

Numerical Simulation of Dynamic Synapse-Dendrite-Soma Neuronal Processes

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Abstract. The nonlinearities play a crucial role in the brain processes. They take place in neuronal system elements: synapses, dendrite membranes, soma of neurons, axons. It is established that the soma nonlinearity, which is of sigmoidal shape, is not so strong as compared with the electric current-voltage relation of a dendrite membrane. The relation is N -shaped with two stable and one unstable points. In dynamics, this leads to the appearance of a switch wave or formation of some logic functions. We present some artificial logic circuits based on an electrical analogy of dendritic membrane characteristics in static and dynamic cases. The nonlinear cable theory and the numerical simulation were used. Basing on the logic circuit construction proposed, we suppose that the dendritic membrane processes are able not only to gather and transfer information but also to transform and classify knowledge.

The theoretical substantiation and numerical experiments are only the first step forward to the proving of neuronal dendritic logic constructions. Of course, extensive neurophysiological tests are necessary to discover the final mechanism of neuronal computing in the human brain.

Key words: neuronal computing, dendritic logic circuit, nonlinearity, cable theory.

1. Introduction

It is well known that the chief function of dendrites in a common neurophysiological chain of synapse-dendrite-soma of a complex neuron is information-gathering. Numerous investigators have used the cable theory for explanation of neuronal dendrites. Some important works in this field have been conducted by Hodgkin and Huxley (1939); Hodgkin and Katz (1949); Rall (1962; 1964; 1967; 1978; 1989); Jack and Redman (1971); Jack *et al.*, (1975); Rall and Shepherd (1968); Rinzel and Rall (1974); Koch *et al.* (1983); Rall and Segev (1987). They considered many different extra complex operations: transferring of information, adaptation to a long-lasting current stimulus, coding information by varying frequencies, repetitive activity in excitable membranes, and transformation signals.

Some theoretical and practical works (Jack *et al.*, 1975; Rall, 1960; Lux and Schubert, 1975; Llinas and Sugimory, 1980; Schwindt and Crill, 1977; Lux *et al.*, 1970; Gutman, 1984; Garliauskas *et al.*, 1991, 1992a, 1992b; Garliauskas, 1994) have proved that a current-voltage relation of a dendrite membrane is not only nonlinear, but also has the N -shaped form with two stable points. The first point occurs at the rest potential state

passing to the hyperpolarization area and the second – in the depolarization area. Special conditions of dendrite threshold action are created by a jump-like transit of a dendrite membrane potential from one stable point to the other. Based upon a conditional mathematical logic has been applied to the case of a simple dendritic branch in a narrow zone of stability (Garliauskas *et al.*, 1991; 1992a; 1992b). Below we will provide the mathematical and numerical treatments of these ideas.

The general mathematical model of neuron activity relying on ideas above fuzzy logic were presented by Gupta (1989, 1992). Some ideas of a neuronal approach are presented by Garliauskas (1994). The origin of the fuzzy signals lies in complex biochemical and electrical processes of the synapse and the dendrite membrane that can be classified into two groups: the first group is associated with the impact of mediators when transferring the potassium, sodium, and chlorine ions in the synapse and the dendrite membrane in the cases of excitation, inhibition, and silent inhibition; the second group is connected with a nonlinear or bistable mathematical representation of electrical processes causing the formation of higher order fuzzy sets.

To explain the functional possibilities of the dendrite, the concrete question has arisen. Does a dendrite fulfill similar operations as the soma: summation, aggregation, logic transform, and classification? If so, what are the somatic operations for? If not, why do such complex nonlinear characteristics of the dendrite exist? We try to answer the second question using knowledge of neurophysiology, nonlinear cable theory of neuronal dendrite by analogy with a simplified neuronal logic and classification functions.

It needs to emphasize that neuronal soma performs complex work on a molecular level. Brown's machine for replication of DNA and Conrad's enzymatic neuron (Conrad, 1985) model this complexity. The natural neuron has some stable states which transform very easily, can change the molecular structure, and has a key-lock like features for recognition of enzymatic molecular components in the environment. The number of existing problems in the soma tells us about its supercomplexity.

Thus, we will try to generalize a consideration of the biological neuronal morphology particularly to the dendrite in a complex neuron.

2. Nonlinear Dendritic Membrane Functions and their Mathematical Description

2.1. Nonlinearities in Synapse-Dendrite-Soma Chain

It is important to emphasize a nonlinearity among many phenomena of brain function. We consider it in the chain of synapse-dendrite-soma. As a rule, in most issues of neurocomputing science, a linear relation between the current and a change of potential in a postsynaptic receptor (Ohm's law) has been used. However, novel studies have confirmed that the current-voltage relation of a synaptic receptor is nonlinear. This occurs when at least three different glutamate receptors were distinguished, especially *N*-methyl-*D*-aspartate (NMDA) (Foster and Fagg, 1984; Mayer and Westbrook, 1984). The current-voltage relation of the synaptic receptor on NMDA has the region where the slope is of negative conductance (Fig. 1).

