ELSEVIER

Bioelectrochemistry 57 (2002) 89–95

Bioelectrochemistry

www.elsevier.com/locate/bioelechem

LoMAPAM—Logical Model of Autowave Processes of Amoebic Movement☆

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Received 1 June 2001; received in revised form 1 February 2002; accepted 6 February 2002

Abstract

This work describes a logical discrete model of the spatiotemporal dynamics of amoebic movement (Logical Model of Autowave Processes of Amoebic Movement (LoMAPAM)) based on finite automata (homogeneous structures) and specified for *Physarum polycephalum*. The basic system of passing rules for the information and regulation levels of the model, describing the contractile behavior of the ectoplasmic walls of *P. polycephalum*, enables a rhythmic generation of contractile waves and their propagation in the ectoplasmic wall due to the created structure of the LoMAPAM model. The finite automata corresponds to elementary square planar elements. This construction is alike homogeneous structures with the only exception is its finite. The planar element is assigned to the pair of integers (i,j). The state vector defined for every element (i,j) in discrete time t will have three components. Each of them will be written in one of the matrices **B**, **C**, or **W**. The information matrix **B** describes the state of the matter. The regulation matrix **C**, the local Ca^{2+} concentration. The flow matrix **W** describes the local flow of endoplasm or ectoplasm. The passing rules for the state vector was written in the form of Boolean functions. Six actomyosin generators placed on a circle and three and five neighbouring ectoplasmatic generators on a line and a layer of endoplasm were analysed.

Keywords: *Physarum polycephalum*; Autowave processes; Model of amoebic movement

1. Introduction

A discrete model of the spatiotemporal dynamics of amoebic movement (Logical Model of Autowave Processes of Amoebic Movement (LoMAPAM)) based on finite automata (homogeneous structures) and specified for *Physarum polycephalum* was constructed. The starting point for the construction of LoMAPAM was the experimental data and the local model by Teplov et al. [1].

The suggested three-level structure of LoMAPAM couples mechanical and chemical oscillations as suggested in the model by Teplov et al. [1] and the conception that autowave processes create the base for these oscillations [2,3].

The basic system of passing rules for the information and regulation levels of the model, describing the contractile behavior of the ectoplasmic walls of *P. polycephalum*, enables a rhythmic generation of contractile waves and their propagation in the ectoplasmic wall due to the given structure of the LoMAPAM model. This is because of the local fluctuation of concentration of the regulation substance (Ca^{2+}). Such contractile waves cause the shuttle streaming of endoplasm, which was observed experimentally as reported (e.g. in Refs. [4–7]).

The autowave processes emerging and sustaining in a nonlinear homogeneous environment create a starting point for discrete modeling of spatiotemporal dynamics of the amoebic movement. The construction of the model was specified for the amoebic movement of *P. polycephalum*, a multinuclear, unicellular organism that is widely used for the experimental study of cell motility (e.g. Refs. [4–7]).

A strand segment of *P. polycephalum* excised from the network of myxomycete plasmodium contracts and relaxes in a certain rhythm and these oscillations become, after a phase of chaotic movements, synchronous. Synchronous contractions of the ectoplasmic walls accompanied by shuttle

☆ This paper was presented at the XVIth International Symposium on Bioelectrochemistry and Bioenergetics, Bratislava from June 1 to June 6, 2001. A collection of these papers has also been published in previous issues of this journal, 55/1–2 and 56/1–2.

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1567-5394/02/$ - see front matter
PII: S1567-5394(02)00060-9

streaming of the endoplasm changing its direction within the period of 1–2 min can be observed. Under the influence of the surroundings, one of the directions can prevail.

The oscillatory behavior of *P. polycephalum* has been studied excessively in the recent years, and papers (e.g. Refs. [8–11]) report on it and on responses of the organism to external signals. Other papers report on the internal regulatory mechanism of the contraction mechanism based on the actomyosin complexes (e.g. Refs. [12–14]).

The character of the mediator — the way how the synchronization proceeds — is still unknown. The membrane of *P. polycephalum* is not excitable and the rhythmic activities also sustain in the systems with disintegrated membrane. It is obvious that the membrane does not play the role of the mediator necessary for the synchronization of local rhythms.

The mechanism for the cytoplasmic Ca^{2+} oscillator to power shuttle streaming in strands of the slime mould *P. polycephalum* uses a phosphorylation–dephosphorylation cycle of myosin light chain kinase, based on a model, was analysed by the Hopf bifurcation theory in Ref. [15].

