Current reinforcement model reproduces centre-in-centre vein trajectory of *Physarum polycephalum*

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Abstract

Vein networks span the whole body of the amoeboid organism in the plasmodial slime mould *Physarum polycephalum*, and the network topology is rearranged within an hour in response to spatio-temporal variations of the environment. It has been reported that this tube morphogenesis is capable of solving mazes, and mathematical model, named the 'current reinforcement rule', was proposed based on the adaptability of the veins. Although it is known that this model works well for reproducing some key characters of the organism's maze-solving behaviour, one important issue is still open: In the real organism, the thick veins tend to trace the shortest possible route by cutting the corners at the turn of corridors, following a center-in-center trajectory, but it has not yet been examined whether this feature also appears in the mathematical model, using corridors of finite width. In this report, we confirm that the mathematical model reproduces the center-in-center trajectory of veins around corners observed in the maze-solving experiment.

Keywords: slime mold, mathematical model, current reinforcement

1 Introduction

The plasmodium of *Physarum polycephalum* (true slime mould) is an expansive (over several cm^2 wide) and multi-nuclear diploid stage of the amoeboid body

and forms an intricate network of veins within the huge body. Through this vein network, protoplasmic material and signals are circulated(Kamiya1959). In 2000 it was reported that the veins are capable of solving mazes: a thick vein developed to connect two food-locations at the exits of the maze, choosing the shortest among many route options (Nakagaki *et al.* 2000; Nakagaki *et al.* 2001; Nakagaki *et al.* 2004a; Nakagaki *et al.* 2004b; Nakagaki *et al.* 2007; Tero *et al.* 2010). As the mechanism behind this vein development it was found that vein growth adapts to the streaming through the veins, which became known as the 'current reinforcement rule' (Nakagaki *et al.* 2000b; Tero *et al.* 2007; Nakagaki & Guy 2008; Ma *et al.* 2012; Guy *et al.* 2011). As this finding sheds light on the interaction between pattern formation of the cell shape and behavioural efficiency, further studies were initiated thereafter (Adamatzky & Jones 2010; Baumgarten *et al.* 2010; Fessel *et al.* 2012; Adamatzky 2014).

Although these studies indicated how the shortest path through the maze between two food-locations was selected, there are still open questions as to the potency of current reinforcement model. In this report, the conventional mathematical model for current reinforcement is examined by comparing it more closely to the results of the maze-solving experiment. In particular, the veins in the real organism follow a center-in-center line when turning at a corner. In this way, the plasmodium attains a shorter total length of the vein network. But it is not yet known whether this character is reproduced well by the model. In the previous studies, such trajectory as a center-in-center line at a corner was presumed and distance of each route in a maze was set along this presumed trajectory. Therefore, we will focus on whether the modelled vein traces a center-in-center trajectory when turning at a corner or crossing a crossroads in the maze.

2 A pending issue left in the mathematical modelling of maze solving by vein morphogenesis

First, in order to elaborate on the objective of this report, we point out the significance of the issue that has been left out in the original reports (Nakagaki *et al.* 2000; Nakagaki *et al.* 2001).

2.1 Topology and configuration of the maze

The configuration of the maze, shown in Fig. 1a, b, was the same as in the original reports (Steinbock *et al.* 1995; Nakagaki *et al.* 2000). Gray parts are walls of the maze and white parts are the corridors. Black dots indicate the locations where the food sources were presented.

Figures 1a and 1b show two possible patterns for the connecting path (thick black line): turning at a corner at a right angle, or cutting the corner by touching its inner edge. In the latter, the total length of the connecting path is smaller.

In particular, in this shape of the maze, there are two opportunities for the organism to choose among two different 'solution' paths, that is, in Figure 1a,

choosing $a1$ or $a2$ in the lower right part of the maze, and choosing $b1$ or $b2$ in the left half of the maze. The trajectories $a1$ and $a2$ are of equal length, but $\alpha 2$ is shorter than $\alpha 1$ in Figure 1b when tracing the inner edge of corner. The trajectory $b1$ is longer than $b2$, but $\beta 1$ is slightly shorter (ca. 2%) than $\beta 2$.

