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# Smart network solutions in an amoeboid organism

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**Abstract**

We present evidence that the giant amoeboid organism, the true slime mold, constructs a network appropriate for maximizing nutrient uptake. The body of the plasmodium of *Physarum polycephalum* contains a network of tubular elements by means of which nutrients and chemical signals circulate through the organism. When food pellets were presented at different points on the plasmodium it accumulated at each pellet with a few tubes connecting the plasmodial concentrations. The geometry of the network depended on the positions of the food sources. Statistical analysis showed that the network geometry met the multiple requirements of a smart network: short total length of tubes, close connections among all the branches (a small number of transit food-sites between any two food-sites) and tolerance of accidental disconnection of the tubes. These findings indicate that the plasmodium can achieve a better solution to the problem of network configuration than is provided by the shortest connection of Steiner's minimum tree.


*Keywords:* True slime mould; *Physarum*; Small world network; Smart behavior

## 1. Introduction

The body of the plasmodium of *Physarum polycephalum* contains a network of tubular elements by means of which nutrients and chemical signals circulate through the organism in an effective manner [1–3]. Circulation is based on streaming through a complicated network of tubular channels. Thus, the geometry of the channel network is related to the exchange of chemicals within the organism. Since the tubes disassemble and reassemble within a period of a few hours in response to external conditions, this organism is very useful for studying the function and dynamics of natural adaptive networks.

When food sources were presented to a starved plasmodium that was spread over the entire agar surface as shown in Fig. 2a1 (the yellow shape corresponds to the organism), it concentrated at each food source. Almost the entire plasmodium accumulated at the food sources and covered each of them in order to absorb nutrient. Only a few

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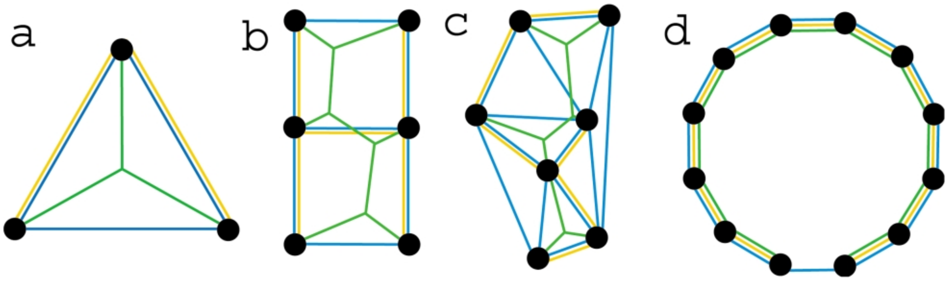


Fig. 1. Schematic illustration of the arrangement of food sources. Black dots indicate positions of the food sources. (a) three food sources at the vertices of an equilateral triangle, (b) 6 food sources at the vertices of two adjoining squares, (c) 7 food sources in an irregular arrangement, (d) 12 food sources at the vertices of a regular 12-gon. The orange, green and blue lines represent the network of minimum spanning tree (MST), Steiner's minimal tree (SMT) and Delauney triangulation network (DTN), respectively. There are other MSTs in arrangement b and c, but a MST with small AS is shown.

thick tubes remained connecting the quasi-separated components of the plasmodium (see for example Fig. 2a3). Since the driving force for transportation is the difference of hydrostatic pressure along the tube, hydrodynamic theory implies that thick short tubes are in principle the most effective for transportation. By forming such a pattern, the organism derives the maximum of nutrient in the minimum of time. Hence this strategy is rather smart; it implies that the plasmodium can solve a complex problem. In order to investigate how this is done we studied the shape and properties of the tube networks formed in response to several different arrangements of food sources, distributed as shown in Fig. 1.

## 2. Methods

### 2.1. Organism and culture

The plasmodium of *Physarum polycephalum* was used. The sclerotia, which is a resting stage in the life cycle, formed on a filter paper ($5\times20$ $cm^2$) were soaked in water once and put on the plain agar gel (1%) in a trough ($35\times25$ $cm^2$). After 10 h, the plasmodium regenerated from the sclerotia and extended over the agar gel. The frontal part of the plasmodium was cut into many pieces ($0.5\times0.5$ $cm^2$), which were served for experiments.

### 2.2. Preparation of required shapes of the plasmodium, as the initial conditions prior to the application of food-sources

For the configuration of three food-sources as shown in Fig. 1a, a negative pattern of the circle shape was cut out from plastic film (Fuji Xerox) and placed on the surface of a plain agar gel. The plasmodium tended to remain on the wet surface of the agar that was not covered with the plastic film, since it avoided dry surfaces. Several pieces of the plasmodium ($0.5\times0.5$ $cm^2$, as described above) were placed on the agar; after a few hours they extended and coalesced into a single organism covering the available agar surface. This is the initial conditions of the plasmodium just before the application of food-sources.

