Slime Mold Imitates the United States Interstate System

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The plasmodium phase of Physarum polycephalum is a champion amongst living creatures used in laboratory prototypes of future and emergent computing architectures. A wide range of problems from computational geometry and logic can be solved by this cellular slime mold. A typical way to perform a computation with the slime mold is to represent a problem’s data as a spatial configuration of nutrients and allow the slime mold to span the nutrients with its protoplasmic network. The architecture of the network represents a solution to the problem. We use a similar approach and exploit foraging behavior of P. polycephalum to imitate the formation of the United States transport network in laboratory conditions. Major urban areas are represented with rolled oats, the plasmodium is inoculated in one urban area, we wait until all oat flakes are colonized by the plasmodium, and then the protoplasmic network developed by the plasmodium is analyzed. The slime mold’s networks are compared with the interstate network and the networks are analyzed in terms of proximity graphs.

1. Introduction

Physarum polycephalum is an acellular slime mold, ordinarily inhabiting forests in many parts of the world. It has a complex life cycle [1] but is usually found in its vegetative stage, a plasmodium. The plasmodium is a single cell, visible by an unaided eye, with myriad nuclei. The plasmodium feeds on a wide range of microscopic particles. During its foraging behavior, which includes undirected and tree-like growth, the plasmodium makes blob-like colonies on sources of nutrients. The colonies are connected in a single organism by a network of protoplasmic tubes. The network is considered to be optimal [2, 3] in terms of efficiency of spatial covering of nutrients, sensitivity to environmental conditions, and cost-efficient transportation of nutrients and metabolites in the plasmodium’s body. Thanks to pioneering works by Toshiyuki Nakagaki [2, 3] and his colleagues, the plasmodium’s foraging behavior can be interpreted as a computation. The spatial configurations of attractants and repellents represent data input for the slime mold computers. The computation is implemented dur-
ing the slime mold’s propagation and colonization of nutrients. The structure of the plasmodium’s protoplasmic network developed on a dataset of nutrients represents the results of the computation [2–4].

The problems solved by the plasmodium of *P. polycephalum* include shortest path [2, 3], implementation of storage modification machines [5], Voronoi diagram [6], Delaunay triangulation [4], logical computing [7], and process algebra [8].

Despite being capable of solving numerous mathematical problems, the only problem *P. polycephalum* is evolutionarily programmed to solve is to build an optimal transport network during its foraging behavior and colonization of its habitats. Thus, using the plasmodium of *P. polycephalum* to imitate human-made transport would be the first obvious problem that comes to mind for anyone wishing to design experimental laboratory prototypes of living amorphous computers. Such imitation may be expected to reveal novel approaches to adaptive reconfiguration of transport networks to dramatically increased demands on long-distance travel [9–11] and efficient planning of transport network structure [12].

An early evaluation of the road-modeling potential of *P. polycephalum* in 2007 [13] came to no definite conclusion. However, significant progress has been made since that time, such as has been reported in our recent papers on approximation of highway systems in the United Kingdom [14], Mexico [15], the Netherlands [16], Canada [17], and Brazil [18]. For all of these countries, we found that the network of protoplasmic tubes developed by *P. polycephalum* matches, at least partly, the network of human-made transport systems, though the closeness of fit varies from country to country. A variable that likely plays an important role in determining the closeness of fit is the constraint that each country’s government design policies place on their unique highway transport networks. This is why we are in the process of collecting data on the development of plasmodium networks in all major countries, in preparation toward undertaking a final comparative analysis.

The United States interstate system, created by Dwight D. Eisenhower, is considered to be an example of simple yet highly efficient transport that changed the lifestyle and the economy of the country [19–21]. The interstate system is an ideal example of a transport system aimed at maximizing the spanning of a territory with a minimal (but still fault-tolerant) number of links. The interstate system was designed by rules of human logic. An interesting question to ask is whether this logic is consistent with that of such primitive living creatures as slime mold. We are trying to provide some answers in the present paper.

Section 2 explains the experimental approach used and specifies the urban areas under consideration. Structures of slime mold’s graphs derived from laboratory experiments are discussed in Section 3. In Section 4, we compare networks built by *P. polycephalum* with the existing interstate network in the United States. Slime molds
and interstate networks are compared with most known proximity graphs in Section 5. In Section 6, we experimentally analyze several scenarios of the transport networks’ response to global disasters. Achievements and deficiencies of our approach are outlined in Section 7.

