendency to maximise both metabolic and statistical efficiency. Poli et al. [23] used partial correlation to identify interconnected neuronal sub-populations and to derive network topology in in vitro cortical networks. By analysing multichannel activity propagation across an engineered axon network, applying pairwise difference analysis of neuronal responses, Chen et al. [24] have shown that neuronal ensembles generally outperformed individual cells in discriminating input patterns. Crago and Makowski [25], by studying action potential patterns with axonal stimulation, pointed out on the role of the relative firing rates of the two sources and the intersite conduction time between them on the firing rate, and the probability distribution of the action potential firing periods in the axonal endpoint. Other authors provided a quantitative theory that predicts brain sizes and quantifies the contributions of temperature-dependent metabolism, body size, and neural density [26, 27].

In our paper, we present quantitative results for both information and information-per-energy efficiency. We discuss these quantitative results, addressing their qualitative consequences. We referred these qualitative implications to the results of other authors. We show how this efficiency depends on the information source (firing rate), neuron parameters (synaptic noise, amplitude fluctuation, activation threshold), and neural architecture (local, inner and long-range connection distributions, size delay effects, inhibition strength). This provides inspired insight into the further analysis of biophysical models of neurons and more advanced neural network architectures [28–30].

2. Theory and models

2.1. Neuron model. Computational threshold neurons are inspired by integrate-and-fire models. The most commonly used artificial cells follow the McCulloch-Pitts approach. Such neurons compute the weighted sum of their inputs and produce responses based on a specific activation function. In this paper, a probabilistic model of a neuron derived from the idea proposed by Levy and Baxter was employed. It turned out that this model provides results consistent with physiologically observed values [31].

Neurons communicate by means of small electric currents, and the information is carried mostly by sudden sharp jumps of these currents, called action potentials or spikes. Assuming that a spike train is being recorded within some time interval, so that in each time slice, a spike is either present or absent, it is natural and justified to represent the spike train as a sequence of bits [32]. Discretisation is one of the most important points of neural communication [33]. Such discretisation allows us to treat both a neuron's stimuli and its response strictly as binary stochastic processes. The input to the neuron analysed in this paper comes from: information source $\{X^{(1)}, \ldots, X^{(n)}\}$, excitatory neurons $\{E^{(1)}, \ldots, E^{(w)}\}$, and a paired inhibitory neuron $\{I\}$. The information source is modelled by discrete binary stationary processes $X^{(i)}$, with the firing rate f_r being the probability of a spike event occurring in a given time slot. Each input signal is then subject to synaptic noise ϕ and amplitude fluctuations Q_i. The synaptic noise ϕ is a Bernoulli zero-one random variable with success probability s. The random variable Q_i is considered continuous and distributed uniformly on interval $[0, 1]$. This means that the output (i.e. bits 0 or 1) from a synapse is multiplied by a randomly chosen number from the interval $[0, 1]$ and this value goes next to the dendrosomatic summation process.

The total excitation of a neuron is expressed as sum $\sigma = \sum_{i=1}^{n} X^{(i)}\phi Q_i + \sum_{i=1}^{w} E^{(i)}\phi Q_i - bI\phi Q_I$. This combined signal σ finally undergoes the spike generator transformation so that the neuron responds with a spike if the magnitude of its excitation exceeds the assumed threshold g. Denoting the resulting spike as 1 and the lack of a spike as 0, the sequence of consecutive neuron responses constitutes an implicit stochastic binary process $\{Z\}$.

To summarise, the basic neuron parameters in the Levy-Baxter model are synaptic noise s, amplitude fluctuation Q_i, and activation threshold height g. An overview of the information flow in the discussed model is pictured in Fig. 1.