2. Model

According to available experimental data, we can assume the following.

(1) Each actomyosin system itself is an autowave system. Single actomyosin systems — pressure generators — are coupled via viscoelastic coupling with endoplasmic core and create a complex autowave network of *P. polycephalum*. The streaming of the endoplasm is carrying the information about the activity of the single generators and takes part in the synchronization process. The mediator can be chemical (Ca^{2+} concentration) or mechanical (fluctuation of the intracellular endoplasmic pressure) and is still not experi mentally specified. The amplitude and frequency of every generator (actomyosin complex) is regulated by a number of biochemical factors (presence or absence of some substances, calcium ions, molecules of ATP, regulation proteins (fragmin, profilin)...).

(2) The observed autowaves phenomena in isolated protoplasmic strands and in the strands in which endoplasm was replaced by an artificial medium allow us to assume that a single network of pressure generators (actomyosin complexes) and viscoelastic fluid can create an autonomous autowave system.

In this way, we can construct a discrete model of the autowave system of *P. polycephalum* in several steps. We divide the model into parts on which the autowave phenomena can be observed:

1. the model of the contractile activity of the actomyosin system;
2. the model of the network of actomyosin generators coupled in a short ectoplasmic fragment via viscoelastic fluid.

In order to model the contractile behavior of *P. polycephalum*, we decided to formulate a discrete model, allowing to study the autowave phenomena not only locally, but also globally. We used the fact that if a spatial model describes an autowave structure, then the simplest discrete model with the suitable coupling among the respective autowave elements has a corresponding spatial nonhomogeneous solution. Conversed argumentation is generally not valid because not all solutions obtained in a qualitative analysis are stable [14].

The second level of the model is created by the so-called passing rules or passing functions, modeling qualitative changes of the state vector of the basic spatial two-dimensional elements. The state vectors of the basic spatial elements create the initial conditions for homogeneous structure, and for each basic spatial element, its defined surrounding consisting of basic spatial elements creates in each time instant an input for the basic automaton of the homogeneous structure. These are the changing and mutually influenced boundary conditions for the passing functions of the basic automaton of the homogeneous structure.

When formulating the model of amoebic movement of *P. polycephalum*, we have to understand the processes in the elementary fragment of *P. polycephalum*, the origin and synchronization of the contractions in the ectoplasmic tube and the streaming of the endoplasm in the elementary fragment. Therefore, we first followed the contractile behavior of such an elementary fragment of *P. polycephalum*.

For simplicity, we first formulate the passing rules for a longitudinal axis section of the strand and restrict ourselves to two-dimensional space. We will operate with the area covered by elementary square planar elements. Each of them can be characterized in terms of the state vector. Therefore, in our two-dimensional space, we can pass from describing the area covered by elementary planar elements of the square net to the square lattice: each elementary planar element of the net creates one junction of the square lattice. The state vector of the planar element is assigned to the pertinent lattice junction. A pair of integers that define the position of the lattice junction in the two-dimensional space can be assigned to each lattice junction. Thus, we can represent the lattice by a matrix. The matrix element (i,j) belongs to the lattice junction with the coordinate (i,j).

The state vector will have three components: a regulation, an information, and a flow one. Each of them will be written in one of the matrices **C**, **B**, **W**. The regulation matrix **C** describes the information about the local Ca^{2+} concentration. The information matrix **B** describes the information about the local state of the matter. The flow matrix **W** describes the local vector flow of the ecto/endoplasm (Fig. 1).

The aim of this work is to create a homogeneous structure and study its behavior in order to study some behavioral abilities of the *P. polycephalum*.

The homogeneous structure S will have three levels: the information level described by matrix **B**, the regulation level

