Cell Motility Viewed as Softness

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ABSTRACT

In this paper, the authors propose a simple model of cell motility inspired by the plasmodium of Physarum polycephalum. The model focuses on the “softness” of aggregations of protoplasm. The model has only two parameters, yet generates a variety of final states, as well as the morphological changes of Physarum according to the condition of the culture medium.

Keywords: Cell Model, Exploration–Exploitation Dilemma, Morphological Changes, Physarum, Softness

1. INTRODUCTION

All living organisms have evolved to survive under some set of external conditions. Put another way, they are organized as an entity capable of sustaining further organization. The plasmodium of the true slime mold Physarum polycephalum, one of the most primitive living organisms, is no exception. The conditions of the culture medium determine the pattern of Physarum’s body formation (Takamatsu, Takaba, & Takizawa, 2009). The plasmodium quickly shows isotropic and homogeneous patterns under favorable conditions, and anisotropic and heterogeneous patterns under unfavorable conditions.

Such morphological changes can be interpreted as a balancing act between the exploration of new possibilities and the exploitation of given certainties (March, 1991). The isotropic body is suited to stable exploitation of food located near the body, a favorable condition. If food is not present near the body, however, the organism must explore. This is not an unfavorable situation, as an anisotropic body form is suited to efficient exploration, making good use of available resources (the body itself). To survive, the organism figuratively takes a gamble by narrowing itself to increase its range of exploration, an example of a living organization facing the choice between exploration and exploitation.

Protoplasm flows easily in the sol state, but less so in the gel state. In this study we focused on these aspects, simplifying the distinction between sol and gel states to the amount of protoplasm in a given location. This simplification enabled a simple model of cell motility, one that describes cytoplasmic streaming using only the amount of protoplasm. We call this integrated representation of the sol and gel states a “representation by softness.” Cell body softness is comparable to the plasticity

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explores its surrounding space by exploiting cytoplasmic resources. Our goal is to elucidate the biological mechanism of exploration by massive cellular organisms, and to understand the underlying mechanism in adaptive plasmodium computation.

2. MODEL

Here we describe our model of cell motility. The model is intended to simulate features of the plasmodium of Physarum polycephalum (Figures 1 and 2). At each site in a two-dimensional square lattice, a nonnegative integer corresponding to the amount of protoplasm is assigned. A zero indicates an absence of protoplasm. The cell body is thus represented by the allocation of positive numbers.

In the next step, two parameters $u$ and $d$ are introduced as follows:

- $u$, the upper limit of the amount of protoplasm at each site.
- $d$, the upper limit of the difference in the amount of protoplasm between two adjacent sites that allows a cytoplasmic flow between them. The protoplasm can move between two sites within this limit.

According to Takamatsu, Takaba, and Takizawa (2009), the contact angle is defined as the angle between the substrate boundary line and a tangential line at the meeting point of the boundaries of the substrate and the plasmodium. The contact angle is therefore directly proportional to the amount of protoplasm. Thus, the amount of protoplasm (and its upper limit $u$) at a peripheral site corresponds to the contact angle. The parameter $d$ directly corresponds to the spread angle defined by Takamatsu et al. as the angle between the tangential lines on the side of a fan (Figure 3). The parameter $d$ is directly proportional to the spread angle. In addition, the model shows various complicated features according to the parameter $u$ and $d$ (Figure 4). In Figure 4(b), the number of protoplasm of the left site is the upper limit $u$, therefore,
the site is “hard” one. In Figure 4(c), the left site has “hardened” because of the value of $d$ though the number of protoplasms is less than the upper limit $u$.

The details of the algorithm based on the parameters $u$ and $d$ are as follows.

1. Initial allocation: A square aggregation of protoplasm is allocated in the center of a sufficiently large square lattice. At each site in the square, a random number of 3 to 10 protoplasms are assigned. A central site of the square is chosen as the initial site $(x, y)$. 

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Figure 1. The plasmodium of Physarum polycephalum

Figure 2. Example time evolution of the plasmodium of Physarum polycephalum: (a) initial state, (b) 630 min, (c) 930 min, (d) 1030 min, and (e) 1090 min
2. With probability 0.9, a new site is randomly chosen from the sites within a circle whose center and radius are \((x, y)\) and 3, respectively. The new site is renamed as \((x, y)\). With remaining probability 0.1, the new site is instead randomly chosen from among all sites with a positive number of protoplasms.

3. A left, right, upward, or downward direction is randomly chosen. The site adjacent to \((x, y)\) in the chosen direction is named \((\text{new}x, \text{new}y)\).

4. If the number of protoplasms at \((\text{new}x, \text{new}y)\) is less than \(u\), and the absolute value of the difference of the number of protoplasms between \((x, y)\) and \((\text{new}x, \text{new}y)\) is less than or equal to \(d\), one protoplasm is moved from \((x, y)\) to \((\text{new}x, \text{new}y)\), and a time counter is incremented by 1.