2.2. Brain-inspired networks. In general, the brain can be regarded as an ensemble of individual cells, interconnected in such a way that the output of one neuron becomes the input to some of the others. The brain-inspired network we propose consists of nodes, each of them being a pair (E, I) of excitatory and corresponding inhibitory neurons. These nodes are allocated uniformly over the circle of radius r. In this case, each node processes information under completely the same circumstances and we have a clear symmetric network. Therefore, as a reference network, we propose already such network. As such reference networks, we propose a network without long-range connections or a network with full long-range connections. Each node $(E, I)_i$ is connected with neighbouring nodes $(E, I)_{i-1}$ and $(E, I)_{i+1}$ through the output of excitatory neurons. Additionally, distant (i.e. not neighbouring) nodes can be connected through long-range connections. For each single node, the strength of the inhibitory neuron in relation to the strength of the corresponding excitatory one is denoted by $b = I/E$. It is assumed that source signals can support excitatory neurons only. The output of one neuron within a given node becomes the input to the other one in the next discrete moment. Excitatory connections outnumber inhibitory ones by at least 5:1 [34]. While the proposed neural network is quite simplified and far from the real brain, it gives inspired intuition for further research in this direction.

After fixing the reference network we consider a complementary architectures (Fig. 3A; all networks in [11], see Fig. 3).

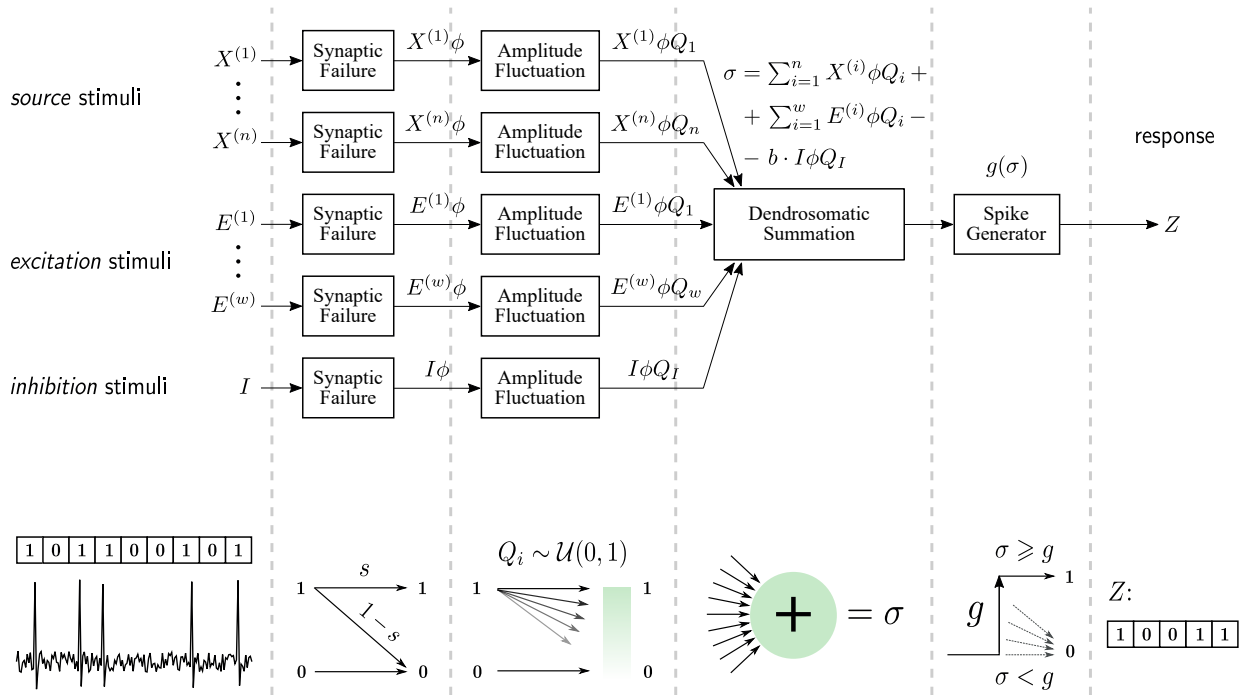*Optimizing information processing in brain-inspired neural networks*