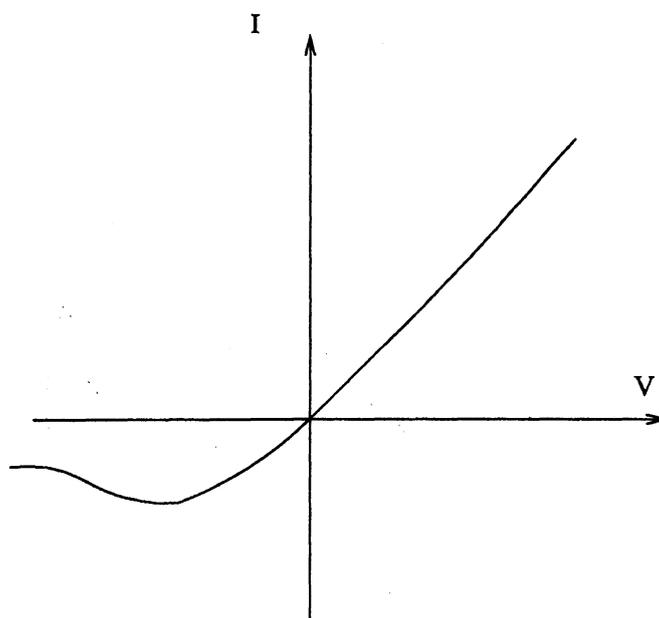


Fig. 1. The current-voltage relation of the synaptic receptor of NMDA.

Action of the NMDA receptor on both the transmitter and postsynaptic potential makes the receptor to behave as an AND logic element (Koch, 1990). Only a simultaneous presence of presynaptic action on the NMDA receptor and depolarizing synaptic potential provides the excited postsynaptic potential.

We are more interested in the electrical properties of dendritic membrane behaviour. Koike *et al.* (1968) suggested that there exists a maximum of the steady input current-voltage relation curve; this curve has slopes of positive and negative conductance arising from the supposed existence of the *N*-shaped current-voltage relation. Measuring the steady input relation at γ -motoneurons by the current clamp method, Lux *et al.* (1970); Lux and Schubert (1975) have observed the current-voltage relation up to the forecasted maximum. Schwindt and Crill (1977) repeated analogous measurements and eventually observed *N*-shaped current-voltage relations of two types (Fig. 2): the type (a) with net inward current inversion, and type (b) without current inversion, both are containing a negative slope. The *N*-shaped current-voltage relation curve (Fig. 3) crosses the abscissa *V* three times in the points V_r , V_u , and V_d where V_r is a rest potential, V_u is a potential where a slope conductance is negative, and V_d is a depolarized potential. Lux and Schubert (1975) have also established that the slow inward current mediated by calcium ions is the reason for a existence of stable depolarization in cat γ -motoneurons.

This was confirmed experimentally by Llinas and Sigumori (1980); they demonstrated directly that the existence of dendritic stable depolarization depends on the inward calcium current.

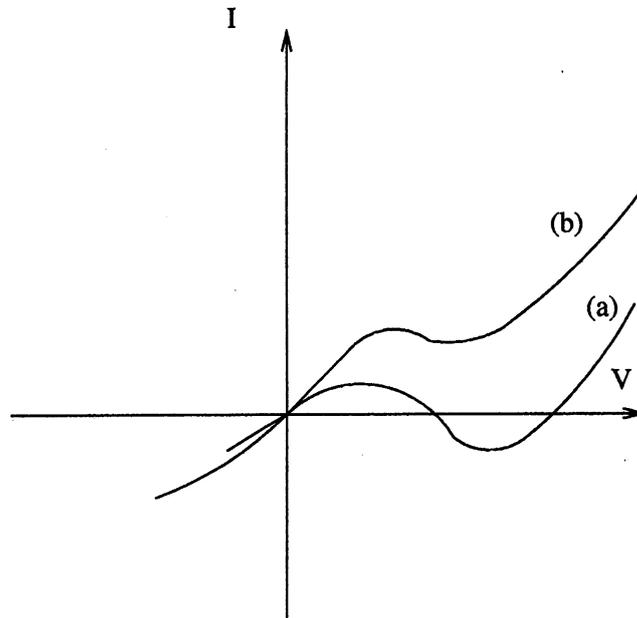


Fig. 2. *N*-shaped current-voltage relation of two types: one type (a) with inward current inversion, and the second (b) without current inversion.

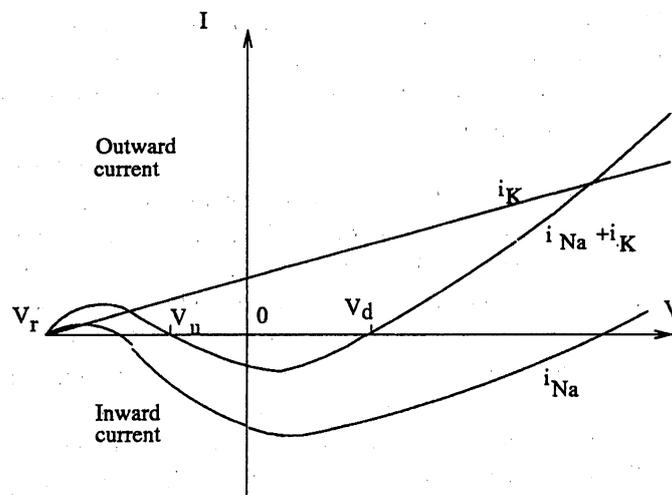


Fig. 3. The current-voltage relation for sodium, potassium and net inward current.

Further we will consider the nonlinear fundamental cable theory. Jack *et al.* (1975) analysed the *N*-shaped current-voltage relation for two currents (potassium and sodium) but not calcium. However, this is not a prerequisite for an artificial intelligence approach. Since our investigations are concentrated on dendritic membrane nonlinearities, we describe some details of the momentary current-voltage relation developed by Jack *et al.*

(1975). The net inward current is the sum of the sodium current as the inward current and the potassium current as the outward current (Fig. 3). The potassium current-voltage relation can be given by a straight line, as in a squid (Hodgkin and Katz, 1949).

We describe the three points V_r , V_u , and V_d shown in Fig. 3 more in detail:

1. The rest potential point V_r occurs where the current-voltage relation has a positive slope conductance. Slight deviations from this point increase the current which returns the membrane potential to its initial value. Thus, the point of resting potential V_r is stable.