In this report, we will reconfirm the real trajectories of the veins in the experiment and examine this character by mathematical modeling of the vein development. We reproduced the same experiments as originally reported before (Nakagaki *et al.* 2001; Nakagaki *et al.* 2007), and indicated the vein trajectory around corners and crossroads of the maze.

2.2 Center-in-center trajectory of connecting veins between two food locations when turning at a corner of the maze

Figures 1c-f show some typical morphologies of vein networks that connected the two food sources (F) in the maze, observed several hours after the presentation thereof. When turning at a corner, the vein tended to cut the inner side of the corner (indicated by the white arrows), although the vein trajectory was often meandering (i.e., not a straight line). When extending across a crossroads of corridors, the veins tended to trace an oblique line relative to the nearby edges and corners (indicated by the white arrow heads). These two characters of vein trajectories were frequently but not always observed.

Another point to be noted is the variety of network patterns. Figure 1c shows that the thick vein passed through the shortest route consisting of paths $\alpha 2$ and $\beta 1$. In Figures d, e, and f, other paths were chosen. This variation was affected by meandering of the vein trajectory, the initial volume of the inoculated organism, and the amount of food, as shown in previous reports (Nakagaki *et al.* 2001; Nakagaki *et al.* 2007b).

3 Re-examination of the current reinforcement rule for vein development

3.1 Outline of current reinforcement dynamics

As a morphogenetic mechanism for the vein network formation, Tero, Kobayashi *et al.* (Tero *et al.* 2007) proposed a simple but potent set of equations for the vein development, the *current reinforcement model*, which represents the plasmodial body as a random meshwork of tubular channels and describes the change of the diameter of tubes according to the following rule. Roughly speaking, the rule is 'flows more, gets thicker' and 'flows less, gets thinner,' similar to the empirical law pointed out by Jean-Baptiste Lamarck in his book Zoological philosophy in 1809 (Lamarck 1914):