Fig. 1. The neuron model studied in this paper is based on the Levy-Baxter approach

The efficiency of these networks was examined both qualitatively and quantitatively. We analyzed the information processing in the network architecture A with added long-range connection with the origin in an excitatory neuron and target neurons being both a not neighbor excitatory neuron and associated with it inhibitory neuron. In this architecture we assume that the excitatory neuron has connection to the source of information (e.g. stimuli). Next, we analyzed the network architecture B also with added the long-range connection with the origin in an excitatory neuron and target neurons being both a not neighbor excitatory neuron and associated with it inhibitory neuron. However, in this architecture we assume that the excitatory neuron has no connection to the source of information. Next, we compared the information (MI) transmitted in the architectures A and B to the information transmitted by the corresponding neurons located in the symmetric architecture. This way we have opportunity to verify how the adding of the long-range connection affects the information being transmitted.

2.3. Mutual information analysis and energetic formulae. Mutual information is one of the key concepts of Shannon's famous communication theory, published in 1948. The MI between two stochastic processes $\{X\}$ and $\{Z\}$ reads

$$I(X; Z) = H(X) - H(X|Z) = \\ = H(X) + H(Z) - H(X, Z), \qquad (1)$$

where $H(X|Z)$ is the entropy of X conditional on Z, and $H(X, Z)$ is the 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 realisation of the other one. This quantity shows its importance especially if one process

(say Z) is an outcome of some transformation of the known process X (i.e. $X \mapsto to f(X) = Z$); e.g., the evolution of the signal transmitted through a neuron. The MI concept can be complementary both to cross-correlation analysis (since it also includes higher correlations [35, 36]) and to the Fisher information approach [37]. Particular entropies in (1) have to be estimated numerically. There are a number of high quality estimators; e.g., [38–42]. We applied the one proposed by Strong et al. [38] which is not computationally expansive. To assure high accuracy of estimation, we applied this entropy estimator to sequences of 1,000,000 bits. Our extensive simulations of Bernoulli and Markov processes have shown that the error between true entropy and the estimated value is on the order of 0.001, and the standard deviation was also on the order of 0.001. We first present an analysis of the MI between the input and output signal for simplified neural architectures [9]. However, biological systems rely mostly on economic energy management; therefore, energetic expenses of information transmission should also be taken into account during optimisation [26]. On the other hand, it is known [43, 44] that the signalling-related energy consumption increases linearly with the spiking frequency. Thus, in this approach, the following information-energetic formula can be considered as a measure of information-energetic efficiency:

$$\Lambda(b) = \max_g \left(\frac{\max_{(f_r, s)} I(f_r, s, b, g)}{\vartheta(f_r^0, s^0)} \right), \qquad (2)$$

where the energy formula $\vartheta(f_r, s)$ is equal to: $s \cdot (n f_r + b f_I + \sum_w f_w)$ for excitatory neurons with access to the source of stimuli, $s \cdot (b f_I + \sum_w f_w)$ for excitatory neurons without access to the source, and $s \cdot \sum_w f_w$ for inhibitory neurons; s^0, f_r^0 are

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the values maximising the numerator. The numerator of the formulae corresponds to the capacity of the channel, while the denominator expresses the energy cost of the transmission and is proportional to the number of spikes actually used to transfer information. The role of inhibitors, long-range connections and size/delay effects are studied and information-energetic optimal parameters are determined.

3. Results

3.1. Feed-forward networks results. For better insight, we start by presenting the results for one-layer feed-forward networks. We show how the following quantities affect the trans-

mission abilities of the networks: synaptic noise, the height of activation threshold, the firing rate, and the type of input source. A number of surprising, non-intuitive effects were observed.

