Insights into Information Processing by the Single Cell Slime Mold *Physarum Polycephalum*

D.S. Hickey and L.A. Noriega.

Faculty of Computing, Engineering and Technology, Staffordshire University, Beaconside, Stafford, England, ST16 9DG
e-mail: s.hickey@staffs.ac.uk

Abstract: The finding that a simple single-celled organism can traverse a maze near optimally provides a challenge to some current ideas in artificial intelligence. In this paper, we present a simple explanation for such behavior and a computational model based on decision trees and ant algorithmics. The behavior of simple biological organisms may provide insights into the nature and evolution of intelligence.

1. INTRODUCTION

The ability to traverse a maze is a standard test of intelligence and behavior in animals: maze learning has been used for many years in psychology to test the intellectual abilities of small mammals and other animals. The difficulty of computing optimal or near optimal paths through mazes is illustrated by their use in puzzle books for human recreation and, occasionally, in tests of intelligence quotient (IQ). Therefore, it came as some surprise when researchers discovered that an evolutionarily simple slime mold, *Physarum polycephalum*, consisting nominally of a single cell, was able to compute a near optimal path through a maze (Nakagaki *et al.*, 2000).

The *Physarum* slime mold is a large multinuclear cell, formed in response to environmental conditions. In Physarum, amoebae are typically haploid. Two Physarum amoebae of different mating types combine to create a diploid cell, which then grows by a process involving repeated division without separation of the cytoplasm. The resulting large plasmodium is a single cell with multiple diploid nuclei.

If *Physarum polycephalum* is subjected to a regular series of shocks, it can learn the pattern and modify its behavior in anticipation of the next stimulus (Ball, 2008). This response may provide clues to the origin of intelligence in animals. The method of information processing utilized by *Physarum* is clearly distinct from standard neural network models, which require intercellular communication. *Physarum's* algorithm has a high computation capacity (Nakagaki, 2001).

1.1 Information Processing Models

Initial models of computation in *Physarum* derived from observations that cytoplasmic waves were associated with the learning behavior (Durham and Ridgway, 1976). These oscillatory mechanisms have been proposed as the system for information processing in the plasmodium. *Physarum* information processing has been modeled as a set of coupled oscillators (Tsuda *et al.*, 2007) and is reported to contain between three and five oscillators, in a ring pattern. The action of these oscillators has been described in terms of dynamical systems using symmetric Hopf bifurcation theory (Takamatsu, 2001).

An analogous computational mechanism is the Belousov-Zhabotinsky (BZ) reaction and its use in robotic control (Adamatzky *et al.*, 2004). The chemical waves of the BZ reaction can control a simple robotic system and, in principle, compute an optimal pathway through a labyrinth (Steinbock *et al.*, 1995).

Recently, we have provided a parsimonious model of information processing in *Physarum* (Hickey and Noriega, 2008), which relates the computation to the underlying biological structure. The model proposes that the venous network in *Physarum* acts as a decision tree, driven by redox and nutrient signals, in a manner analogous to ant algorithmics. Here, we extend the exposition and provide additional insight into the algorithmic implications.
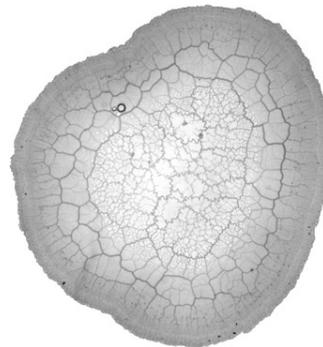
2. BIOPHYSICS AND MICROANATOMY

Fig. 1. *Physarum* "resting", with a lace-like arrangement of veins. (Image courtesy Ragnhild Halvorsrud).

2.1 The internal venous structure

In considering *Physarum*, one of the most notable features is its network of veins. These veins interact with peristaltic rhythmical signals, which are associated with cytoplasmic streaming and movement (Durham and Ridgway, 1976). The veins appear to exist as a lacework in the resting organism, as shown in Figure 1. The network changes according to conditions and the geometry follows the movement of the organism. Figure 2 illustrates the radial arrangement of veins that is associated with movement and maze optimization.
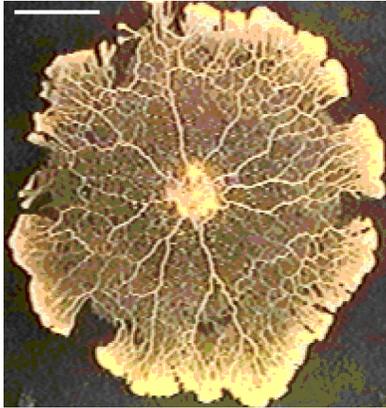

Fig. 2. The structure of *Physarum*. Dendritic veins radiate from the centre, diverging and bifurcating, to follow the shape and movement of the organism. The graphic distance bar has a length of 1 cm. (Courtesy Toshi Nakagaki).