2. Methods

The plasmodium of *P. polycephalum* is cultivated in plastic containers, on paper kitchen towels sprinkled with still drinking water and fed with oat flakes (Asda’s Smart Price Porridge Oats). For experiments, we use 12×12 cm polyestyrene square Petri dishes. Agar plates, 2% agar gel (Select agar, Sigma Aldrich), are cut in a shape of the contiguous United States of America (USA). We consider the 20 most populated urban areas U of the USA (Figure 1(a)):

1. New York area, including Philadelphia, Baltimore, and Washington, DC
2. Boston
3. Charlotte, NC
4. Atlanta
5. Jacksonville, FL
6. Chicago area, including Detroit, Indianapolis, Columbus, and Louisville
7. Milwaukee
8. Nashville
9. Memphis
10. Kansas City
11. Denver
12. Oklahoma City
13. Dallas and Fort Worth
14. Houston area, including San Antonio and Austin
15. Albuquerque
16. Phoenix area, including El Paso and Tucson
17. Los Angeles area, including San Diego
18. San Jose area, including San Francisco
19. Seattle area, including Portland
20. Las Vegas

To project regions of U onto agar gel, we place oat flakes in the positions of the regions of U (Figure 1). In each experiment, we tried to match the size and shape of areas in Figure 1 by selecting a rolled oat of corresponding size and shape. At the beginning of each experiment a piece of plasmodium, usually already attached to an oat flake from a cultivation box, is placed in the New York area (region 1 in Figure 1(a)). The Petri dishes with plasmodium are kept in darkness, in the temperature range 22–25 °C, except for observation and image recording. Periodically (usually in 24-hour intervals) the dishes are scanned using an Epson Perfection 4490. We undertook 29 experiments.
Figure 1. Experimental setup. (a) Urban areas to be represented by oat flakes. (b) Snapshot of protoplasmic transport network developed by *P. polycephalum*; the snapshot is made on a map of the states.
3. Protoplasmic Networks

A few hours after being inoculated at the site of the New York area, the plasmodium of *P. polycephalum* begins its colonization of the substrate. In Figure 2, we see that in the first 12 hours the plasmodium spans the New York area with Boston and Charlotte and starts colonizing Atlanta and Nashville (Figure 2(a)). In the next 24 hours, the plasmodium propagates to and colonizes Milwaukee in the north, Atlanta and Jacksonville in the south, and the Chicago area, the Kansas City area, and Oklahoma City in the west (Figure 2(a)). In the early stages of colonization, a fine network of protoplasmic tubes is formed. Later on, the network is roughened up, and some tubes are abandoned and others increase in size. The rest of the urban areas of U are colonized in an additional 24 hours.

![Image of plasmodium colonization](image)

**Figure 2.** Example of plasmodium colonizing the experimental area. Images are recorded at (a) 12 hours, (b) 36 hours, and (c) 60 hours after inoculation.
The plasmodium of \textit{P. polycephalum} rarely repeats its foraging pattern and almost never builds exactly the same protoplasmic network twice (Figure 3). To generalize our experimental results, we constructed a \textit{Physarum} graph with weighted edges.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{networks.png}
\caption{Grayscale images of protoplasmic networks developed in laboratory experiments. The images are recorded c. 48 hours after inoculation of the plasmodium in the New York area.}
\end{figure}

A \textit{Physarum} graph is a tuple $P = \langle U, E, w \rangle$, where $U$ is a set of urban areas, $E$ is a set of edges, and $w : E \rightarrow [0, 1]$ are frequencies of edges from $E$ appearing in laboratory experiments. For every two regions $a$ and $b$ from $U$, there is an edge connecting $a$ and $b$ if a plasmodium’s protoplasmic link is recorded in at least one of $k$ experiments, and the edge $(a, b)$ has a frequency calculated as a ratio of experiments where the protoplasmic link $(a, b)$ occurred in the total number of experiments $k = 29$. For example, if we observed a protoplasmic tube connecting areas $a$ and $b$ in five experiments, the weight of edge $(a, b)$ will be $w(a, b) = \frac{5}{29}$. We do not take into account the exact configuration of the protoplasmic tubes but merely their existence. Further, we will be dealing with threshold \textit{Physarum} graphs $P(\theta) = \langle U, T(E), w, \theta \rangle$. The threshold \textit{Physarum} graph is modified from the \textit{Physarum} graph by the transformation $T(E) = \{ e \in E : w(e) > \theta \}$. That is, all edges with weights less than or equal to $\theta$ are removed.

A “raw” \textit{Physarum} graph $P\left(\frac{0}{29}\right)$ is shown in Figure 4.
Figure 4. Configurations of a Physarum graph $P(\theta)$ for various cutoff values of $\theta$. The thickness of each edge is proportional to the edge’s weight.