2. The next intersection point is at V_u where the slope conductance is negative, and there is no equilibrium point between depolarizing and hyperpolarizing currents. This point is obviously unstable and leads to the appearance of the voltage threshold and a relevant action potential.

3. The right-hand intersection is at V_d with a positive slope conductance. This point is stable and, thus, the membrane current-voltage relation has two stable points V_r and V_d . However, Jack *et al.* (1975) showed that during potassium activation n and sodium inactivation h reactions, the current-voltage relation would spontaneously shift outward, the point V_d would disappear completely, and the membrane would repolarize back to V_r .

The third member in the synapse-dendrite-soma chain is the soma of a neuron. Its main characteristic is an input-output threshold function analogous to an amplifier with a saturating gain function. Examples of high-gain limit and other functions of the soma have been shown by Gupta and Rao (1994).

Following our overview of the synapse-dendrite-soma chain, we now will concentrate our attention on a mathematical description and synthesis of stability in the dendrite using the nonlinear cable theory.

2.2. Mathematical Description of Dendritic Membrane Functions and Minimum Threshold Value

First, as shown by (Jack *et al.*, 1975; Gutman, 1984; Segev *et al.*, 1989; Garliuskas *et al.*, 1991; Garliuskas, 1994), the current-voltage relation can be approximated by a third-order polynomial of the common form. Now we use such a polynomial:

$$i_i(V) = f(V) = V + V^2(V - a)/a(1 - b^2), \quad (1)$$

where V is the membrane potential, a is the constant ($a = 3$) and b is a parameter (range is from 0.5 to 0.8).

The approximation (1) of the current-voltage relation describes Hodgkin and Huxley-like electrical characteristic of the membrane rather well.

Second, the basic mathematical description of a dendrite as a cable is founded on partial differential equations of the linear or nonlinear cable theory. The main Hodgkin and Huxley (1939) differential equation is the following

$$c_m \frac{\partial V}{\partial t} = (1/r_a) \frac{\partial^2 V}{\partial x^2} + V/r_m, \quad (2)$$

where r_a is the intracellular resistance per unit length of the cable, c_m and r_m are the capacitance and resistance of the membrane per unit length of the cable, respectively.

After introducing membrane time τ_m and space λ constants, one obtains

$$\tau \frac{\partial V}{\partial t} = \lambda^2 \frac{\partial^2 V}{\partial x^2} + V, \quad (3)$$

where $\lambda = (\tau_m/r_a)^{1/2}$ and $\tau_m = r_m c_m$.

The membrane time constant is given by the time at which the voltage rises by approximately two-thirds of its steady-state value. The space constant of the membrane is a very important value for transferring excited signals through the dendritic line. Quantitatively, the membrane space constant is given by the length $x = \lambda$ when the potential V in a steady-state decays up to e^{-1} of its initial value. This value, defined from the canonical electrotonic equation near the rest potential, is named the electrotonic length constant. According to the Rall (1962) theory of ohmic dendritic cables, the spikes are not only in the soma of neurons or in the initial axonal segment but also along dendrites. This excited potential exists in dendrites at transduction as long as the electrotonic distance of a semi-infinite cable is not exceeded the electrotonic length constant λ three times.

Partial differential Eqs. 2 and (3) are parabolic and have a unique solution, if we denote suitable initial data and certain boundary conditions at $x = 0$ and $x = l$ in finite cable case.

The initial conditions are as follows

$$V(x, 0) = V(x), \quad 0 \leq x \leq l, \quad (4)$$

or in a uniform resting state

$$V(x) = 0, \quad 0 \leq x \leq l. \quad (5)$$

The boundary condition as a voltage clamp (some fixed value of potential) at $x = 0$ is

$$V(0, t) = V_c, \quad t > 0, \quad (6)$$

or, if applied at $x = l$, is

$$V(l, t) = V_c, \quad t > 0, \quad (7)$$

where V_c is the voltage clamp equal to the depolarizing potential.

Another boundary condition ($x = 0$) is a sealed end that means there is no longitudinal current at the end, then

$$V_x(0, t) = 0, \quad t > 0, \quad (8)$$

or if the end at $x = l$ is sealed,

$$V_x(l, t) = 0, \quad t > 0. \quad (9)$$

In Eqs. 2 and (3), initial and boundary conditions (4) and (5) in the linear cable theory r_a , r_m , and c_m are independent on V , x , and t . However, the value r_m in longer ranges of potentials is usually strongly dependent on V and t . Thus, instead of Eq. 2, we must use:

$$c_m \frac{\partial V}{\partial t} = (1/r_a) \frac{\partial^2 V}{\partial x^2} + i_i(V), \quad (10)$$

where $i_i(V)$ is the membrane ionic current density related to the membrane area on a unit length of the cable versus potential.

Substituting (1) to Eq. 10 with some new notation of parameters, a strongly nonlinear differential equation is as follows

$$c_m \frac{\partial V}{\partial t} = (1/r_a) \frac{\partial^2 V}{\partial x^2} + (V + pV^2 + qV^3), \quad (11)$$

where $p = -(1 - b^2)^{-1}$, $q = 1/a(1 - b^2)$.

In view of the dendrite model as a homogeneous cable (Jack *et al.*, 1975; Torre and Poggio, 1978) and taking into consideration the transmembrane current, we obtain such a dimensionless canonical partial differential equation:

$$\frac{\partial V}{\partial t} = \frac{\partial^2 V}{\partial x^2} + f(V). \quad (12)$$

Taking into account that in the bistable active medium a potassium current has been taken.