As movement begins, the leading edge veins form a bulbous network, while the trailing section is skeletonized into major vessels, as shown in Figure 3. *Physarum* is able to respond to simple environmental signals, such as chemical signals and temperature gradients, with chemotactic or thermotactic movement.
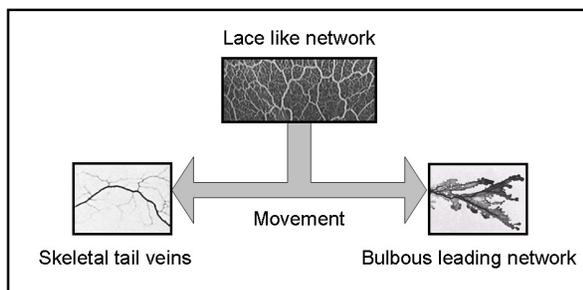

Fig. 3. Movement can induce a leading "bulbous" network, with trailing sparse veins that include relatively large vessels

2.2 Basic mechanisms

In considering *Physarum*, we noticed a similarity with signaling in colonial hydroids. These small animals (often confused with plants) have a lace-like venous network, which connects their polyps. Blackstone has modeled the response of a colonial hydroid network to nutrients and redox active (antioxidant-oxidant) signaling molecules, such as vitamin C (Blackstone, 2001; Blackstone, 2006). Growth and differentiation of the network can be controlled by changing the nutrient and redox status, as shown in Figure 4. Similar redox regulation occurs in higher animals, for example in angiogenesis (Maulik, 2002). Blackstone's model for redox and nutrient mitochondrial control (Blackstone, 2005) provides a potential mechanism for local control of the veins in *Physarum* (Hickey and Noriega, 2008).

As with colonial hydroids, *Physarum's* maze traversal involves responding to nutrient and redox signals. Cytoplasmic streaming in *Physarum* is calcium dependent (Ridgway and Durham, 1976) which, in turn, is dependent upon the redox state (Allen and Venkatraj, 1992). *Physarum* provides a model for redox control of differentiation (Yu, 1993).
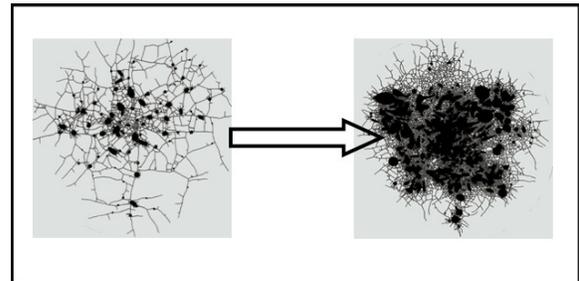

Fig. 4. Increased growth in colonial hydroid stimulated by vitamin C, illustrating redox control of biological tubular networks (Images courtesy Neil Blackstone).

3. ALGORITHMICS

3.1 Ant algorithms

Path optimization in *Physarum* when traversing a maze is related to ant algorithmics. Ants in a formicary undertake coordinated behavior for the location and transportation of food. Their organization depends on a pheromone signaling mechanism that is found extensively in nature. A foraging ant searches for food on an apparently random radial path. Having located food, the ant retraces its steps to the formicary, leaving a pheromone trail for other ants to follow.

The pheromone signal evaporates over time, so the longer the path an ant travels, the greater the signal loss. If two ants find the same food source, then the ant that took the shorter path leaves a stronger pheromone signal. As the number of ants increases, the shortest route from the formicary to the food source is determined. This basic algorithm is used in artificial intelligence (AI) and is particularly suited for navigation related search problems.

For AI purposes, the world in which the ant operates is modeled as a graph, with the formicary representing the

starting point, and the food source representing the search destination. The graph to be searched is represented using an $n \times n$ adjacency matrix P, where n refers to the number of nodes in the graph. The probability of moving from node i to node j in graph P is denoted $p_{i,j}$. If there is no direct connectivity between these two nodes, then the probability is zero, otherwise the probability is calculated directly. Initially, the probabilities are set to a suitable value, so if node k has two connecting nodes, each of those may be arbitrarily accorded a probability of 0.5, or if node m has three connecting nodes, then each is set to a probability of 0.33, and so on.

As the algorithm progresses, the pheromone signal is applied and modifies the associated connection probabilities, i.e.

$$p_{i,j} = \begin{bmatrix} \dfrac{S_{i,j}}{\sum_{l \in Ni} S_{i,l}} & \text{if } j \in N_i \\ \\ 0 & \text{if } j \notin N_i \end{bmatrix} \qquad 1$$

where N_i refers to the neighborhood of i (the nodes in the graph connected to i), and $S_{i,j}$ refers to the strength of the signal (the amount of pheromone on the arc connecting nodes i and j).