**Finding 1.** The Physarum graph is planar for $\theta \geq \frac{5}{29}$ and disconnected for $\theta \geq \frac{18}{29}$.

When $\theta$ increases from $\frac{17}{29}$ (Figure 4(c)) to $\frac{18}{29}$ (Figure 4(d)), the graph loses its connectivity due to removal of the link from the Phoenix area to the Dallas area. The link roughly corresponds to Interstates 10 and 20. Also the links from Seattle-Portland to Las Vegas and Seattle-Portland to Denver, although not responsible for keeping
connectivity of the transport network, are removed in the transition \( \mathbf{P} \left( \frac{17}{29} \right) \rightarrow \mathbf{P} \left( \frac{17}{29} \right) \).

The link is strong if it appears in over 75% of laboratory experiments (Figure 4(e)) and super-strong if it appears in over 95% of experiments (Figure 4(f)).

**Finding 2.** The *Physarum* imitation of the USA interstate transport network has the following strong components:

- route from the San Jose area to Las Vegas
- chain of links connecting Denver to Albuquerque to the Phoenix area to the Los Angeles area
- chain of links connecting Kansas City to Oklahoma City to the Dallas area to the Houston area
- two chains: Milwaukee to the Chicago area to Nashville to Memphis and Boston to the New York area to Charlotte to Atlanta to Jacksonville, bridged by a link from the Chicago area to New York

**Finding 3.** Links from the Dallas area to the Houston area, the Chicago area to Milwaukee, and the New York area to Boston are super-strong links of USA transport networks from a perspective of slime mold foraging behavior.

The super-strong links of the *Physarum* graph are shown in Figure 4(f). They roughly correspond to Interstate 35 (Dallas to Houston) and Interstate 96 (New York area to Boston).

### 4. How Well Does Slime Mold Approximate Interstates?

We construct the interstates graph \( \mathbf{H} \) as follows. Let \( U \) be a set of urban regions; for any two regions \( a \) and \( b \) from \( U \), the nodes \( a \) and \( b \) are connected by an edge \((a–b)\) if there is an interstate starting in the vicinity of \( a \) and passing in the vicinity of \( b \) and not passing in the vicinity of any other urban area \( c \in U \). Interstates graph \( \mathbf{H} \) shown in Figure 5(b) is extracted from a scheme of the USA interstate network (Figure 5(a)). Intersections of *Physarum* graphs \( \mathbf{P}(\emptyset) \) and \( \mathbf{H} \) are shown in Figure 6.

**Finding 4.** The *Physarum* graph \( \mathbf{P}(0) \) approximates 36 of 41 edges of the interstates graph \( \mathbf{H} \).

The following transport routes of \( \mathbf{H} \) are not represented in protoplasmic networks (Figure 6(a)):

- Denver to San Jose area
- Houston area to Albuquerque
- Houston area to Jacksonville
- New York area to Nashville
- Boston to Chicago area
Figure 5. Transport network of the USA. (a) Scheme of interstates [22]. (b) Interstates graph $H$. 
Finding 5. Slime mold overdoes the interstates network by producing additional links:
- San Jose area to Las Vegas
- Denver to Seattle area
- Albuquerque to Las Vegas

This is obtained by direct comparison of $P_{17}^{29}$, $P_{18}^{29}$, and $P_{22}^{29}$ (Figure 4) and intersections of these graphs with the interstates graph $H$ (Figure 6).

![Figure 6. Intersection of threshold Physarum graph $P(\theta)$ with interstates graph $H$ for $\theta = 0, \frac{8}{23}, \frac{17}{23}, \frac{18}{23}, \frac{22}{23}$.]

5. Proximity Graphs

A planar graph consists of nodes that are points on the Euclidean plane and edges that are straight segments connecting the points, and the edges do not intersect. A planar proximity graph is a planar graph where two points are connected by an edge if they are close in some sense. A pair of points is assigned a certain neighborhood, and points
of the pair are connected by an edge if their neighborhood is empty. Here we consider the most common proximity graphs.

- Gabriel graph GG: Points \( a \) and \( b \) are connected by an edge in GG if a disc with diameter \( \text{dist}(a, b) \) centered in the middle of the segment \( a \, b \) is empty \([23, 24]\) (Figure 7(a)).

- Relative neighborhood graph RNG: Points \( a \) and \( b \) are connected by an edge in RNG if no other point \( c \) is closer to \( a \) and \( b \) than \( \text{dist}(a, b) \) \([25]\) (Figure 7(b)).