It is important to investigate the stability points of equation (12) and possible transitions from one stability point to the other, as well as the conditions for the appearance of switch waves. The switch wave moving in velocity $c \geq 0$ from the stability point $V_0 = h_0$ to $V_2 = h_2$ and vice versa is represented by a partial solution of equation (12).

Including new variable

$$\xi = x - ct, \quad V = V(\xi), \quad (13)$$

the such limiting conditions are existed:

$$\xi \rightarrow -\infty, \quad V \rightarrow h_2; \quad \xi \rightarrow +\infty, \quad V \rightarrow h_0. \quad (14)$$

After substituting solution (13) into equation (12) we get an ordinary second order differential equation

$$V'' + cV' + f(V) = 0. \quad (15)$$

Let us introduce a potential field function

$$I(v) = \int_0^v f(V) dv, \quad (16)$$

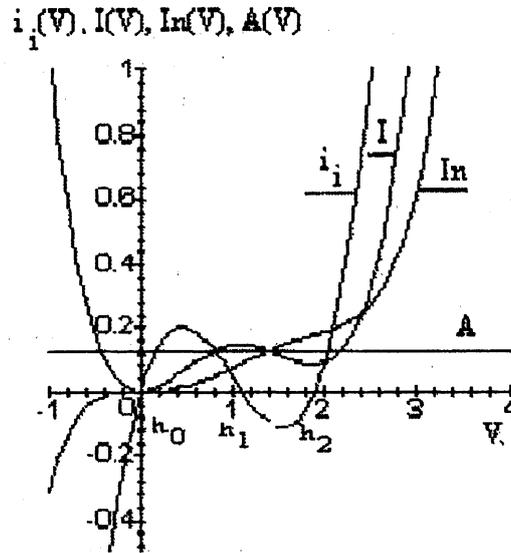


Fig. 4. Ionic current and its integrals versus potential.

and assume v as the coordinate of a particle and ξ as the time. In fact the dynamic might be interpreted as a particle moving in the potential field with velocity c , i.e., with the front velocity of the switch wave. The value of function (16) achieves maxima at the points h_0 and h_2 .

If $A = \int_{h_0}^{h_2} f(V)dV > 0$ (Fig. 4), then $V(h_2) > V(h_0)$, and if $A < 0$, the particle jumps from h_0 to h_2 at $c = c_0$ (critical value); if $A < 0$ and $V(h_2) < V(h_0)$, the particle jumps from h_2 to h_0 .

It is evident that saddle points $(h_0, 0)$ and $(h_2, 0)$ are existing. The results of modelling of equation (15) for four variants of initial conditions are presented in Fig. 5.

Further, we use the expression from the Cole theorem (Cole and Curtis, 1941) for nonterminated cables

$$i_a(di_a/dV) = i_i(V)/r_a, \quad (17)$$

where i_a is an applied current density, and show some general properties relevant to voltage threshold conditions.

We find the applied current $I = 2i_a$ at $x = 0$ from a theoretical i_i relation by integrating to give

$$\int_{i_0}^{i_a} i_a(di_a/dv) dv = 1/r_a \int_{V_r}^V i_i(v) dv. \quad (18)$$

After integrating of left side member we obtain

$$i_a^2 - i_0^2 = 2/r_a \int_{V_r}^V i_i(v) dv, \quad (19)$$

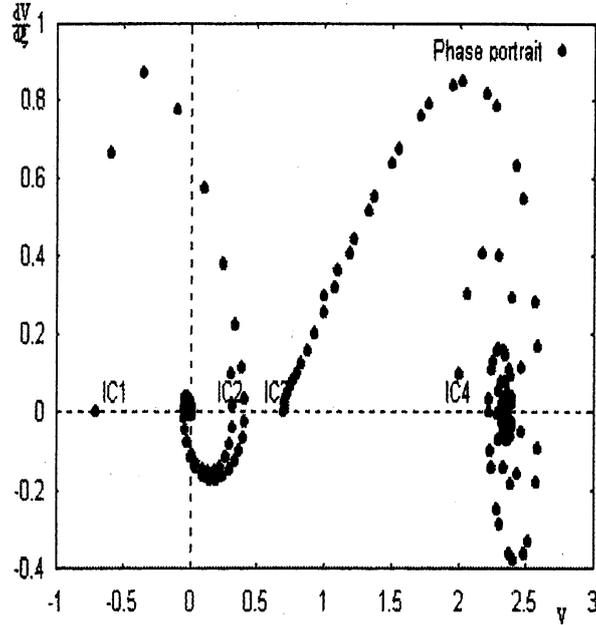


Fig. 5. The phase portrait of neuronal dynamics at initial conditions (IC): IC1- $V(0) = -0.7$, the derivative of V equals 0; IC2- 0.3, 0.1; IC3-0.7, 0.0; IC4-2.0, 0.1, respectively.

where i_0 is the value at $V = V_r$.

Since no current is required in the cable at the resting potential, $i_0 = 0$, and Eq. 19 becomes

$$I_1(V) = 2 \left[2/r_a \int_{V_r}^V i_i(v) dv \right]^{1/2}. \quad (20)$$

Some conclusions from Eq. 20 are:

1. The cable input current-voltage relation $I_1(V)$ is less nonlinear than $i_i(V)$ because I depends on the integral of $i_i(V)$. More extreme nonlinearities are smoothed in the cable.
2. The minimum threshold voltage $V = V_{th}$ occurs at this conditions:

$$\int_{V_r}^V i_i(v) dv = 0 \quad (21)$$

or

$$\int_{V_r}^{V_u} I_1(v) dv = \int_{V_u}^{V_{th}} I_1(v) dv. \quad (22)$$

A change of integrals of Eq. 22 is presented by $In(V)$ in Fig. 4. $V = V_{th}$ is the *minimum threshold value* for the voltage in the dendrite as a cable.