> 'In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually

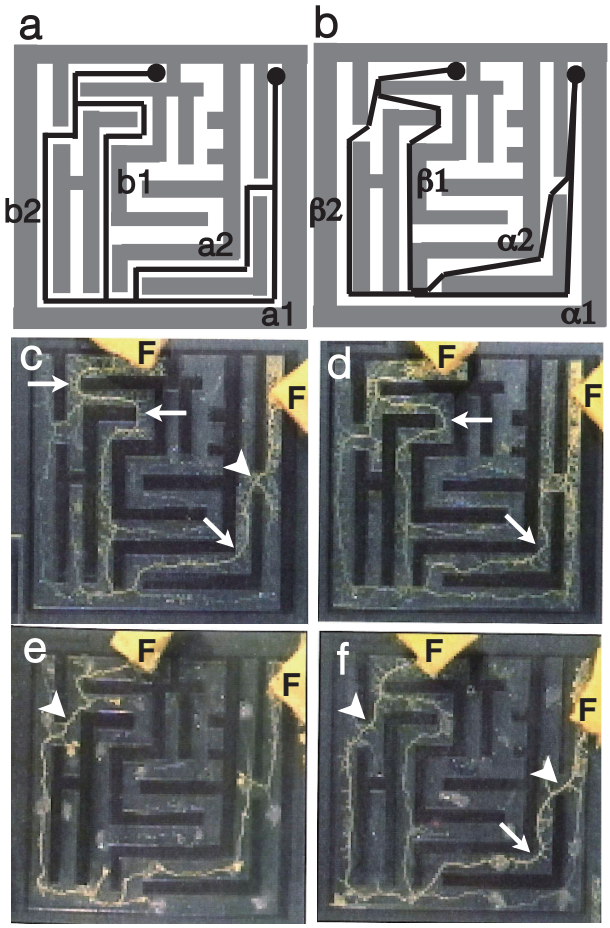

Figure 1: Snapshot of vein networks that connected two food locations (F) in the maze. (a)-(b) Schematic illustration of the maze geometry used in the experiment. The food sources are represented by black dots (a): Thick solid lines indicate the trajectories of veins turning at right angles. (b): Shorter trajectory with oblique lines passing through the crossroads of corridors. There are two routes through the lower right (namely a1 and a2 in Fig. 1a) and through the left (b1 and b2). The length of routes a1 and a2 (a) is equal, but $\alpha 1$ is longer than $\alpha 2$ (b). Route b1 is longer than b2 (a) but $\beta 1$ is slightly shorter than $\beta 2$. (c)-(f): Some typical examples of vein trajectories in the real organism. Arrows indicate a curving trajectory at a corner and arrowheads point out an oblique trajectory. (c) 6 hours and (d-f) 13 hours after the the presentation of food sources. This data reproduced results of experiments previously performed (Nakagaki *et al.* 2000; Nakagaki *et al.* 2001).

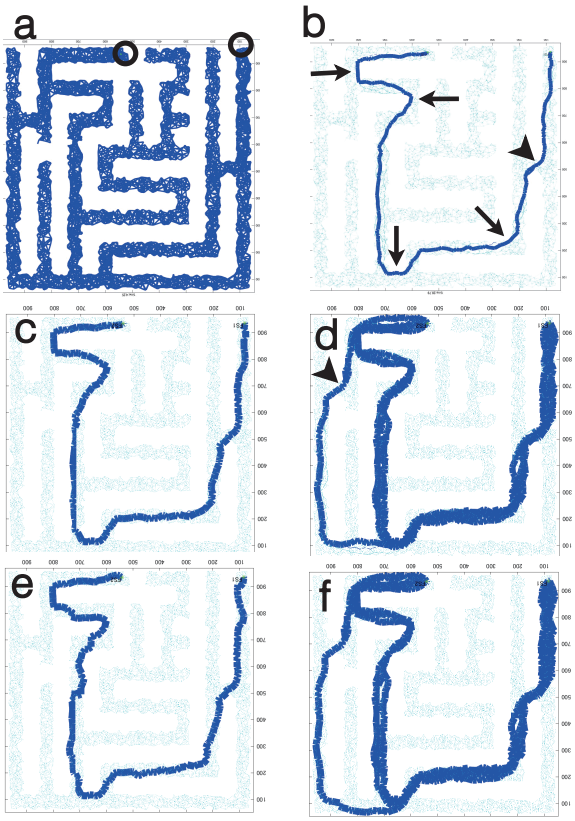

Figure 2: Numerical simulation of the mathematical model for the current reinforcement rule in the 2-dimensional maze. (a) Setup. The body filled all corridors of the maze, represented by a random meshwork of veins. The open circles indicate the locations of the food sources. The trajectory of the remaining vein has a degree of freedom: which course it traces within the corridor, in particular, when turning at a corner or crossing a crossroads. (b) Steady state of the numerical simulation when $f(|Q|) = |Q|^{1.33}$ and $Q_0 = 1$. (c)-(f) Trajectory of the remaining vein when $f(|Q|) = \{(1+a)|Q|^{\mu}\}/\{1+a|Q|^{\mu}\}$ and $Q_0 = 1$. (c) $(\mu, a) = (1.5, 0.5)$, (d) $(\mu, a) = (1.5, 10)$, (e) $(\mu, a) = (3, 6)$, (f) $(\mu, a) = (3, 1000)$. Arrows indicate a curving trajectory at a corner and arrowheads point out an oblique trajectory through a crossroads. The single vein was formed between two food-sources in (b), (c) and (e). Multiple veins were formed in (d) and (f). The thickness of the line indicates the flow through the vein.

> strengthens, develops and enlarges that organ, and gives it a power proportional to the length of time it has been so used; while the permanent disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity, until it finally disappears.'

Compared with other models for network formation in *Physarum* (Gunji *et al.* 2008; Jones 2010; Liu *et al.* 2013; Liu *et al.* 2015), it is characteristic of current reinforcement dynamics to have an expression as differential equations and to consider fluid dynamics. Here we begin with a brief summary of the Tero-Kobayashi model (Tero *et al.* 2007).