We begin with a synaptic noise analysis. One would intuitively expect the transmission to be less effective if this information-losing factor is present. However, we found that high synaptic noise maximises mutual information for model neurons with a relatively low activation threshold. It turned out that MI is maximised in a very noisy environment where less than half of the already-generated spikes (or even only one-third of their total number) are allowed two passes through synapses further to the network. Moreover, the value of this maximum (in fact efficiency) can be more than two times greater than that achieved in noise-free conditions (i.e., if $s = 1$) Fig. 2A.
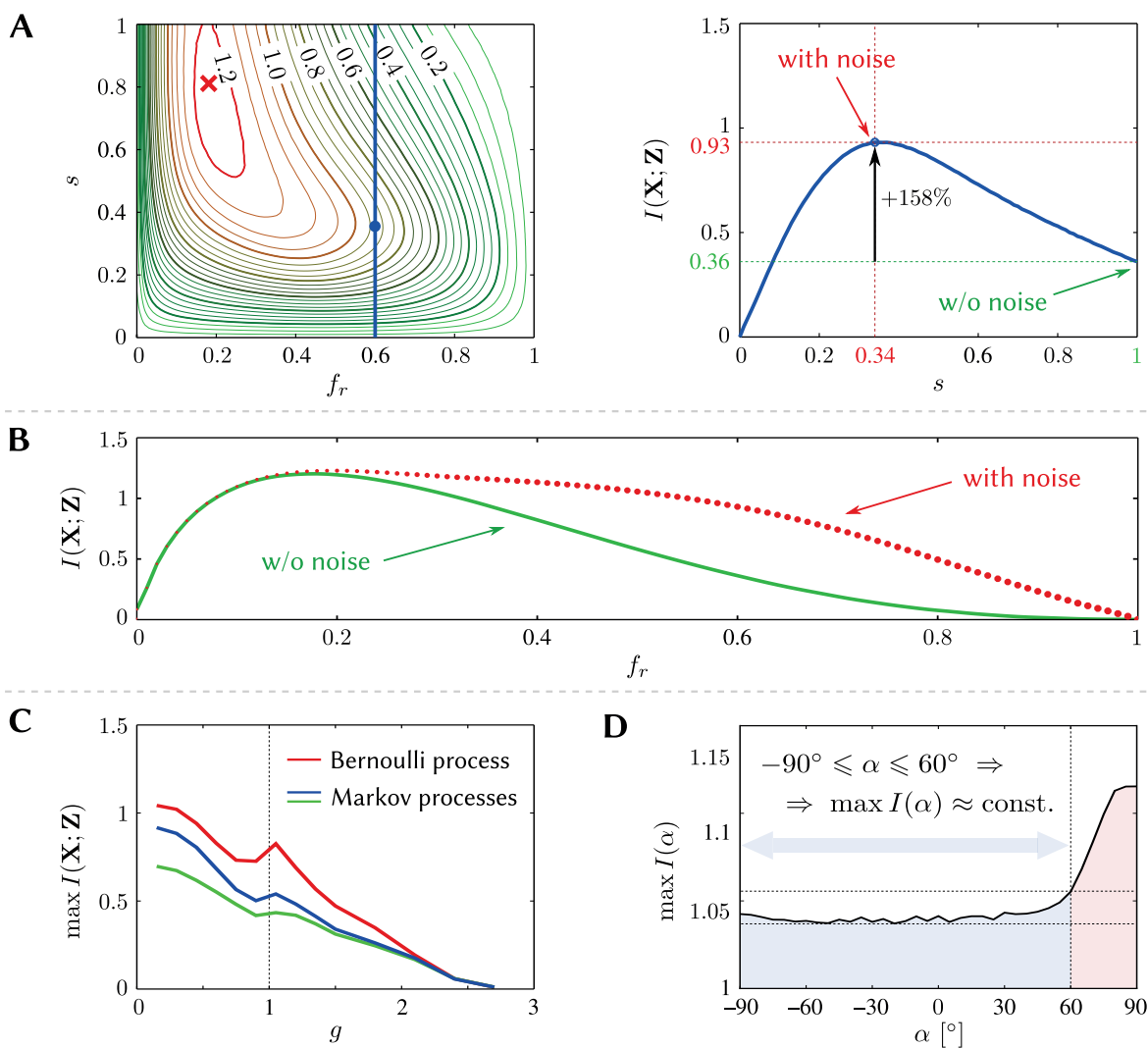