3. A negative chord conductance region (Fig. 3, area near V_u) is not the reason for the appearance of the threshold voltage.

Thus, we have obtained the main conditions for voltage thresholds in the dendrite as a cable with strong N -shaped nonlinearities. Now we have to show how this dendritic membrane phenomenon may be used to construct artificial intelligence logic functions.

3. Modelling by the Compartment Approach

3.1. Propagation of Excitation in Dendritic Membrane Circuits

When the threshold potential of excitation is exceeded, the all-or-nothing potential wave propagates in dendritic media. Now the cable current flows from excited to resting areas, this propagation has been proven experimentally by Hodgkin (1937) but a quantitative theory was formulated only in 1952 (Hodgkin and Huxley, 1952). Full numerical solutions of propagation excitation appeared rather late (Coley and Dodge, 1966; Noble and Stein, 1966).

We now consider a simple electric circuit to explain the potential wave propagation in the cable. Let a scheme of membrane consist of the resting resistance, capacitance, and a sodium current circuit which are placed in parallel through the axial resistance of the cable (Fig. 6a).

Let, in the beginning, the left-hand circuit be in a state similar to the right-hand circuit after an external generator was applied to charge the capacitor c_m . Then, a switch K in the sodium circuit turns on and the sodium current from its battery passes also to the capacitance charging it more. Now the left-hand circuit becomes as a generator which charges the right-hand circuit, and after achieving threshold voltage, the right switch is off and the inward current charges the right-hand capacitance. In such a way, the excited potential will be propagated along the line of dendrite. The switching event is shown in Fig. 6b.

Let the electric circuit be turned on by external sources, I_s be given from G (Fig. 6a). Let $I_s = 0$. The remaining circuit will be a natural termination circuit with the end of a dendrite sealed by the membrane. On the basis of current conservation at $x = 0$, the current through the terminal membrane at $x = 0^-$ will be equal to the longitudinal current at $x = 0^+$. Then

$$c_m V_t(0, t) = (1/r_m) V_x(0, t) + 1/r_m V(0, t), \quad t > 0. \quad (23)$$

If an external current I_s is now applied at $x = 0^-$, we obtain

$$c_m V_t(0, t) - 1/r_m V_x(0, t) - 1/r_m V(0, t) = I_s(0, t), \quad t > 0. \quad (24)$$

These circuits considered allow us to construct new ones which in turn provide logic operations.

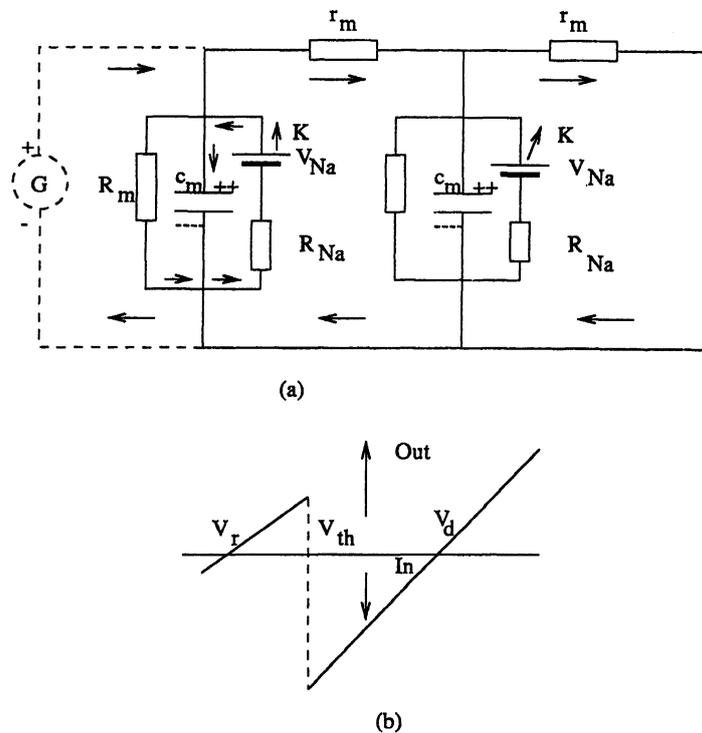


Fig. 6. Simple electrical circuit of potential wave propagation in the cable (a). Current-voltage diagram in the switch-line of conductance (b).

3.2. Main Differential Equations for the Compartment Approach

We begin by discussing some aspects of biological neuron morphology point of view. A biological neuron includes, in sequence synapses, dendrites, soma, axon, and once again synapses. The synapse is a long-term memory element where an experience accumulates on behalf of synaptic strengths.

Now we suppose, that three main mathematical operations: aggregation, thresholding, and nonlinear mapping, which usually occur in the soma, may be transferred to the dendritic region. We have shown above that dendrites have abilities similar to that of soma. After that, a reasonable question arises. What is the function of soma for? We suppose that soma fulfills similar operations only on another cognitive level of abstraction of information processing.

Now we present some artificial logic circuits based on *N*-shaped nonlinearities of the dendritic membrane. A logic circuit of the OR operation has been implemented by two nonlinear synapses and one stimulus current which are connected as a natural termination circuit with the lumped termination of synapses and stimulus currents (Fig. 7).