As each virtual ant passes over an arc, the pheromone is incremented by a value determined by the distance travelled. The shorter the distance, the greater the amount of pheromone deposited on the trail. In this case, the amount of pheromone added to the trail is calculated at each iteration of using

$$S_{i,j}(t) = \rho S_{i,j}(t-1) + \Delta S \qquad 2$$

where ρ is a coefficient that represents the evaporation rate of the pheromone, and ΔS is the change in pheromone occasioned by the traversing ants.

$$\Delta S \propto \frac{1}{d(start, end)} \qquad 3$$

where d(start, end) is the distance travelled by a virtual ant between its starting point and destination. In pseudo-code:

```
foreach ant
    generate a random route from start to destination
    calculate the distance travelled
    increment the signal strength
    recalculate the probabilities
next ant
```

The algorithm converges when ants predominantly follow the same route and the probabilities in the matrix for a near optimal route approach unity.

3.2 Physarum algorithm

Maze traversal in *Physarum* can be modeled using modified ant algorithmics. *Physarum* spreads out searching for food, which is conveyed through veins to the centre of the organism (see Figure. 2). When food is located, the nutrient transportation veins dilate and flow increases. Meanwhile, veins that are connected to areas of the organism that have failed to find food contract. The diameter of the vein relates to the flux, or flow, which can be modeled by the number and speed of traversing virtual ants.

Dilation and contraction of the veins are processes that, in principle, are similar to the increase and evaporation of pheromones in the ant colony model. In *Physarum,* we tentatively liken the action of nutrients on mitochondria and their associated redox responses with the virtual ant pheromone trail (Hickey and Noriega, 2008). Both models include a probabilistic adjacency matrix. With *Physarum*, the matrix is determined by the arrangement of veins, which constrains the flow. The arrangement of veins, shown in Figure 2, therefore specifies a standard decision tree, as used throughout artificial intelligence and cybernetic systems.

The formulae for updating the probabilities that we used with *Physarum* differ from standard ant algorithmics. In *Physarum*, the biophysics of the process provides a large signal gain, because the flow depends on the diameter of the vessel. The physical basis of modeling the flow of nutrients through the veins in *Physarum* is based on the Hagen-Poiseuille law.

$$Q_{i,j} = \frac{\pi r_{i,j}^4 [pr_i - pr_j]}{8 v L_{i,j}} \qquad 4$$

where $Q_{i,j}$ is the flow, or flux, between nodes i and j, pr_i is the pressure at node i, υ is the viscosity, and $L_{i,j}$ is the length of the connecting vein. Thus, the radius of the vein, r, allows a flow of nutrients (or virtual ants) by an amount proportional to its fourth power.

Equation 4 can be broken down into two separate components, a term for the radius effect

$$D = \pi r_{i,j}^4 / 8v \qquad 5$$

and a term for the length effect

$$Q_{i,j} = D_{i,j} [pr_i - pr_j] / L_{i,j} \qquad 6$$

The length effect in Equation 6 refers to the length of an individual arc in the graph. The vein dilation and length effects correspond to the route taken by virtual ants from start node to destination node. These values can be used to calculate the adjacency probability matrix, based on the radius of the vein connecting neighboring nodes.

$$p_{i,j} = \begin{bmatrix} \dfrac{Q_{i,j}}{\sum_{k \in N_i} Q_{i,j}} \text{ if } j \in N_i \\ \text{otherwise} \quad 0 \end{bmatrix} \qquad 7$$

The vein contraction process is modeled by finding a suitable value for $\rho \in [0, 1]$, in Equation 2. The dilation process is a little more involved. The gain in flow is sensitive to small increments in the radius. A function of the flow $Q_{i,j}$ can therefore be used to determine the increment. Note that the flow may be represented by the number of virtual ants traversing a vein,

$$\frac{d}{dt} D_{i,j} = f\left(\left|Q_{i,j}\right|\right) - \rho D_{i,j} \qquad 8$$

after Taro *et al.* (2007).

Changes in D can be directly related to r using Equation 5 and the flow and probability of traversal using Equation 7. In our simulations, we used a simple learning rate function to model the increment

$$\Delta f\left(\left|Q_{i,j}\right|\right) = \varepsilon f\left(Q_{i,j}\right) \qquad 9$$

where $\varepsilon \in [0, 1]$ and, for reasonable convergence, is set to a small value (i.e. < 0.1). The algorithm adopted to implement the *Physarum* model for an individual virtual ant is based on the standard ant algorithm:

```
foreach iteration
    generate a random route from start to destination
    calculate the distance
    increment the vein radii
    recalculate the probabilities
next
```

Individual virtual ants may be tracked, or a population of ants may disperse over the network, as required in the investigation. With our population studies, we tracked numerous virtual ants simultaneously throughout the network to simulate the flux, and the effect of the signal was restricted to the local connecting vein.