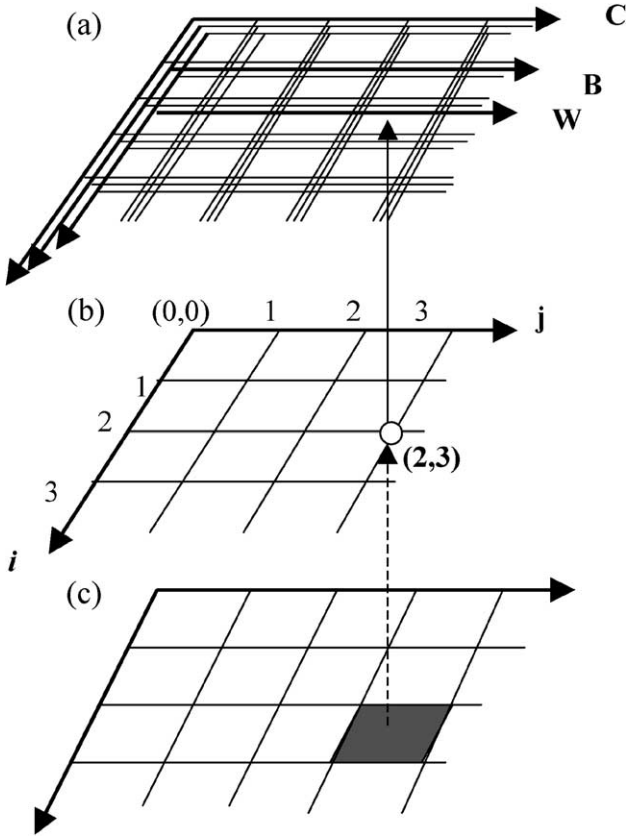


Fig. 1. Two-dimensional case with basic space element (c) and the corresponding node of the lattice (b). (a) shows the distribution of the state vector among three matrices: flow matrix $\mathbf{W}=(w_{ij})$, regulation matrix $\mathbf{C}=(c_{ij})$, and information matrix $\mathbf{B}=(b_{ij})$.

described by matrix **C**, and the flow level described by matrix **W**. Among the matrices **B**, **C**, **W**, we can identify horizontal relations — the state of the element of the matrix is determined by its surroundings in the given matrix and vertical relations, the state of the element of a matrix is determined by the states of the elements of one of the other two matrices. Simplified relations between the matrices are defined in the following way.

Horizontal–vertical relations — the state of the b_{ij} element of the information matrix is determined by the surroundings of the element b_{ij} and by the state of the c_{ij} element of the regulation matrix.

Vertical relations — a change of the state of the information matrix element b_{ij} influences the change of the regulation matrix element c_{ij}; a change of the state of the flow matrix element w_{ij} influences the change of the regulation matrix element c_{ij}; a change of the state of the information matrix element b_{ij} influences the change of the state of the flow matrix element.

The system of the matrices **C**, **B**, **W**, whose elements are from the sets E_c, E_b, E_w, will be called configuration.

The application of the set of the passing rules to every element of the three matrices will be called evaluation of a configuration.

We define the ordered surroundings of the first order $O_1(i,j)=\{(i,j),(i,j+1),(i-1,j),(i,j-1),(i+1,j)\}$. The state of the appurtenant lattice junctions will be assigned S0, S1, S2, S3, S4.

Not violating the generality of the case, we will fix the z-axis to the axis of the ectoplasmic strand and the x-axis to the cross-section of the ectoplasmic strand.

We identify the states of the information, regulation, and flow matrices that are given in the following tables.

Information matrix	
State 0	vicinity of *P. polycephalum*
State 1	surroundings of *P. polycephalum*
State 2	endoplasm, positive gradient of the pressure in axis $+z$
State 3	endoplasm, positive gradient of the pressure in axis $-z$
State 4	ectoplasm, contraction state
State 5	ectoplasm, noncontraction state

Regulation matrix	
State 0	underthreshold Ca^{2+} concentration
State 1	overthreshold Ca^{2+} concentration

Flow matrix	
State 0	no flow of the substance
State 1	flow of the substance in direction $+z$
State 2	flow of the substance in direction $+x$
State 3	flow of the substance in direction $-z$
State 4	flow of the substance in direction $-x$

The configuration and its change on the regulation level will be coded in the following way. The first number codes the state of the surroundings of the central element and the state of the central element in time t. The number in brackets codes the regulation substance concentration in time t. The number written after the arrow codes the state of the central element in time $t+1$ and the second number in brackets codes the state of the regulation substance in time $t+1$.

The basic passing rules for the anterior wall of *P. polycephalum* (in direction of the axis $+z$) are defined:

$10111(0) \rightarrow 5(0)$ — the endoplasm strikes the anterior wall (the boundary between *P. polycephalum* and its surroundings), the ectoplasm is being condensed;
$10111(0) \rightarrow 1(0)$ — the endoplasm in the area of increased Ca^{2+} concentration stays fluid and *P. polycephalum* moves forward;
$50515(0) \rightarrow 2(0)$ — the wave is reflected, the pressure induces increase of Ca^{2+} concentration;
$50525(1) \rightarrow 1(0)$ — the anterior wall under influence of increased Ca^{2+} concentration is being diluted, the conditions for the forward movement of *P. polycephalum* are created.