For the different configurations of 6 and 7 food-sources as shown in Fig. 1b,c, the initial shape of the plasmodium were a rectangle and a pentagon, respectively, which were the smallest convex polygons which contained all sites of food-source. For 12 food-sources in Fig. 1d, the initial shape was a circle. In these preparations of initial shapes, a negative pattern of the required shape was cut out from plastic film and put on a plain agar gel. Then the following procedures were the same as the case of 3 food-sources.

### 2.3. Application of food-sources

The plasmodium was presented with food sources according to one or the other of two

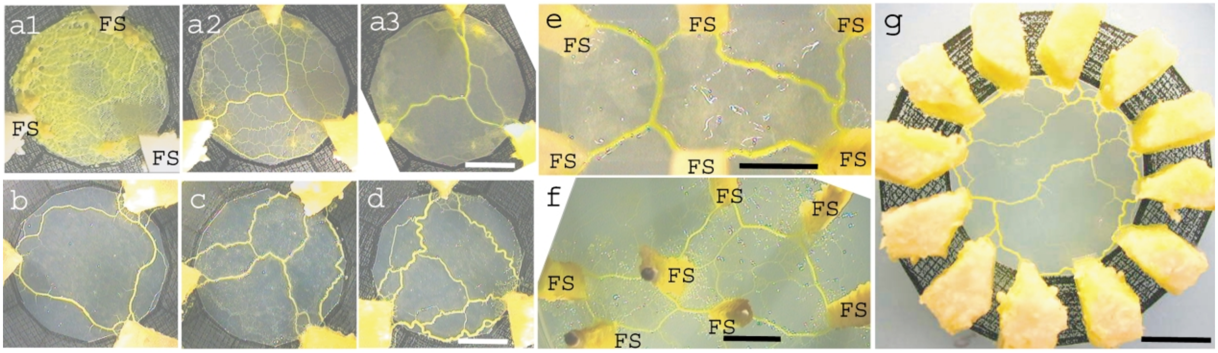


Fig. 2. Typical tube networks with (a–d) three, (e) 6, (f) 7 and (g) 12 food sources. The organism itself is yellow. (a) Networks at 0 (a1), 6 (a2) and 36 (a3) h after application of the food sources. (b–d) three typical networks in ascending order of TL at 30–35 h after application of the food sources. Scale bars at the bottom right of each figure represent 1 cm. FS: food source. Figures (e) and (f) were obtained by experimental procedure 2, and these networks are not viewed from right above but from diagonally above, in order to give a good picture of the networks.

procedures. Procedure 1: when the set of positions of the food sources was convex, as shown in Fig. 1a,b,d, agar blocks containing ground oat flakes (0.1 g/ml) were placed on the plastic film with a small part of the block exposed to the plasmodium. Procedure 2: when the set of positions was not convex, as shown in Fig. 1c, columns of food-agar supported by a stick (5 cm in height) were stood on the agar plate after removing the plastic film. In each case, tube morphology was observed at regular intervals after presenting the food. The results obtained using the configurations of Fig. 1a,b,d, were the same whichever procedure was used, but procedure 1 was generally employed because it is easy to handle and convenient for observing the network from above.

### 2.4. *Evaluation of smartness in network shape*

In order to evaluate the shape of a tube network, we introduce criteria derived from the recent theory of adaptive self-organizing networks [4–7]: 'average degree of separation (AS)' and 'fault tolerance (FT)', and, in addition, total length of the tubular system (TL). Some modification of these measures is, however, necessary when applying them to the plasmodial network. Thus, degree of separation is here defined as the number of transit food sources through the shortest path between two food sources. If two sources are connected directly by a tube, the degree of separation is zero because no transit site is necessary. Notice that a bifurcating tube counts as one tube. AS is the degree of separation averaged over all pairs of food sources, and decreases as food sources are more closely coupled. Here we focus on the connectivity of food sources and neglect the effect of tube length on AS.

FT is the probability that the organism is not fragmented if an accidental disconnection occurs at a random point along the tubes. Since the probability of disconnection of a tube is proportional to its length, a longer tube has a higher risk of disconnection. We use the combined index FT/TL, which expresses the ratio of benefit to cost. The networks are thus characterized by AS and FT/TL (see Fig. 3). For comparison, we refer to some well known networks: the minimum spanning tree (MST), the Steiner minimal tree (SMT) and the Delaunay triangulation network (DTN). Roughly speaking, the former two have short TL and low FT, while DTN has relatively high FT at the expense of TL. Fig. 1 depicts these three types of network for the spatial configurations used in our experiments.