Fig. 2. The influence of a neuron and neural network on transmission efficiency, measured as mutual information (MI). **A)** MI dependence on synaptic success s in a feed-forward network consisting of 5 neurons with the threshold set to $g = 0.25$. Analogous results were presented in [9] for $g = 0.30$. The cross-section (marked by the blue line) for $f_r = 0.6$ is presented in the right panel. This cross-section was chosen to illustrate that maximal information transmission can be reached in a very noisy synapse (i.e. the probability s that spike will be transmitted is less than 0.4). **B)** Comparison [9] of maximal MI values (red dotted line) with those achieved as $s = 1$ (green solid line). Size of a dot is proportional to $1 - s$ (noise), indicating that the bigger the dot, the corresponding mutual information value is achieved at a lower s. **C)** MI dependencies on threshold g for Bernoulli source (red solid line) Markov (green and blue solid line). **D)** MI as a function of the strength of amplitude fluctuation maximized over all other parameters (f_r, s and g) – see Section 3.1 and 3.2 for details

We observed non-zero synaptic noise ($s < 1$) in all ranges of parameters that globally maximise *MI*. The important role in the justification of this benefit of noise could be the stochastic resonance effect, which is a form of noise-enhanced signal transmission in a wide variety of nonlinear physical and biological systems [3].

The threshold is a neural mechanism that prevents weak signals (in the sense of their cumulated amplitude) from being passed down through an axon to other neurons. Since only signals strong enough to exceed the barrier are able to make a neuron fire, intuition suggests that the maximal amount of information transmitted within a given neural structure falls as the value of the threshold grows. However, our calculations show that transmission efficiency turns out to be a non-monotonic function of the activation threshold. For comparison, we consider two types of processes as information sources. We consider Bernoulli processes and two-state Markov processes. In turn, in the case of Markov sources, we studied two cases. In the first case the conditional probability that, after spikes, there will be no spike, is equal to 0.1 and in the second case it is 0.05. Presence of spike corresponds to "1" in bits' sequence. We observed a universal value of the threshold for which MI has a local maximum (Fig. 2C). This value is achieved for most of the model neural architectures, regardless of the type of information source (correlated and non-correlated) [45].

The study of feed-forward networks was finalised with an analysis of the influence of signal amplitude fluctuations (damping, uniform, amplifying); another important component in neural computations [31]. It was found in [10] that the more amplifying the fluctuations are, the more beneficial to transmission efficiency the synaptic noise becomes. Furthermore, it turned out that maximal efficiency remains nearly constant, almost regardless of the fluctuation type. The efficiency stays at the same level for all networks, except these with strong amplifying fluctuations, for which transmission is slightly more efficient (Fig. 2D). Finally, it was exposed that for a wide range of thresholds, both for damping and amplifying fluctuations, the MI behaves in the opposite way to the corresponding correlations between input and output signals. Moreover, it was shown in [46, 47] that the role of mutual information in the Shannon fundamental theorem, describing the limits of optimal decoding schemes, can not be replaced by straightforward correlations.

3.2. Brain-inspired networks results. The results obtained for simple feed-forward networks form an adequate introduction to the analysis of more complex neural communication systems. The information transmission rate per energy used (2) in a class of brain-inspired networks (Fig. 3A) involving components such as excitatory and inhibitory neurons or long-range connections was studied by [11]. It was shown that all network components in a broad range of parameters significantly improve the information-energetic efficiency.