These passing rules will be written in the form of Boolean functions:

$$c_0^{t+1} = g(b_{01}^t, b_{02}^t, \ldots, b_{42}^t, c_0^t),$$
$$b_0^{t+1} = (b_{01}^{t+1}, b_{02}^{t+1}) = (f_1, f_2),$$

where

$$f_1 = f_1(b_{01}^t, b_{02}^t, \ldots, b_{42}^t, c_0^t), \quad f_2 = f_2(b_{01}^t, b_{02}^t, \ldots, b_{42}^t, c_0^t).$$

To describe the process on the information level, the states 0, 1, 2, 5 are sufficient.

Thus, the partial Boolean functions f_1, f_2, g with respect to the basic behavioral rules for the anterior wall of *P. polycephalum* are defined as follows:

$$g = 0,$$

$$f_1 = x_{02}\bar{x}_{11}\bar{x}_{12}x_{22}\bar{x}_{31}x_{32}x_{42}y(\bar{x}_{01}\bar{x}_{21}\bar{x}_{41} \vee x_{01}x_{21}x_{41}),$$

$$f_2 = \bar{x}_{01} \vee \bar{x}_{02} \vee x_{11} \vee x_{12} \vee \bar{x}_{21} \vee \bar{x}_{22} \vee x_{31} \vee \bar{x}_{32} \vee \bar{x}_{41} \vee \bar{x}_{42} \vee y,$$

where $x_{ij} = b_{ij}^t$, $y = c_0^t$.

The basic passing rules for the rear wall of *P. polycephalum* (in direction of the axis $-z$) are defined as:

52505(0) → 5(1) — reflection of the wave on the rear wall;
52505(1) → 2(0) — melting of the rear wall;
22202(0) → 5(0) — condensation of the rear wall;
22202(1) → 2(0) — backward movement of *P. polycephalum*.

The corresponding partial Boolean functions f_1, f_2, g for the rear wall of *P. polycephalum* can be written as follows:

$$g = x_{01}x_{02}x_{11}\bar{x}_{12}x_{21}x_{22}\bar{x}_{31}\bar{x}_{32}x_{41}x_{42}\bar{y},$$

$$f_1 = \bar{x}_{01} \vee x_{02} \vee \bar{x}_{11} \vee x_{12} \vee \bar{x}_{21} \vee x_{22} \vee x_{31} \vee x_{32} \vee \bar{x}_{41} \vee x_{42} \vee \bar{y},$$

$$f_2 = \bar{x}_{01} \vee \bar{x}_{02} \vee \bar{x}_{11} \vee x_{12} \vee \bar{x}_{21} \vee \bar{x}_{22} \vee x_{31} \vee x_{32} \vee \bar{x}_{41} \vee \bar{x}_{42} \vee \bar{y}.$$

Let us consider a simplified model with the ectoplasmic cortex consisting of one layer. We introduce the reduced surroundings O_{red}. The configuration and its change will be coded in the following way: the first three numbers code the reduced surroundings of the information matrix, the second three numbers code reduced surroundings of the regulation matrix. Basic passing rules:

555,010 → 5(1) — local Ca^{2+} fluctuation in ectoplasm;
535,010 → 3(0) — contractable ectoplasm relaxation;
535,101 → 5(0) — change of a contractable state into a noncontractable one;
535,101 → 5(1) — increase of Ca^{2+} concentration stimulated by contraction;
353,010 → 3(1) — origin of contractable area in the ectoplasm;
333,111 → 3(1) — contraction area;
355,100 → 5(1) — increase of Ca^{2+} concentration stimulated by contraction;
553,011 → 5(1) — increase of Ca^{2+} concentration stimulated by contraction.