Following Segev *et al.* (1989) the dynamic differential equations in the middle of the dendrite as a distributed electric line circuit added by synapses and stimulus will be

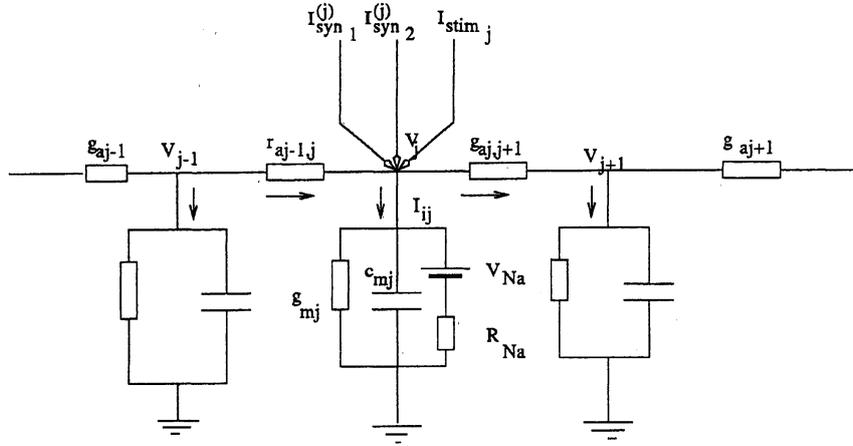


Fig. 7. Electrical circuit of external current applied at termination $x = 0$.

represented as

$$\begin{aligned} c_m dV_j/dt + I_{syn_1}^{(j)} + I_{syn_2}^{(j)} + I_{stim_j} + I_{leak_j} + I_{i_j} \\ = g_{a_{j-1,j}}(V_{j-1} - V_j) - g_{a_{j,j+1}}(V_j - V_{j+1}), \end{aligned} \quad (25)$$

where $g_{a_{j-1,j}}$ is the axial conductance between the $(j - 1)$ th and the j th compartment of the line.

The synaptic and other currents may be induced by as a product of the potentials as follows

$$I_{syn_1}^{(j)} = g_{syn_1}^{(j)}(V_j - E_{syn_1}^{(j)}); \quad I_{syn_2}^{(j)} = g_{syn_2}^{(j)}(V_j - E_{syn_2}^{(j)}), \quad (26)$$

where $g_{syn_1}^{(j)}$, $g_{syn_2}^{(j)}$ are synaptic conductances at the j th point between compartments usually accepted as time-dependent, but voltage-independent (conductive pathway based on the "alpha" function) (Rall, 1967; Jack *et al.*, 1975; Segev *et al.*, 1989).

$E_{syn_1}^{(j)}$, $E_{syn_2}^{(j)}$ are reversal constant voltages for two synapses, respectively.

I_{stim_j} is the stimulus current at the point j presented by the passive part of the dendritic membrane circuit.

The leakage current is as follows

$$I_{leak_j} = g_{leak_j}(V_j - E_{leak_j}), \quad (27)$$

where g_{leak_j} is a constant battery voltage at the j th point of the line.

At last, I_{i_j} is the ionic current of the dendritic membrane at the j th point. It is presented as follows

$$I_{i_j} = g_{i_j}(V, t)(V_j - E_{i_j}), \quad (28)$$

where $g_{i_j}(V, t)$ is, in general case, a voltage-and time-dependent conductance at the j th point of the line; we consider it as only a voltage-dependent conductance.

E_{i_j} is the reversal constant voltage in the ionic current branch at the j th point.

After substituting Eqs. 26–28 to Eq. 25 and regarding that the j th point of the circuit (Fig. 7) is the original one at $x = 0$, the dynamic differential equation looks like this

$$c_m dV_0/dt + g_{syn_1}^{(0)}(V_0 - E_{syn_1}^{(0)}) + g_{syn_2}^{(0)}(V_0 - E_{syn_2}^{(0)}) + I_{stim} + g_{leak_0}(V_0 - E_{leak_0}) + g_{i_0}(V)(V_0 - E_{i_0}) = g_{a_01}(V_0 - V_1). \quad (29)$$

This equation is the boundary condition at $x = 0$ for differential Eq. 24 in a semi-infinite cable. The solution of Eqs. 24 and 29, as shown by Segel *et al.* (1989), may be obtained using the numerical nonstandard means of SPICE software (Vladimirescu *et al.*, 1981). We used the GENESIS (GEneral NEural Simulation System) developed by J. Bower's group at the California Institute of Technology and described by Bower and Beeman (1994).

4. Logic Circuits in Static and Dynamic Approaches

4.1. Static Dendritic Logic Circuits

Neurophysiological simple logic operations in a natural dendrite were observed in Koch *et al.* (1983). Some rather descriptive considerations on their possible existence were presented theoretically by Gutman (1984). The numerical experiment was carried out on an elementary dendritic branch by principle possibilities of constructing dendritic logic circuits. Afterwards we present the numerical model results in dynamics.

In a steady-state $dV/dt = 0$ at $t \rightarrow \infty$ and the potential depends on the distance x . For simplicity, consider that the important variables are: synaptic conductances g_i , the difference of pre-and postsynaptic potentials V_i , and the stimulus current that remains constant at the point $x = 0$.

The construction of dendritic logic circuits is founded on the following rule: if the sum of all external currents (including the inward ionic reversal current charged the membrane capacitance) becomes larger than the threshold current I_{th} (the depolarizing potential is higher than the threshold voltage V_{th}), then a jump potential will appear; if the sum of all currents is smaller or equal to I_{th} and potential is lower or equal to V_{th} , the jump potential will appear, then

$$V_{jump} = \begin{cases} V_{th} & \text{if } g_1 V_1 + g_2 V_2 + I_{stim} + i_m > I_{th}, \\ 0 & \text{if } g_1 V_1 + g_2 V_2 + I_{stim} + i_m \leq I_{th}, \end{cases} \quad (30)$$

where i_m is the sum of ionic and leakage currents which are not changed in dependence of the variables of synapses and the stimulus current.