In the model, the body of the plasmodium is represented by a network of veins, and the flow through the network is considered according to the law of mass conservation under some assumptions for the sake of simplicity. Then, the current reinforcement rule adapts vein thickness and flow conductivity of the vein according to the flow rate through the vein itself.

An assumption of the model is volume conservation of the flowing fluid. In the model, the vein network in *Physarum* is represented by a graph consisting of edges and vertices. Suppose that vertices i and j, at which the pressure is P_i and P_j, respectively, are connected by the channel ij with uniform diameter r_{ij} and length L_{ij}. The flow rate Q_{ij}, with consideration of the flow direction, is now defined as

$$Q_{ij} = \frac{\pi r_{ij}^4}{8\eta L_{ij}}(P_i - P_j). \tag{1}$$

Then, flow conservation is implemented at vertex i as

$$\sum_j Q_{ij} = J_i, \tag{2}$$

where J_i is a nonzero constant only if vertex i is a source or sink of the current (the food-source). In addition, J_i is assumed to satisfy

$$\sum_i J_i = 0 \tag{3}$$

for feasibility of finding flows.

Here, letting D_{ij} denote the conductivity per length $\pi r_{ij}^4/8\eta$, which means

$$Q_{ij} = \frac{D_{ij}}{L_{ij}}(P_i - P_j), \tag{4}$$

we set the current reinforcement rule (Nakagaki *et al.* 2000b; Tero *et al.* 2007; Nakagaki & Guy 2008; Ma *et al.* 2012; Guy *et al.* 2011):

$$\frac{\mathrm{d}D_{ij}}{\mathrm{d}t} = f(|Q_{ij}|) - D_{ij}, \tag{5}$$

where f is a monotonically increasing continuous function satisfying $f(0) = 0$ (here we call this function $f(|Q_{ij}|)$ 'current reinforcement function'). Essentially,

Eq. (5) is a differential equation of the radius r_{ij}, because we assume constant viscosity η and length L_{ij}.

If the current sources and sinks are given with J_i at the food-sources, and L_{ij} and r_{ij} of all channels are known, all Q_{ij} can be determined by solving the system of linear equations (Tero *et al.* 2007). Once the flow through the network is known, the current reinforcement rule can modify the thickness of each channel for the next time step according to the flow it is carrying.

Eq. (5) contains two antagonistic components: $f(|Q_{ij}|)$ represents a thickening factor that increases with the current, whilst $-D_{ij}$ is an intrinsic thinning factor. Thus, the thickening component dominates for a channel with a larger current, and the thinning effect dominates for one with smaller current at each time step. The complete temporal evolution of the network is then calculated iteratively with the updated conductivities. Regarding food sources as sources and sinks, the current reinforcement dynamics reproduce vein networks of slime mold (Nakagaki *et al.* 2007a; Tero *et al.* 2007; Tero *et al.* 2010).

3.2 Numerical simulation for the vein network in the maze

Figure 2a shows the setup of plasmodial veins as a fine meshwork that fills the maze, the two black circles indicating the location of food sources. At the initial condition, the thickness of the network's veins was homogeneous.

Figure 2b shows the single trajectory of a vein that connected the two food locations when the current reinforcement function was $f(|Q_{ij}|) = |Q_{ij}|^{\mu}$ with $Q_0 = 1$. We assumed $\mu = 1.33$ because of the recent suggestion from a comparison between experiment and model (Akita *et al.* 2017). As indicated by the black arrows, the vein tended to cut to the inner side when turning at a corner. This character was similar to what was observed in the actual organism.

When passing a crossroads of the maze, the vein traced an oblique line relative to nearby walls (indicated by the black arrow heads in Figure 2b). This, too, is similar to the trace of actual plasmodial veins.

Figures 2c-f show the network shapes for different forms of the current reinforcement function $f(|Q_{ij}|) = \{(1+a)|Q_{ij}|^{\mu}\}/\{1+a|Q_{ij}|^{\mu}\}$ and $Q_0 = 1$: the model parameters (μ, a) were $(1.5, 0.5)$, $(1.5, 10)$, $(3, 6)$, $(3, 1000)$ in Figures c, d, e and f, respectively. It can be seen that different values of the model parameters change whether or not parallel veins are maintained, but the vein trajectories around the corners is unaffected by a change in parameters presented in Figure 2. A consequence of this is that, while there is, of course, a dependence of the solution on the form of the current reinforcement function and its parameters, the characteristics of the solutions are robust over a certain range of parameters. For example, all vein trajectories shown in Figures 2c - f traced a center-in-center line.