It turned out that the presence of inhibitory neurons (i.e. if $b > 0$); can improve information-energetic transmission efficiency by 50 percent in comparison to networks lacking inhibitory connections (if $b = 0$); Fig. 3B. Transmission is most information-energetic effective if the inhibitory-excitatory strength ratio is below 0.5.

It was found (Fig. 3C) that long-range connections can lead to a significant improvement in target neurons' information-energetic efficiency, even by 70 percent, if the neuron starting this connection has no access to the source of stimuli (Fig. 3C right). If the connection originates from a neuron that has such access, it can bring a 40 percent loss to the target neuron's efficiency (Fig. C left), however this connection increases the efficiencies of the starting neuron and the neurons neighbouring the target neuron by up to 24 percent.

It was established (Fig. 3D) that the most effective network is the one with the smallest size r (the most compact one): we observed that a twofold increase in the size can cause even a threefold decrease of information-energetic efficiency [11].

4. Discussion and conclusions

Evaluation of the efficiency of information transfer in biological systems–in particular in the human brain–requires calculation of both the amount of information transmitted and the energy cost used in that process. This justifies the information-energetic transmission (2) that we proposed and then optimised in this paper. A mathematical framework that provides tools for the quantification of information content and its transfer is information theory [2]. The estimation of energy required to maintain the signalling activity of neurons is subject of interest for many authors in many contexts [26, 48-51]. It was shown that the signalling-related energy consumption increases linearly with the average spiking frequency [51]. Moreover, recently for the characterisation of connectivity effectiveness within neurons population transfer entropy, which quantifies the information transferred between variables in terms of strength, time scale, and direction, was applied [52]. General questions arise: how do neurons and neural networks adapt to make the transmission more efficient? In particular, the role of synaptic noise, the activation threshold, and the amplitude fluctuations for a single neuron are of special interest. The efficiency should strongly depend on how neurons cooperate in the transmission process. The question is in fact about the essence of the role of long-range connections and the balance between excitatory and inhibitory neurons in the network architecture.