Now we consider simple logic circuits OR, AND, and MAJOR. The example of OR circuit (Fig. 8) is built on the basis of such illustrated values. Let $g_1 = g_2 = 10nS$;

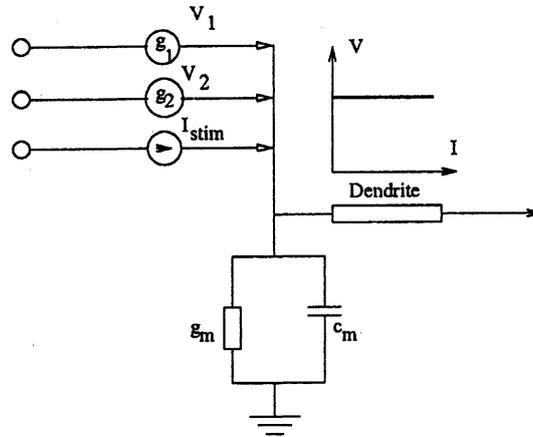


Fig. 8. Dendrite OR logic circuit.

Table 1
The OR logic circuit operation

$g_1 V_1$	$g_2 V_2$	$I_{stim} + i_m$	Sum	$V_1 \text{ OR } V_2$
10×0	10×0	7	7	<10: ClassA
10×1	10×0	7	17	>10: ClassB
10×0	10×1	7	17	>10: ClassB
10×1	10×1	7	27	>10: ClassB

Table 2
The AND logic circuit operation

$g_1 V_1$	$g_2 V_2$	$I_{inh} + i_m$	Sum	$V_1 \text{ AND } V_2$
10×0	10×0	-3	-3	<10: ClassA
10×1	10×0	-3	7	<10: ClassA
10×0	10×1	-3	7	<10: ClassA
10×1	10×1	-3	17	>10: ClassB

$V_1 = V_2 = 1mV$; $I_{stim} = 5nA$; $I_m = 2nA$; $I_{th} = 10nA$, and $V_{th} = 20mV$ as hypothetical data. The operations of OR circuit and the result of classification are presented in Table 1.

The AND logic circuit is obtained if the current of the inhibition synapse for hyperpolarizing the membrane potential is taken instead of the stimulus current, that is $I_{inh} = -3nA$ (Fig. 9, Table 2).

If we take three or more excited synapses and one inhibited synapse, we can simply build MAJOR dendritic logic circuit (Fig. 10). In this case, class A will be represented when one synapse is excited, that is, class A: $(0, 0, 0,)$, $(0, 1, 0)$, $(0, 0, 1)$, $(1, 0, 0)$, and

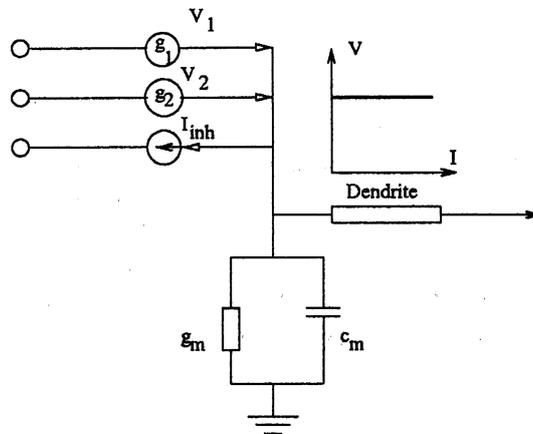


Fig. 9. Dendrite AND logic circuit.

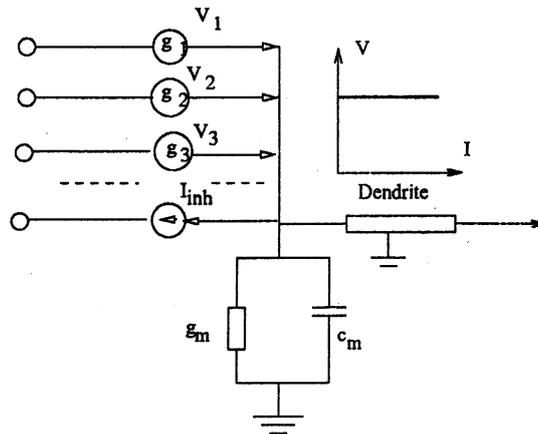


Fig. 10. Dendrite MAJOR logic circuit.

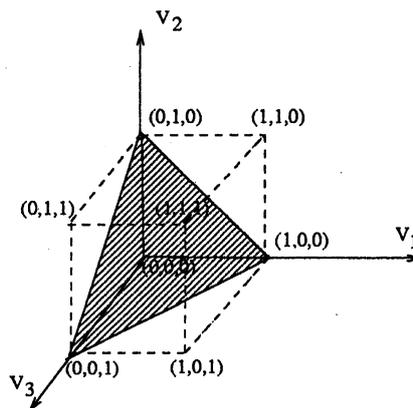


Fig. 11. The geometrical illustration of MAJOR logic circuit.

class B – when two or more are excited, that is, class B : (1, 1, 0), (1, 0, 1), (0, 1, 1), (1, 1, 1). A geometrical illustration of MAJOR logic circuit classification at unity values is given in Fig. 11. Here the values inside the area of the plate including it form class A , and outside – class B .

According to Koch *et al.* (1983), when synapses are situated close to each other on the dendrite, the veto operation may be observed, especially between a silent inhibition and excitation. This operation is like an analog version of a digital NOT AND gate.

Further, if we let the negation (inversion) operation which is like the veto one, we easily succeed on obtaining the universal Shepher's and Pirson's logic circuits NOT OR and NOT AND, respectively. Basing upon some of them and the inversion element, all necessary logic functions may be built.