5. If the number of protoplasm at \((x, y)\) becomes 0, a continuity check over all sites with a positive number of protoplasm is performed (i.e., the presence of isolated parts is determined). If isolated parts exist, the move and the time counter increment are canceled.

6. Steps 2 through 5 are iterated until the time counter reaches a predefined number.

Figure 3. Behavior of the model according to the parameter \(d\). If \(d\) is low, movable directions may be limited though other conditions are identical.

Figure 4. Behavior of the model according to the parameters \(u\) and \(d\). (a) Both directions are movable. (b) Only right direction is movable because of the value of \(u\). (c) After one protoplasm moves from the right site to the left one, both directions become immovable because of the value of \(d\).
into \((x, y)\) decreases. At a site, a relatively large number of protoplasms indicate a “hard” state, while a small number of protoplasms indicate a “soft” state. For example, if \(u = 10, d = 4\) at a site with 8 protoplasms and 2 protoplasms in each adjacent site, then no protoplasm can move to or from the adjacent sites, despite the number of protoplasms being below the upper limit 10. As another example, if \(d = 4\) and a protoplasm moves from a site with 2 protoplasms to an adjacent site with 6 protoplasms then no subsequent moves between the two sites are possible, because the difference in the number of protoplasms becomes 6. Figuratively speaking, the movement has “hardened” the boundary between the two sites. The parameters \(u\) and \(d\) and protoplasm movement represent “hard” and “soft” states.

Note that some values such as the probability which gives a new site \((x, y)\), the radius of a circle, and the total number of protoplasms are arbitrarily determined. However the values within a certain range do not affect the behavior of the model much. Details are described in a later section.

3. RESULTS

Figure 5 shows examples of morphological development of the model. The initial allocations are identical, but the final figures vary with different settings of the parameters \(u\) and \(d\). When \(u = 10\) and \(d = 10\), an isotropic figure with dense extensions develops. If \(u = 4\) and \(d = 4\), the extension is isotropic but sparse. If \(u = 10\) and \(d = 6\), the extension is both anisotropic and sparse. This case corresponds to taking chances, exploration with limited resources. Figure 6 shows more comprehensive results, with all figures at time \(t = 50000\).

Note that in the cases of \(u = 10, d = 4,\) and \(u = 8, d = 4,\) the figures remain similar to the initial state due to an overabundance of initial protoplasm for those values. Most of the protoplasm is concentrated in the initial sites, so there is little extension to the outside. These are special cases of overly “hard” initial conditions.

To analyze the figures numerically, we use the measures \(E_i\) and \(E_r\) from Gunji et al. (2011) as follows:

- \(O\), the center of gravity of the figure.
- \(A\), the farthest point from the point \(O\).
- \(B\), the farthest point from the point \(A\).
- \(E_i\) (efficiency of exploitation), the length between the points \(A\) and \(B\), normalized according to the area of the figure.
- \(E_r\) (efficiency of exploration), the occupancy rate of the figure in the part of the circle \(OA\) without the circle \(OB\).

Figure 5. Time-evolution examples of the model. Each grayscale dot represents a site. Dots with lower populations are drawn lighter.
Figure 6. Figures of final states (t = 50000). A variety of forms emerge, including a very anisotropic one (u = 10, d = 6). When the difference between u and d are large (u = 10, d = 4; u = 8, d = 4), the figures remain similar to the initial state.

Note that the occupancy rate of $E_r$ is given after each point is covered by a circle with a given radius. $E_i$ is a measure of efficiency of the length between the points A and B. $E_r$ is an index indicating the extent of exploration around the figure’s perimeter.

Table 1 shows $E_i$ and $E_r$ for the final states resulting from various values of $u$ and $d$. When $d$ is fixed, $E_i$ increases in proportion to increases in $u$. If $u$ is fixed, $E_i$ decreases as $d$ increases. In addition, there is a trade-off between $E_i$ and $E_r$ (Figure 7), observable if the two special cases that resulted in negligible transformation ($u = 10, d = 4; u = 8, d = 4$) are ignored. This means that each aggregation of protoplasm in the model chooses between exploration and exploitation, varying its body according to its environment as does Physarum.