Noise is an inherent ingredient of biological systems [13, 53]. Zhang et al. [54] showed that even in a homogeneous neural network, noise can produce a variety of complicated dynamic spiking phenomena. Recent results indicate that synaptic noise may be beneficial [55, 56]. Kanitscheider et al. [57] have found that it is possible to improve the efficiency of the code by optimising the tuning and noise correlations. Axonal and synaptic failure suppress the transfer of firing rate oscillations, synchrony and information during high-frequency deep brain stimulation [13]. It turned out that axonal variability may have a considerable impact on synaptic response variability. It was shown in [58] that action potential height and width
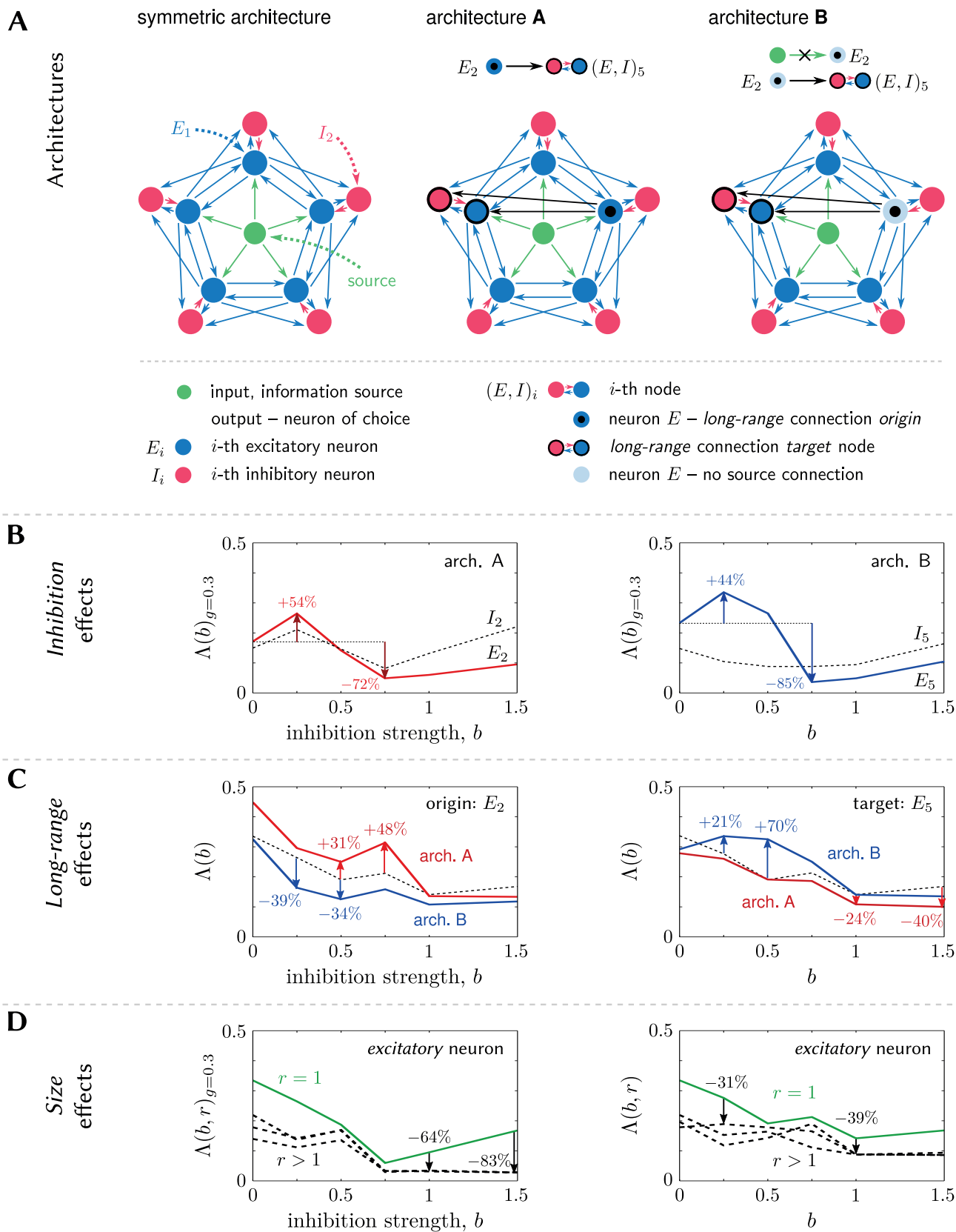
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Fig. 3. Brain-inspired network model; note that on the scheme, the position of the input source in the centre is only figurative. We consider four five-node architectures, each powered with a three-dimensional source of information, drawn in the centre of each diagram. **A)** Information-energetic characteristic across chosen brain-inspired architectures. **B)** Inhibition effects. **C)** Long-range connection effects for origin and target neurons. **D)** Size effects for fixed threshold g and globally – see Section 3 and [11] for details

variabilities increase with a 3/4 power-law as the diameter decreases and translates these fluctuations into post-synaptic response variability. Malyshev et al. [59] presented that neural networks can combine high sensitivity to perturbations and operation in a low-noise regime. Moreover, certain patterns of ongoing activity favour this combination and energy-efficient computations. The interaction of two of the most common plasticity mechanisms – intrinsic and synaptic plasticity – was studied in [55]. It turned out that this interaction leads to representations that allow spatiotemporal computations. It was also pointed out that these representations are structured to tolerate noise and to even benefit from it. The authors suggest noise as a possible mechanism for avoiding ineffective dynamics. The information-theoretic approach was also used to characterise learning phenomena in the presence of noise [60]. In [3], the authors address the effect of suprathreshold stochastic resonance in the process of signal transmission in a parallel array of independently noisy identical threshold nonlinearities, including model neurons. It turned out that capacity is achieved when the signal distribution is the Jeffreys prior (as formed from the noise distribution) or when the noise distribution depends on the signal distribution via a cosine relationship. In our considerations, noise is included in synapses and in amplitude fluctuations. Our quantitative research demonstrates that even significant synaptic noise can play a very positive role, as it can lead even to a twofold increase of the information transmission efficiency. Moreover, the more amplifying the amplitude fluctuation mechanism is, the more positive is the role of synaptic noise in efficient information transmission.