- Minimum spanning tree MST: The Euclidean minimal spanning tree (MST) \([26]\) is a connected acyclic graph that has the minimal possible sum of edges’ lengths (Figure 7(b)).

![Figure 7. Principle proximity graphs computed on a set \( U \) of urban areas. (a) Gabriel graph. (b) Relative neighborhood graph. (c) Minimum spanning tree.](https://doi.org/10.25088/ComplexSystems.21.1.1)

In general, the graphs relate as \( \text{MST} \subseteq \text{RNG} \subseteq \text{GG} \) \([24, 25, 27]\).

**Finding 6.** Slime mold’s protoplasmic network includes minimum spanning of the urban areas \( U \).

This is because \( P \left( \frac{0}{29} \right) \cap \text{MST} = \text{MST} \) (Figure 8(a)). The minimum spanning component of slime mold’s network is stable: \( P (\theta') \cap \text{MST} = P (\theta'') \cap \text{MST} \) for any \( 0 \leq \theta', \theta'' \leq \frac{19}{29} \).
Figure 8. Intersections of (e–g) *Physarum* graphs $P(\theta)$ with proximity graphs, and (h) the interstates graph $H$ with minimum spanning tree $MST$. 
Finding 7. The transport link connecting the New York area and the Chicago area is the only strong link not presented in the minimum spanning tree MST.

This is because $P\left(\frac{28}{29}\right) \cap \text{MST} = P\left(\frac{28}{29}\right) - \text{(New York, Chicago)}$ (Figure 8(b)); see also Finding 2.

Finding 8. Super-strong links are edges of the minimum spanning tree on MST.

As we see in Figure 8(c), $P\left(\frac{28}{29}\right) \cap \text{MST} = P\left(\frac{28}{29}\right)$, which are indeed the links described in Finding 3.

Finding 9. The “raw” Physarum graph $P(0)$ includes all the proximity graphs considered: $\text{MST} \subseteq \text{RNG} \subseteq \text{GG} \subseteq P(0)$.

This is in agreement with our previous studies on relationships between slime mold’s protoplasmic networks and proximity graphs, for example [4]; see also Figure 8(a, d, e).

Finding 10. The Physarum graph $P(\theta)$ is a subgraph of the Gabriel graph $\text{GG}$ for $\theta \geq 17$.

See examples in Figure 8(f, g).

Finding 11. The minimum spanning tree MST is almost a subgraph of the interstates graph H.

The following links are missing from $H \cap \text{MST}$ (Figure 8(h)): Memphis to Kansas City, Las Vegas to Albuquerque, and the San Jose area to Las Vegas.

6. Reconfiguration in Disasters

To imitate a large-scale disaster, we place a crystal of sodium chloride (SAXA Coarse Sea Salt, a crystal weight around 20 mg) in the places of agar plate corresponding to nuclear generating stations as shown in Figure 9. Inorganic salt is a repellent for $P.\ polycephalum$, therefore the sodium chloride diffusing into the plasmodium’s growth substrate causes the plasmodium to abandon domains with high levels of salinity. An immediate response to diffusing chloride, plasmodium withdraws from the zone immediate to the epicenter of contamination (Figure 10). Further response usually fits into two types: hyper-activation of transport at an attempt to deal with the situation and migration away from contamination and even beyond growth substrate as an attempt to completely avoid the situation (Figures 11 and 12). The following scenarios are observed in laboratory experiments.
Figure 9. Sites of contamination epicenters are shown by stars and arrows: (a) Palo Verde Nuclear Generating Station, (b) South Texas Nuclear Generating Station, and (c) Vermont Yankee Nuclear Power Plant.

Figure 10. Early stages (8 hours) of the plasmodium’s response to contamination with the epicenter in South Texas Nuclear Station. The boundary of the contaminated area is marked by a line.
Figure 11. Examples of plasmodium response to large-scale contamination of the USA with epicenters in (a–c) South Texas Nuclear Generating Station, (d–f) Vermont Nuclear Power Plant, and (g–l) Palo Verde Nuclear Generating Station. Images are scanned in 15–24 hours after the start of contamination and binarized by the following procedure. Only pixels from the original scans of experimental dishes in which red and green components exceed 100 and the blue component is less than 100 are drawn as black pixels; otherwise they are white.
Figure 12. Schematics of the plasmodium’s response to a large-scale contamination with epicenters in (a) South Texas Nuclear Generating Station, (b) Vermont Nuclear Power Plant, and (c) Palo Verde Nuclear Generation Station. Transport routes enhanced in a response to contamination are shown by lines. Routes of attempted emigration are shown by arrows.

