If BZ medium did spanning trees these would be the same trees as *Physarum* built

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A sub-excitable Belousov–Zhabotinsky (BZ) medium exhibits self-localized wave-fragments which may travel for relatively long time preserving their shape. Using Oregonator model of the BZ medium we imitate foraging behavior of a true slime mold, *Physarum polycephalum*, on a nutrient-poor substrate. We show that given erosion post-processing operations the BZ medium can approximate a spanning tree of a planar set and thus is computationally equivalent to *Physarum* in the domain of proximity graph construction.

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1. Introduction

Physarum polycephalum,[1] commonly known as a true or multi-headed slime mold, is – at one stage of its complicated life cycle – a single cell with many diploid nuclei. This syncytial mass of protoplasm, called plasmodium, looks like amorphous yellowish mass. The plasmodium behaves and moves as a giant amoeba. It feeds on bacteria, spores and other microbial creatures. When foraging for its food the plasmodium propagates towards sources of food particles, surround them, secret enzymes and digest the food. Typically the plasmodium forms a congregation of protoplasm in a food source it occupies. When several sources of nutrients are scattered in the plasmodium's range, the plasmodium forms a network of protoplasmic tubes connecting the masses of protoplasm at the food sources. When we think of food sources as nodes and protoplasmic tubes as edges, we say the plasmodium develops a planar graph.

Nakagaki et al. [15–17] shown that topology of the plasmodium's protoplasmic network optimizes the plasmodium's harvesting on distributed sources of nutrients and makes more efficient flow and transport of intra-cellular components. Therefore the plasmodium is considered as a parallel computing substrate complementary [5] to existing massive-parallel reaction–diffusion chemical processors [3].

Experimental observations suggest that during development of its protoplasmic network the plasmodium undergoes transitions between various classes of proximity graphs [6]. It starts with spanning trees [4] and may complete its protoplasmic network development as a Delaunay triangulation [23].

One of the key differences between reaction–diffusion chemical processors and *Physarum* machines could be in how they deal with computation of planar graphs [5]. Minding that Belousov–Zhabotinsky (BZ) medium plays a central role in the family of reaction–diffusion computers [3] we can express the difference as follows:

*Given a finite set **P** of planar points, Physarum polycephalum computes a spanning tree of **P** while Belousov–Zhabotinsky medium could not.*

In the Letter we demonstrate that excitation waves in sub-excitable BZ medium behave similarly to pseudopodia of *Physarum*, when sources of nutrients, chemo-attractants for the plasmodium, are represented by illumination gradients, 'photo-attractants' for excitation waves, in BZ medium. The wave-fragments are capable for navigating shortest paths towards source of attraction. Moreover trajectories of the wave-fragments represent edges of a tree spanning the attractant points. In simulation experiments with BZ medium and laboratory experiments with *Physarum* we show the following.

If wave-fragments in sub-excitable BZ medium did leave permanent traces the BZ medium would compute the same spanning trees as Physarum polycephalum does.

The Letter is structured as follows. In Section 2 we outline experimental setup for *Physarum* and numerical models of sub-
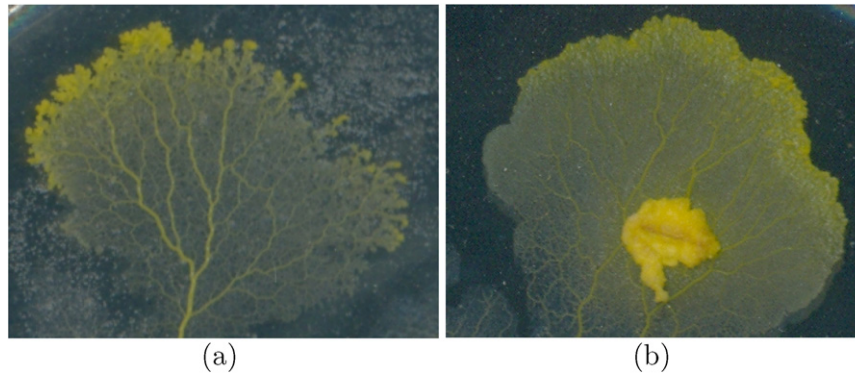

Fig. 1. Photographs of propagating pseudopodia of *Physarum polycephalum*. In (a) pseudopodium propagates following gradients of chemo-attractants and humidity. In (b) the pseudopodium just occupied the oat flake, source of nutrients, and then expands further.

excitable BZ medium. Results of simulation and analogies between excitation wave-fragments and pseudopodia are discussed in Section 3. Some limits of the approach analysed and possible directions of future research are outlined in Section 4.

2. Methods

The plasmodia of *Physarum polycephalum* were cultured on wet Letter towels, fed with oat flakes, and moistened regularly. We sub-cultured the plasmodium every 5–7 days. Experiments on growing spanning trees were undertaken in standard Petri dishes, 9 cm in diameter. A substrate was a wet filter Letter. We preferred the filter Letter not 2% agar gel, because the Letter offers less favoured conditions for the plasmodium growth, and thus less branching of the propagating pseudopodia is observed (see details in [7,27]). The Petri dishes with plasmodia were kept in darkness and only exposed to light during observation and recording of images.