Basic passing rules can be written in the form of passing functions:

$$b_0^{t+1} = f_{ek}(b_0^t, b_1^t, b_3^t, c_0^t, c_1^t, c_3^t),$$
$$c_0^{t+1} = g_{ek}(b_0^t, b_1^t, b_3^t, c_0^t, c_1^t, c_3^t).$$

The corresponding partial Boolean functions can be written as:

$$g_{ek} = \bar{x}_1 \vee \bar{x}_3 \vee (\bar{x}_2 \vee y_1 \vee y_2 \vee y_3)(x_2 \vee (y_1 \vee \bar{y}_2 \vee y_3)(\bar{y}_1 \vee y_2 \vee \bar{y}_3))$$

$$f_{ek} = \bar{y}_2 \vee (\bar{x}_1 \vee y_3(\bar{x}_2 \vee \bar{x}_3 \vee y_1)(x_2 \vee x_3 \vee \bar{y}_1)) \wedge (x_1 \vee x_3 \vee (\bar{x}_2 \vee y_1 \vee y_3)(x_2 \vee \bar{y}_1 \vee \bar{y}_3)),$$

where $x_i = b_i^t$, $y_i = c_i^t$, $i = 0,1,3$.

In the case of endoplasm, we formulated only one basic rule — the prevailing direction of the surroundings is being expressed. Ca^{2+} concentration does not influence the mentioned.

3. Results

Involving the refracted state of endoplasm and the basic passing rules, we can generate contraction waves sustaining in a modeling ectoplasmic wall. The local fluctuation of Ca^{2+} concentration plays the role of energy of *P. polycephalum* for this generation.

The starting state is a relaxed ectoplasmic wall. The matrix elements describing the wall of the strand are in the state 5. The corresponding regulation matrix elements are in the state 0 (underthreshold Ca^{2+} concentration value). The state of a net node is coded $x(y)$, where x is the code of an information matrix element, and y is the code of a regulation matrix element.

3.1. Basic cycle of the ectoplasmic wall

A matrix node of a relaxed ectoplasmic wall is coded 5(0). In the local fluctuation of Ca^{2+} concentration, a matrix node is coded 5(1). A contractable state, an increase of Ca^{2+} concentration, causes the node of the information matrix change its state to state 3. A matrix node is described by 3(1). In a relaxation of a contractable state, calcium ions are closed into intracellular stores, Ca^{2+} concentration decreases below the underthreshold value. A matrix node is described by 3(0). The decrease of Ca^{2+} concentration leads to the change of the state 3 to the state 5. The viscous ectoplasmic wall is being built up again. A matrix node is coded 5(0).

Thus, the basic cycle of the ectoplasmic wall can be written as:

$$5(0) \rightarrow 5(1) \rightarrow 3(1) \rightarrow 3(0) \rightarrow 5(0) \rightarrow \ldots$$

If the area of the contractable ectoplasm is wider than two elements of the surroundings, then good contraction conditions (overthreshold Ca^{2+} concentration) sustain in such an area.

3.2. The rhythmic generation of ectoplasm contractions caused by a local Ca^{2+} fluctuation

Let us consider three neighbouring matrix nodes and the following starting configuration 5(0)5(1)5(0). Due to the passing rules, the temporal evolution can be written as:

5(0) 5(1) 5(0)
5(0) 3(1) 5(0)
5(1) 3(0) 5(1) ←
3(1) 5(0) 3(1)
3(0) 5(1) 3(0)
5(0) 3(1) 5(0) ←

The cycle sustains.

3.3. The rhythmic generation of ectoplasmic contractions caused by local Ca^{2+} fluctuation and the streaming of endoplasm

Let us consider five neighbouring ectoplasmic generators on a line and a layer of endoplasm. (a)–(g) describes the temporal development of such a configuration, (a) is the starting configuration with the local fluctuation of Ca^{2+}.

t ↓

(a) 5(0) 5(1) 5(0) 5(0) 5(0)
1(x) 1(x) 1(x) 1(x) 1(x)

(b) 5(0) 3(1) 5(0) 5(0) 5(0)
1(x) 1(x) 1(x) 1(x) 1(x)

(c) 5(1) 3(0) 5(1) 5(0) 5(0)
1(x) 4(x) 1(x) 1(x) 1(x)

(d) 3(1) 5(0) 3(1) 5(0) 5(0)
1(x) 1(x) 1(x) 1(x) 1(x)

(e) 3(0) 5(1) 3(0) 5(1) 5(0)
4(x) 1(x) 4(x) 1(x) 1(x)

(f) 5(0) 3(1) 5(0) 3(1) 5(0)
1∨2 1(x) 1(x) 1(x) 1(x)

(g) 5(1) 3(0) 5(1) 3(0) 5(1)
1∨2 4(x) 1(x) 4(x) 1(x)

