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Development of the deterministic and stochastic Markovian model of a dendritic neuron

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ABSTRACT

In this study, we propose a model of the dendritic structure of the neuron (referred to as a neural network – NN), which can be viewed as an extension of the models that are currently used in the description of the potential on the neuron's membrane. The proposed extensions augment the generic model and offer a fuller description of the neuron's nature. The common assumption being used in most of the previous models stating a single channel (forming component of the neuron's membrane) can be positioned in only one of the two states (permissive – open and non-permissive – closed), is now relaxed by allowing the channel to be positioned in more states (five or eight states). The relationship between these states is expressed in terms of Markov kinetic schemes. In the paper, we demonstrate that the new approach is more suitable for a larger number of applications than the conventional Hodgkin–Huxley model.

The study, by providing the mathematical background of the new extended model, forms a significant step towards a hardware implementation of the biologically realistic neural network (NN) of this type. To reduce the number of components required in such implementation, we propose a new optimization technique that significantly reduces the computational complexity of a single neuron.

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1. Introduction

The developments of the model of the biological neuron have been witnessed since 1950s, when the first model of the potential of the membrane of the neural cell has been developed by Alan L. Hodgkin and Andrew Huxley. During the past years many efforts have been undertaken to generalize or to simplify this model, see [5,14,17,24,26,27], however the Hodgkin–Huxley model still remains the basis for the most of these modifications.

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Let us recall, that the Hodgkin-Huxley model is described inthe following form

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$$C\frac{dV}{dt} = I - g_{Na}m^{3}h(V - V_{Na}) + g_{K}n^{4}(V - V_{K}) + g_{L}(V - V_{L})$$
(1)

$$\frac{dn}{dt} = \alpha_n(\mathbf{V}) \cdot (1-n) - \beta_n(\mathbf{V}) \cdot n$$

$$\frac{dm}{dt} = \alpha_m(\mathbf{V}) \cdot (1-m) - \beta_m(\mathbf{V}) \cdot m$$

$$\frac{dh}{dt} = \alpha_h(\mathbf{V}) \cdot (1-h) - \beta_h(\mathbf{V}) \cdot h$$
(2)

3ł (1) describes the dynamics of the potential V of the cell's 34 membrane, where I is an external current, and C is the 35 membrane capacitance. The parameters g_{Na} , g_K , g_L and V_{Na} , V_K , V_{t} denote conductivities and reversal potentials of the ions, 36 respectively, where Na stands for sodium, K – for potassium 37 and L for chloride type of ions. Parameters n, m, and h are called 38 'gating variables', they range from 0 to 1, and equations for 39 their derivatives describe the process of movement of ions 40 41 through the membrane. The Hodgkin–Huxley model assumes 42 that the membrane is built from channels, that are composed 43 from gates, which control the movement of certain types of 44 ions through the membrane. The set of Eq. (2) describes probabilities of transfer of these ions. Each gate can be in one of 45 46 two states, namely a permissive or non-permissive one. The 47 component $\alpha_k(V) \cdot (1-k)$ standing in (2) refers to the transition from non-permissive to permissive state, while a part $\beta_k(V) \cdot k -$ 48 49 from permissive to non-permissive state, where α and β are the rate functions that refer to the probabilities of transfer 50 51 between states.

52 In most models, it is assumed that the potential is equal in each point of the neuron's membrane [2,17,26]. Hodgkin and 53 Huxley have proposed a model described by (1) and (2) [2,17], 54 which in the consecutive years was the subject of the 55 56 optimization realized in different ways. For example, FitzHugh 57 and Nagumo have proposed a simplification of the original 58 model [17]. In this work, four equations of the form (1) and (2) 59 have been replaced with two equations describing the dynamics 60 of the potential as well as the dynamics of the current that flows 61 through the membrane. The model with two equations has been presented also in [23]. Another simplification has been 62 proposed in [25], where the model with four variables has been 63 reduced to a single-variable threshold model. 64

In some previous studies the purpose was to arrive at a 65 more comprehensive model to offer a realistic description of 66 67 the potential on the neuron's membrane, resulting in more complex equations [4,27]. From the implementation point of 68 69 view, the extensions proposed in [4,27] have a negative 70 influence on both the software and the hardware implementations. On the other hand, these models make the description 71 72 of processes that take place in the neuron, more accurate, thus 73 increasing the area of its potential applications in areas that more accurate models are required. Furthermore lower 74 75 computational complexity of proposed model may enable 76 the use of it in areas where more accurate models are too 77 complex.

Another modification of the Hodgkin–Huxley model
assumes the introduction of stochasticity [5,16,29]. The
simplest way to realize this is either by adding some random
fluctuations to the main equation of the model [35] or to the

remaining three equations, which describe the movement of ions through the membrane [16]. Different possibility is to consider that the ion channels can be in more than only two states, which are described on the basis of the kinetic Markov schemes [29]. The neuron's membrane is built from channels, which are built from small gates. These gates control the movement of ions through the membrane. In the classic approach it is assumed that each ion channel can be only in one of the two states, permissive (open) and non-permissive one (close) [19]. It is possible to consider a simple model, described by Eq. (1), but with the assumption that each gate can be in more than only two states, where one is permissive and the remaining ones are non-permissive. 82

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In Eq. (1) term n^4 show that exactly four gates must be permissive so the potassium channel is opened [29]. Similarly term m^3h indicates that there need to be three 'm-gates' and one 'h-gate' so the sodium channel is opened [29]. We can then consider different configuration of opened and closed gates with use of Markov kinetic schemes where states represent number of opened gates and thus give the information whether the channel is permissive or non-permissive [7].

It is worth noting that the real neuron does not exhibit a point-like structure. In the simple models described above it was commonly assumed that the potential is equal across the entire cell. In the next generation models, it is assumed that the neuron has a dendritic structure, in which each point of it can have different potential. In this paper we will commonly use phrase neural networks (NN) for tree-like structure of the neuron and neuron to the point-like structure. Such models described, for example, in [2,17] are called compartmental models.

One of the extensions, proposed already by Hodgkin and Huxley in [20], also assumes that the neuron has a dendritic structure. In this approach, a derivative of the potential expressed in the space has been added to the main equation of the model [20]:

$$\frac{a}{2R}\frac{\partial^2 V}{\partial x^2} = C\frac{\partial V}{\partial t} + g_{Na}m^3h(V-V_{Na}) + g_Kn^4(V-V_K) + g_L(V-V_L), \quad (3)$$

while the three other equations retain the same form as before, see (2), where we consider partial derivatives $\partial n/\partial t \partial m/\partial t \partial h/\partial t$, as the variables *n*, *m* and *h*, are the functions of time and space.

There exists also a simple extension of this model, in which the noise is added to the main equation of the original model proposed by Hodgkin and Huxley given by (3). The results are presented in [21,22]. The addition of the noise to the main equation of Hodgkin–Huxley model (1) or (3) or even to Eq. (2) enables to observe different behaviours of the potential on the membrane (i.e. moments of hyperpolarization and depolarization [27]).

In this paper, we propose a new model of the NN that augments the original model given by (3) and (2). In the comparison with the approach presented in [8] this new model is more complex, but simultaneously enhances a modelling flexibility. In the proposed approach we replace Eq. (2) with differential equations obtained from the Markov kinetic schemes of certain sizes. More specifically, as discussed in [15,29], we consider a scheme with five states for potassium channels and eight states for sodium channels.

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