## 3. Results

Fig. 2a–d reproduce some plasmodial tube networks we observed in response to food sources

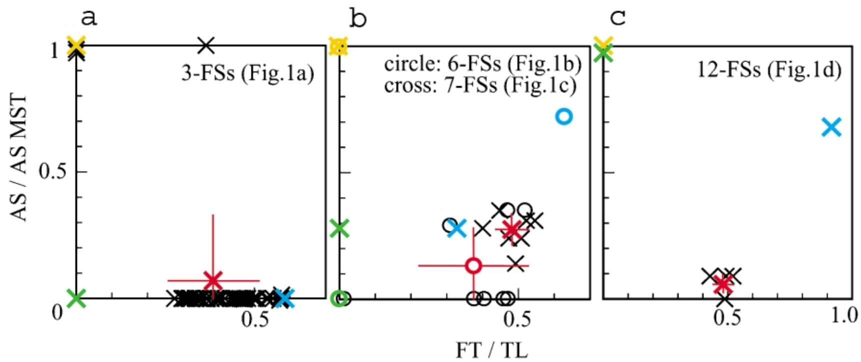


Fig. 3. Properties of the plasmodial transportation networks, defined by AS and FT/TL. Black symbols indicate the values for each specimen of plasmodium, and red, the averages of these values (mean and S.D.). Orange, green and blue symbols give the values of MST, SMT and DTN, respectively, depicted in Fig. 1. (a) three food sources, (b) 6 (circle) and 7 (cross) food sources, (c) 12 food sources. Values of AS are normalized to that of MST.

located at the vertices of an equilateral triangle. At the outset the plasmodium formed a fairly uniform circular sheet of tubes over the surface of the wet agar (a1:0 h). After the food sources had been present for a while most of the tubes had disappeared and a network of fine tubes took their place (a2:6 h). Later there remained only a few thick tubes connecting all three major components of the plasmodium (a3:30 h). The shape of the tube network varied considerably on different agar plates, as shown in Fig. 2b–d in ascending order of TL, where TL is normalized to TL of SMT. In each case only a few thick tubes connected the three plasmodial components.

Typical tube networks formed in response to 6, 7 and 12 food sources located as shown in Fig. 1b–d are presented in Fig. 2e–g. Again only a few thick tubes connect the plasmodial components. Fig. 3 presents diagrams of FT/TL against AS in the networks obtained in our experiments. An effective network requires both low AS and high FT/TL. In the case of the three food sources, the networks observed have high FT/TL, comparable to DTN, as well as the lowest AS (Fig. 3a). With the 6 food sources (circles in Fig. 3b), both AS and FT/TL are favorable, while SMT has the best AS and the worst FT/TL and DTN has worse AS and better FT/TL. In the 7 food sources (crosses in Fig. 3b), the network is similar to SMT and DTN in AS, and superior to them in FT/TL. Thus, the tube networks formed meet the requirements of low AS combined with high FT/TL.

The favorable properties of the tube network were especially clear with the larger numbers of food sources. Fig. 3c shows that the networks formed in response to 12 food sources (Fig. 1d and crosses in Fig. 3c) had both low AS and high FT/TL. Thus, this organism ‘designs’ a sophisticated transportation network.

## 4. Discussion

How does the organism obtain the smart solution? Two empirical rules describing changes in body shape are known: (1) tube of open ends are likely to disappear in the first step and (2) when two or more tubes connect the same two food sources, the longer tubes tend to disappear [3]. These changes in the tubular structure of the plasmodium are closely related to the spatio-temporal dynamics of cellular rhythms [1]. Shuttle streaming of protoplasm, which is driven by hydrostatic pressure induced by rhythmic contraction, may affect the morphogenesis of tubular structures. Hence a key mechanism underlying network formation may involve the spatio-temporal dynamics of oscillatory fields with complex shapes and moving boundaries [8,9].

## 5. Conclusions

The *Physarum* plasmodium can construct an efficient transportation network which meets the multiple requirements of short length of network and low degree of separation between food sources, as well as tolerance of accidental disconnection at random position. The plasmodium can achieve a better network configuration than that based on the shortest connection of Steiner's minimum tree, which is impressive considering that it is very hard for humans even to deduce Steiner's connections for just a few locations. This amoeboid organism must be quite smart.

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