Figure 7. Trade-off relation between $E_i$ and $E_r$. Rightmost two dots are the values of $u = 10, d = 4$, and $u = 8, d = 4$. 
4. DISCUSSION

In our model, a “hard” site with a large concentration of cytoplasm has some functions: (i) it has a relatively large number of protoplasms, and thus constitutes the main morphological body; (ii) it serves as a source of protoplasm when pseudopods are extended; and (iii) it serves as a breakwater that prevents an outflow of protoplasm. Here, we demonstrated that functional traits can emerge from a simple model of preferential movement. This is important because the model itself is not designed to be functional. It does not have defined goals or procedures for reaching some state. In the experiments performed there is obvious emergence of an interplay between functionless constituent parts and the organized whole of the system. This is important because the model itself is not designed to be functional. It does not have defined goals or procedures for reaching some state. In the experiments performed there is obvious emergence of an interplay between functionless constituent parts and the organized whole of the system. The cytoskeleton in cells forms tubular structures, while the cytoskeleton itself is formed from tubular structures. The cytoskeleton function emerges as a result of intrinsic properties of tubules constrained by external factors. In the model presented here, such a duality exists between emergent figures and their constrained local points. Another result matching those in organized systems is the observed trade-off between $E_i$ and $E_r$ (Figure 7). Increased exploration leads to decreases in exploitation efficiency, creating further constraints on figure formation and growth. Along with the abovementioned functions of “hard” sites, this is another example of emergence of potentially functional traits. This also suggests that system growth requires the development of some form of multiple centrality, here represented as $(x, y)$. How this can be most simply achieved is a topic for future research.

Step 5 of the algorithm excludes the presence of isolated extensions, confirming unity of the cell body. This setting corresponds to the fact that it is hard for Physarum to break apart. The probability of selecting a new neighboring site in Step 2 is 0.9. This setting promotes a certain level of transformation of the figure. Neither setting is essential for the model. In fact, even if the probability is 0.0, i.e., the new site is randomly chosen from among all sites with a positive number of protoplasms each time, the similar trade-off is observed. If the radius of a circle is 1 instead of 3, the model shows the similar tendency. If the total number of protoplasms increases, the final figure becomes larger; however, the similar tendency still remains.

The directional tendency of Physarum to move in response to external stimuli, for example, thermal stimuli, has been applied within various contexts (Shirakawa, Gunji, & Miyake, 2011; Aono & Hara, 2008; Tsuda, Zauner, & Gunji, 2006). In the present model, a directional tendency for movement can be easily introduced by adjusting the directional probability in Step 3 of the algorithm. For example, rather than assigning equal probabilities for each direction, assigning 0.4 to the right and upward directions

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Table 1. $E_i$ (upper) and $E_r$ (lower) final states. $E_i$ and $E_r$ of the initial state are 0.127 and 1.000, respectively. The covering radius for $E_r$ is 2.
and 0.1 to the left and downward directions would result in an aggregate protoplasm with a tendency to move up and to the right.

Figure 8 shows the morphological change of a protoplasm with such a directional tendency. The protoplasm mass first separates as if unpeeling. It then extends pseudopods composed of protoplasm and serving to convey additional protoplasm. Once pseudopods are fully extended, the body is “dissolved” and used as a resource for further extension in a secondary protoplasm wave.

The parameters \( u \) and \( d \) are constant at all sites in the present model, but we can also introduce interplay between \( u \) and \( d \) after protoplasm movement, and doing so may better mimic actual protoplasm flow. Use of food sources has allowed Physarum to solve mazes (Nakagaki, Yamada, & Toth, 2000; Nakagaki, 2001) and form adaptive networks (Nakagaki, Yamada, & Hara, 2004; Shirakawa & Gunji, 2007) and dynamic changes to \( u \) and \( d \) may allow for representation of similar phenomena with the model. Actual implementation of dynamically changing \( u \) and \( d \) values and analyzing the behavior of the resulting model are topics for future investigation.

As many studies (Adamatzky & Jones, 2008; Adamatzky, 2007, 2010; Adamatzky, DeLacy Costello, & Shirakawa, 2008; Shirakawa, Gunji, & Miyake, 2011; Aono & Hara, 2008; Tsuda, Zauner, & Gunji, 2006; Nakagaki, Yamada, & Toth, 2000; Nakagaki, 2001; Nakagaki, Yamada, & Hara, 2004; Shirakawa & Gunji, 2007) have demonstrated, the plasmodium shows a network-like organized morphology. For instance, the plasmodium explores for nutrients until finding a food source and then transforms its network structure to optimize transportation. In this way, the plasmodium mediates between exploration and exploitation, implying that the plasmodium can shed new light on novel forms of computing.

5. CONCLUSION

We formulated a simple model for representing cell motility. The figure corresponding to a cell is composed of just one type of material. Low and high material concentrations represent sol (“soft”) and gel (“hard”) states, respectively, providing a simple representation of sol-to-gel transformation.

The model has two parameters, which correspond indirectly to features of Physarum, and changing parameters reveals morphological variety similar to that of Physarum. In addition, figures generated by the model represent the dilemma between exploration and exploitation.

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Figure 8. Move implemented with a directional tendency towards the upper right. Secondary wave-like protoplasm movement occurs by use of protoplasm from the dissolved body.
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