Data points, to be connected by protoplasmic graphs, were represented by oat flakes. Photographs of the protoplasmic networks, developed by the plasmodium, were made using the digital camera FinePix S6500.

A profile of pseudopodium's tip is isomorphic to shapes of wave-fragments in sub-excitable media. When pseudopodium propagates, two processes occur simultaneously – propagation of the wave-shaped tip of the pseudopodium and formation of the trail of protoplasmic tubes. Examples are shown in Fig. 1(a), (b). We simulate the first process, tactic traveling of pseudopodia, by excitation wave-fragments, and the second process is imitated by erosion operation applied to the history of excitation in the medium.

We simulate foraging behaviour of *Physarum* with two-variable Oregonator equation [11,30] adapted to a light-sensitive BZ reaction with applied gradients of illumination [8,13]:

$$\frac{\partial u}{\partial t} = \frac{1}{\epsilon}\left(u - u^2 - (fv + \phi)\frac{u - q}{u + q}\right) + D_u \nabla^2 u,$$

$$\frac{\partial v}{\partial t} = u - v.$$

The variables u and v represent local concentrations of bromous acid HBrO$_2$ and the oxidized form of the catalyst ruthenium Ru(III), ϵ sets up a ratio of time scale of variables u and v, q is a scaling parameter depending on reaction rates, f is a stoichiometric coefficient, ϕ is a light-induced bromide production rate proportional to intensity of illumination.

The ϕ is an excitability parameter. Moderate intensity of light will facilitate excitation process, higher intensity will produce excessive quantities of bromide which suppresses the reaction.

There is no diffusion term for v because we assume the catalyst is immobilized. To integrate the system we used Euler method

with five-node Laplasian operator, null boundary conditions. time step $\Delta t = 5 \times 10^{-3}$ and grid point spacing $\Delta x = 0.25$, with the following parameters: $\phi = \phi_0 - \alpha/2$, $A = 0.0011109$, $\phi_0 = 0.0766$, $\epsilon = 0.03$, $f = 1.4$, $q = 0.022$.

When adjusting parameters of the model we took into account that a decrease in ϵ results in unbounded growth of excitation activity, while by increasing f we may roughly control shapes of propagating wave-fronts. The parameters correspond to a region of higher excitability of the sub-excitability mode [18,22]. When a medium is in excitable mode a local disturbance leads to formation of circularly expanding target waves (classical excitable medium). In the sub-excitable mode local stimulation does not usually cause a propagating patterns of excitation. However, media being at the edge of sub-excitable and excitable modes exhibit self-localized excitations: a local disturbance leads to formation of traveling excitation wave-fragments which preserve their shape for finite period of time and then either expand or collapse. Exact fate (collapse or expand) of a wave-fragment is determined by size and geometry of initial local disturbance and particulars of the illumination profile.

The parameter α imitates source-dependent gradient of illumination in BZ medium, which corresponds to a gradient of chemo-attractants emitted by sources of nutrients in *Physarum* environment. Let P be a set of attraction sites, sources of nutrients, and x be a site of a simulated medium then $\alpha_x = 2 \times 10^{-2} - \min_{p \in P}\{d(x, p): \gamma(p) = \text{TRUE}\} \cdot b^{-1}$ where $3100 \leqslant b \leqslant 4900$ and $d(x, p)$ (for the simulated medium 400×400 sites) is an Euclidean distance between sites x and p. Parameter $\gamma(p) \in \{\text{TRUE}, \text{FALSE}\}$ characterizes activity of the attraction site (a source of nutrients). At the beginning of simulation $\gamma(p) = \text{TRUE}$ for all sites of P. A site p becomes inactive as soon as it is covered by an excitation wave-front: if $u_p > 0.1$ then $\gamma(p) = \text{FALSE}$. This conditions allows us to take into account that a source of nutrients covered by *Physarum*'s pseudopodium ceases its production of chemo-attracts, and thus does not influence behavior of other pseudopodia.

The medium is perturbed by an initial excitation, when 11×11 sites are assigned $u = 1.0$ each. The perturbation generates a circular excitation wave, which later splits into one or more wave-fragments when affected by heterogeneous illumination field α. The simulation ends when all source of nutrients are inactive: for any $p \in P$ $\gamma(p) = \text{FALSE}$.

The simulation setup above allows us to imitate propagation of protoplasmic pseudopodia by excitation wave-fragments and navigation of pseudopodia in gradient fields of chemo-attractants. Additional constructs are required to simulate transformation of pseudopodium's tip to protoplasmic tubes.

During the simulation values of variable u are stored in matrix L. For any site x and time step t if $u_x > 0.1$ and $L_x = 0$ then $L_x = 1$. At the end of simulation we repeatedly apply the erosion operation to matrix L. For any site x if $L_x = 1$ and $m_1 \leqslant \sigma_x < m_2$