(h) 3(1) 5(0) 3(1) 5(0) 3(1)
1∨2 1∨2 1(x) 1(x) 1(x)

(i) 3(0) 5(1) 3(0) 5(1) 3(0)
4(x) 1∨2 4(x) 1(x) 4(x)

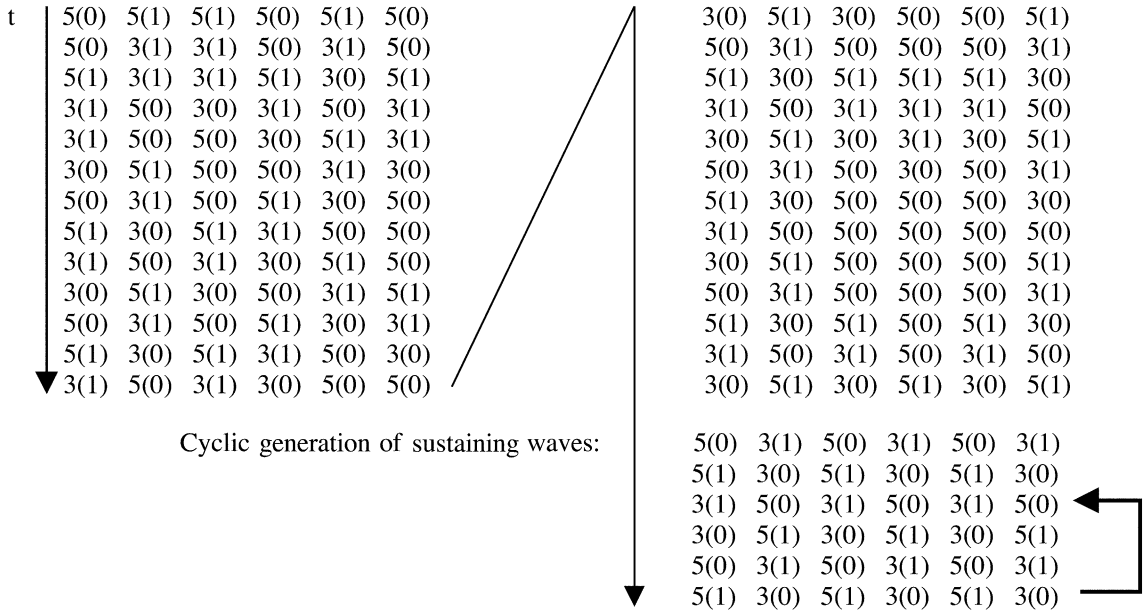
(j) 5(0) 3(1) 5(0) 3(1) 5(0)
1∨2 1∨2 1∨2 1(x) 1∨2

Cycle (g)–(j) sustains.

By (x), we denote that the flow of regulation substance is not considered. By 1∨2, we denote the state of endoplasm when the boundary conditions are not sufficient for the estimation of the state of endoplasm.

3.4. Six actomyosin generators placed on a circle

Let us consider the starting configuration as described in the previous case — a local fluctuation of Ca^{2+} concentration. We will show that such casually excited configuration leads to sustaining synchronous contraction waves.



Generation of a transmitting wave of condensed and diluted endoplasm areas generated by hydrostatic pressure, thanks to the contractions of the ectoplasmic wall.

An active contractable state of the endoplasm is coded by 3(1). This state generates the local increase of Ca^{2+} concentration in the relaxed areas coded 5(0) of its surroundings. Let us assume that in this way, the concentration reaches an overthreshold value (state 1 in the information matrix). If a matrix element is coded by 3(1) and there is an endoplasm in the state 1 or 2 in its surroundings, the endoplasm reaches only one of the state 1 or 2.

If a matrix node, coded 3(0), creates the surroundings of endoplasm in the state 1 or 2, the endoplasm reaches the refracted state coded by 4.

4. Conclusion

The defined homogeneous structure allows the modeling of sustaining cyclical wave-like processes with the coupling of only basic defined qualitative states of the *P. polycephalum* with the notion of a regulation trigger (in our case, we assumed fluctuations of Ca^{2+}, however, the regulatory mechanism can be more complicated without harming the usage of the model). A few simple initial states were discussed. Further, we are aiming for deeper computer simulations and study of the basic set of passing rules.

Acknowledgements

This work was financially supported by Slovak Grant Agency No. 1/7673/20.

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