The crucial role in neural information transfer is played by excitatory neurons, while inhibitory neurons play an auxiliary role [61–63]. Many authors examine this mechanism in terms of excitation and inhibition balance [64–66]. Researchers agree that inhibitory neurons play a positive role in brain activity, which corresponds to the results presented in our paper. Dehghani et al. [67] have found experimentally in human and monkey neocortexes that in all states of the wake-sleep cycle, excitatory and inhibitory neuron ensembles are well balanced, and co-fluctuate with slight instantaneous deviations from perfect balance, mostly in slow-wave sleep. Analysis of inhibitory interneurons and their circuits suggest [68] a possible revision of the dominant view that neurons represent information with firing rates corrupted by Poisson noise. Instead, the tight excitatory/inhibitory balance may be a sign of a highly cooperative code, orders of magnitude more precise than a Poisson rate code. The relationship between network inhibition and the scaling of the power spectral density exponent of avalanche activity in a neuronal network model was studied in [69]. It turned out that this scaling exponent depends on the percentage of inhibitory synapses. The results indicated that the level of inhibition affects the frequency spectrum of resting brain activity and suggests an analysis of the power spectral density scaling behaviour as a possible tool to study pathological conditions. We observed that inhibitors can strengthen the effectiveness of transmission by up to 50 percent.

A full description of brain networks (and evaluation of their efficiency) requires detailed characterisation of their architectures. Not only the placement of neurons is important, but also the distribution of specific connections, including long-range connections and linkage with the information source [70]. While many authors describe the significance of connections [71], relatively little attention is paid to their–and networks overall–topology [72]. It was shown in [73] that long-range interaction in Hindmarsh-Rose neural networks can induce different features of information transmission among coupled neurons, pictured by complex waves, zigzag fronts and quasi-periodic structures. It turned out that these features depend strongly on the specific range parameter. Memories are acquired and encoded within large-scale neuronal networks spanning different brain areas. It was demonstrated in [74] that, although intermingled locally, long-range connectivity defines distinct subpopulations of amygdala projection neurons and indicates that the formation of long-term extinction memories depends on the balance of activity between two defined amygdala-prefrontal pathways. Long-range projections from the frontal cortex are known to modulate sensory processing in multiple modalities. In [75], virus-assisted circuit mapping was used to identify the brain networks for top-down modulation of visual, somatosensory and auditory processing. The approach, based on information theory [9], produced results consistent with other researchers' findings, proving the positive effects of long-range connections. It turned out that when it comes to connectivity, the key role in information transmission efficiency is played by the position of the starting and target neurons of a given connection. It was observed that long-range connection improves the efficiency of the network, provided that the neuron starting the connection is not stimulated directly by the information source.

Recent research suggests that organisms evolve in such a way that entails improvement of the neural information-energetic transmission efficiency [76]. Moreover, if one compares the measures of mutual information and the corresponding correlations, the results support the argument that neural coding is much more subtle than the straightforward link between input and output, i.e. efficient neural transmission does not necessary coincide with high input-output correlation.

Nevertheless, the question of what is optimised during information transmission in the brain still remains open. The hypothesis that organisms evolve to optimise the transmission in terms of energy efficiency seems promising. The results presented in this paper give inspired insight for further research in this direction, applying other models of neurons, such as the biophysical Hodgkin–Huxley model, the Izhikevich model, or integrate-and-fire models, and more advanced neural networks.

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