4 Discussion

The length of the path between two locations in a maze depends on the position of the vein within the width of the corridor. When turning at a corner or passing a crossroads, it is efficient for connecting veins to follow a line closer to the edge of the corner so as to reduce the total length of the trajectory. If there are multiple crossroads and corners close to each other, it may not be trivial to find the shortest path. We showed that the current reinforcement rule alone, described by a set of simple equations, works well even in the complicated situation of a maze. This finding, therefore, sheds light on the the mechanism behind the surprising ability of *Physarum polycephalum* to find efficient paths through complicated arenas.

The vein trajectory generally depends on the form of the function $f(|Q_{ij}|)$ as shown in the numerical simulation and previous reports. When $f(|Q_{ij}|)$ is $|Q_{ij}|^{\mu}$ and $\mu = 1$, the shortest trajectory is selected from the random meshwork (Tero *et al.* 2007; Tero *et al.* 2010). However, it may take an unpractically long time to find the shortest out of many routes whose distances are very similar, since the speed of competition among these options depends on the difference of the distances. In the random meshwork tested in this report, there are many combinations of edges with similar overall length, especially around corners and crossroads. This means that we often couldn't observe single thick veins appearing around corners, while they clearly appeared in straight parts of the corridor. As such behaviour was not observed in the experiments, the assumption of $\mu = 1$ was not realistic.

In the recent comparison of the parameter μ with experimental results, it turned out that $\mu = 1.33$ was plausible. For this value, the speed of competition between veins of similar distance is much higher than at $\mu = 1$. Therefore, we suggest that $\mu = 1.33$ is reasonable when we assume the current reinforcement function of the form $f(|Q_{ij}|) = |Q_{ij}|^{\mu}$.

However, in $f(|Q_{ij}|) = |Q_{ij}|^{1.33}$, the shortest trajectory was not always selected, and a trajectory with a slightly greater length was selected due to initial small fluctuations of the vein thickness. In the actual experiments, too, we often observed that a vein developed along a longer route, and not only along the shortest one in the maze. This hints at this form of the current reinforcement function modelling the mechanism in the actual organism quite well.

Next, we want to briefly discuss the assumption of Hagen-Poiseuille flow in the mathematical model. As experimental facts on protoplasmic streaming within the plasmodium, studies in the 1950s using cinematographs found that the velocity profile across the diameter of the vein is a parabola whose apex is flattened when the flow speed is very slow (Kamiya 1959). In 2009, the imaging technique employed by Bykov *et al.* obtained a parabolic velocity profile at the top speed of shuttle streaming (Bykov *et al.* 2009). Both these findings support the assumption of Hagen-Poiseuille flow.

The current reinforcement rule was studied from a physical and/or molecular point of view in *Physarum* (Stockem & Brix 1994; Takamatsu *et al.* 2000; Takamatsu & Fujii 2002), and in general (Murray 1926; Sherman 1981; Kunita

et al. 2012; Haskovec *et al.* 2015; Haskovec *et al.* 2016), as similar rules are observed in other systems of biological transport networks. On the overall organisation of transport networks in living and nonliving systems, some physical laws have been found and studied physically and mathematically (West *et al.* 1997; Banavar *et al.* 1999; Dodds 2010; Corson 2010; Katifori *et al.* 2010; Hu & Cai 2013). The *Physarum* network is a very tractable model system to study the transport capacity of networks in living systems and its underlying physical principles since modelling studies on physically and biologically well-examined dynamics of cell movement have been published very actively in the last several years (Teplov *et al.* 1991; Radszuweit *et al.* 2010; Ueda *et al.* 2011; Alim *et al.* 2013; Radszuweit *et al.* 2013; Radszuweit *et al.* 2014; Alonso *et al.*2016; Lewis *et al.* 2015).

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