4.2. Numerical Simulation of Dendritic Logic Circuits in Dynamics

The numerical simulation of dendrite membrane processes in dynamics was carried out by numerical integration methods according to Bower and Beeman (1994). There was the Eq. 29 integrated by the exponential Euler method. The current brief pulse (2 msec.) injection was applied to the soma of the uniform cable.

For numerical simulation of OR and AND dendritic logic circuits three uniform compartments of dendrite and soma circuits were taken. The injection current pulse was applied to soma. The input of the dendritic logic circuit was the point between the second and third compartments similarly that shown in Fig. 7. Two excited synapses and a stimulus current were also applied, or in the case of AND logic circuit, an inhibitory current. Both the stimulus and the inhibitory current present a bias of logic circuits.

Numerical simulation of OR and AND dendritic logic circuits has performed by GENESIS (Bower and Beeman, 1994) specialized for modelling of neurobiological phenomena in brain.

Under the stimulus current influence upon soma the membrane potential has changed in time (Fig. 12, 13, curves, V_m). If we take the threshold potential, $V_{th}=12$ mV, the OR logic circuit works in such a way.

There are such combinations of two synapses: 00 means no synapses (Fig. 12, $V_m:00$), 01 and 10 mean that only one synapses is excited (Fig. 12, $V_m:01$), and 11 means two excited synapses (Fig. 12, $V_m:11$).

In the case of 00, the maximum of membrane potential courses in time at the output of the third compartment does not exceed the threshold potential; in the cases 01, 10, and 11 the maximum becomes higher than the threshold potential. It means that the OR logic circuit operations shown in Table 1 are confirmed. At the same threshold potential AND dendritic logic circuit operations are also confirmed.

According to Fig. 13, $V_m:00$ and $V_m:01$ the maximum potential is lower than V_{th} and it stands for class A (Table 1). Class B is coincidental with a combination of two excited synapses. This event is presented in Fig. 13, curve $V_m:11$.

Thus, we have confirmed the possibilities to build dendritic logic circuits based upon numerical dynamical simulation.

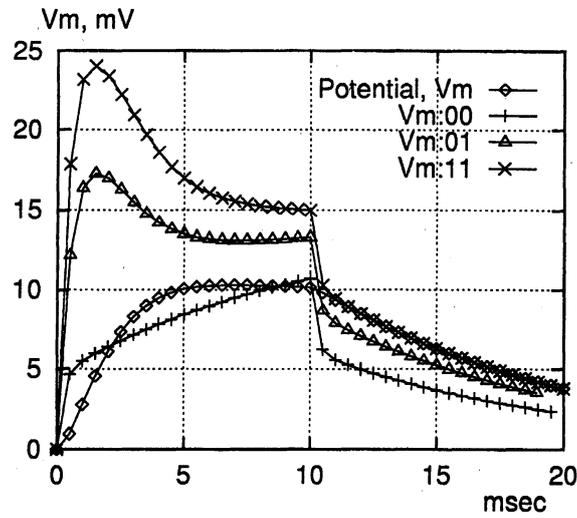


Fig. 12. Dendritic OR logic circuit potentials versus time.

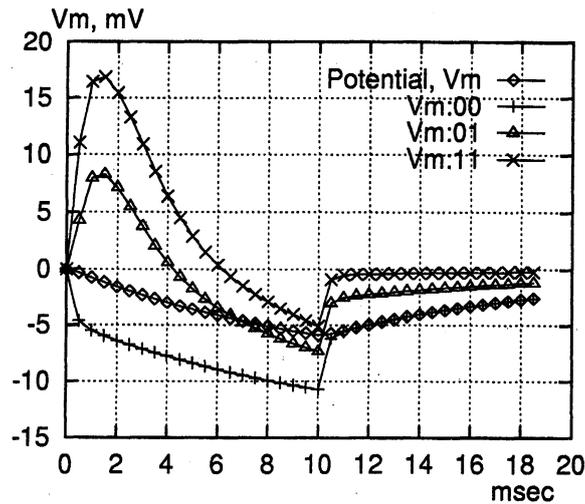


Fig. 13. Dendritic AND logic circuit potentials versus time.

5. Conclusions

Basing upon the extended theoretical studies of nonlinearities and possibilities of a dendritic logic construction in the neuronal structure we would like to emphasize the following:

- (1) The dendrite membrane nonlinear current-voltage relation with two stable points creates a presumption of carrying out some logic functions;
- (2) Using the bistable dynamic theory in physical systems, switch waves in a dendrite medium of neurones were discovered instead of forming hysteresis as it has been

proposed in recent works. Under our considerations the existing threshold potential switch wave carries modulated information in the medium as a non-homogeneous line of cable;

- (3) The electrical analogy used to describe the static and dynamic processes in the neuronal medium allowed us to simulate main simple logic constructions: OR, AND, MAJOR;
- (4) Note that the theoretical substantiation and numerical experiments are only the first step forward to the proving of neuronal dendritic logic constructions for generalised imagination of neuronal computing in the brain.

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Dinaminių sinapsė–dendritas–ląstelė neuroninių procesų skaitmeninis modeliavimas

Algis GARLIAUSKAS

Smegenų veiklos procesuose ypatingą vaidmenį vaidina netiesiškumo charakteristikos. Be žinomų netiesinės sigmoidinės neurono ląstelės priklausomybės, ypatingą reikšmę turi *N*-formos dendrito membranos charakteristika. Remiantis ja parodyta loginių operacijų konstravimo galimybė. Atliktas šių operacijų skaitmeninis modeliavimas prie statinių ir dinaminių sąlygų.

Pabrėžiama, kad apart modeliavimo tik intensyvus neurofiziologinis tyrimas gali atverti galutinį žmogaus smegenų neuroninio skaičiavimo mechanizmą.