6.1 Epicenter of Contamination in Palo Verde Nuclear Generating Station

Normal activity in the area as far from Palo Verde as San Jose and San Francisco, Seattle-Portland, Albuquerque, and Oklahoma City are totally disrupted. Plenty of abandoned protoplasmic tubes can be found in the contaminated zone. Transport links at the boundary between contaminated and clean areas are substantially enhanced. A huge increase in diameter, equivalent of throughput, of protoplasmic tubes is observed in the routes from Seattle-Portland to Denver, from Denver to Kansas City, and from Kansas City to Milwaukee and Memphis. A slightly but yet clearly visible increase of transport links is also recorded in routes from Dallas and Fort Worth to Memphis and from the Houston area to Memphis. Sometimes we can also note that tubes connecting the Chicago area with Nashville and New York, and from Atlanta to Charlotte and from the New York area to
Boston become hypertrophic (Figures 11(g–l) and 12(d)). At the same time, we observe the plasmodium migrating in the following directions:

- from Jacksonville to Miami and then toward Cuba;
- from Houston, San Antonio, and Austin across the Mexican border toward Monterrey and Ciudad;
- from Vermont, New Hampshire, and Maine across the Canadian boundary toward New Brunswick and Quebec;
- the hugest wave of migration is directed from the USA to Calgary, Edmonton, and Saskatoon in Canada: directed links of migrating plasmodium are observed propagating from Milwaukee, Denver, Seattle, and Portland toward and across the Canadian boundary.

### 6.2 Epicenter of Contamination in Texas Nuclear Generating Station

Three types of migratory response to contamination spreading from Texas Nuclear Generating Station are observed in laboratory experiments:

- from Los Angeles and San Diego to Tijuana and Ensenada;
- from Jacksonville to Miami and then toward Cuba;
- from Seattle and Portland toward Vancouver and further in British Columbia.

Transport links from Los Angeles and San Diego via San Jose and San Francisco to Seattle and Portland, and from Seattle-Portland to the Houston area and Milwaukee are substantially increased in their size. Infrequent hypertrophic reaction is also observed in routes from Milwaukee to the Chicago area, and from the New York area to Boston and to Chicago (Figures 11(a, b, c) and 12(a)).

### 6.3 Epicenter of Contamination in Vermont Nuclear Power Plant

In the situation when the epicenter of contamination is located at Vermont Nuclear Power Plant, we observe migration and the shift of the plasmodium’s activity toward the south and southwest parts of the USA. Namely, hypertrophy of the following transport routes is recorded in experiments (Figures 11(d, e, f) and 12(b)):

- Seattle-Portland to San Jose, San Francisco, and Las Vegas;
- Los Angeles area to Phoenix area to Dallas area and Houston area;
- Las Vegas to Albuquerque to Dallas and Forth Worth;
- Dallas area to Memphis to Jacksonville.
Attempted migration of the plasmodium outside the USA boundaries are observed almost everywhere along the south and southwest boundaries. The most pronounced sites of migration are the Houston area, the Phoenix area, Los Angeles and San Diego, San Jose and San Francisco, and Seattle and Portland.

7. Discussion

We represented 20 major areas of the United States of America (USA) with rolled oat placed on an agar plate in the shape of the USA, inoculated the plasmodium of Physarum polycephalum on the oat flake representing the New York area, and analyzed networks of the plasmodium’s protoplasmic tubes spanning the oat flakes (Figure 13). We found that the slime mold approximates almost all interstates excluding routes directly connecting Denver to the San Jose area, the Houston area to Albuquerque, the Houston area to Jacksonville, the New York area to Nashville, and Boston to the Chicago area. We discovered that the slime mold’s network includes the Gabriel graph and relative neighborhood graph and has a strong core corresponding to a minimum spanning tree on major urban areas. We identified Interstates 10 and 20 as responsible, at least from the slime mold’s “point of view,” for connectivity of the USA transport network: when these interstates are removed, the network becomes separated into western and eastern components. In laboratory experiments, we imitated an abstract major disaster leading to spreading contamination and outlined several possible scenarios of how the transport network will restructure in a response to such disasters. Despite a range of impressive findings, we must admit that our experimental approach suffers from low resolution and also does not take into account terrain and other geographical conditions. These deficiencies will be dealt with in further experiments.

References


Figure 13. Examples of protoplasmic networks on the interstate map of the USA.