4. RESULTS

4.1 Ant population studies

For our virtual ant population studies, Nakagaki *et al.* (2004) provided a simple experimental arrangement and results for computer modeling, as shown in Figure 5. In Nakagaki's biological experiment, *Physarum* provided a solution in 72 hours.
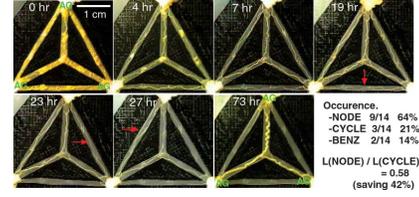

Fig. 5. Triangular model system for experimental investigation of maze traversal, with multiple food sources, by *Physarum* (Courtesy Toshi Nakagaki).

This experimental arrangement provided the basis for a simple but demanding model. There are three food sources, four nodes, and six veins. For each input node, there are three output veins. The radius of the veins was initially set to unity, while arc (i.e. vein) lengths were determined by the geometry of the graph. The graphical representation in Figure 6 shows initial results at the start and the end of training. These preliminary findings are consistent with the experimental results obtained by Nakagaki *et al.* (2004).
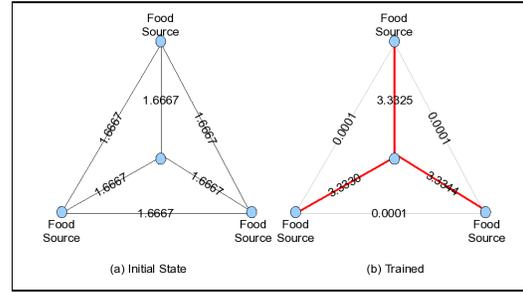

Fig. 6. Simulation of Nakagaki's experimental arrangement (three food sources). In (a), initial vein radii are shown (in arbitrary units). Diagram (b) shows results from a population of 400 virtual ants modeling the flow and resultant signaling over 800 time steps.

4.2 Individual ant tracking

We compared the standard ant algorithm with the *Physarum* variant in a series of simple experiments, with graphs of increasing complexity. In these simulations, we tracked the response to individual virtual ants acting independently, as shown in Figure 7. This figure illustrates the *Physarum* algorithm, studied using graphs of increasing complexity.
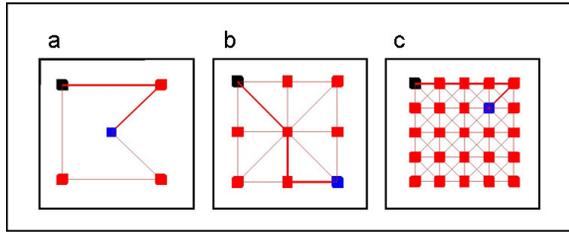
Fig. 7. Simulation of graph traversal by individual virtual ants in the *Physarum* algorithm, with a single source and destination. Image (a) has five incompletely connected nodes, image (b) nine fully connected nodes and image (c) has 25 fully connected nodes. The resulting path is indicated by the width of the connections.

The *Physarum* algorithm has many of the features expected of standard ant algorithmics, including shortcomings of dependence on initial conditions and the comparatively large number of permutations of possible paths. However, *Physarum's* radial network geometry, shown in Figure 2, has the appearance and logical structure of a decision tree. This geometry imposes a constraint on the method and provides an informational guide, limiting the complexity of the computation for the organism when compared with an arbitrary graph.

5. CONCLUSIONS

Maze traversal in *Physarum* can be modeled as a simple decision tree, optimized by ant algorithmics. This provides a simple explanation for apparently anomalous information processing by a single-celled organism. The mechanism can be viewed as a biological implementation of straightforward artificial intelligence techniques. The virtual ant model serves to model the flow of nutrients and thus the induced redox or related signals acting on the veins.

Life is characterized in terms of information processing and single-celled organisms show remarkably advanced information processing capabilities. A neural network with inter-cellular connections is not necessary for biological computation, which may have implications for brain studies.

The outline algorithm we propose for *Physarum* is only a partial explanation of information processing in this organism. The formation and movement-induced changes in the venous network modulate the algorithm. A more biophysically appropriate approach would be to use the flow and mitochondrial transduction directly. However, virtual ant algorithmics provide a simple approximation to the flow and signaling.

Physarum's information processing capabilities are relatively advanced, as single-celled organisms have evolved to behave in a demanding evolutionary environment. We return to our old friend, W. Ross Ashby, and his law of requisite variety. Evolution of simple organisms provides a severe constraint on the parsimony of solutions. There needs to be a sufficient number of ants (or routes) to model the required range of permutations in paths. A minimal number of routes must be generated to approximate the optimal route. Moreover, evolutionary selection in algorithm development will be subject to Occam's razor. *Physarum* appears to optimize its network search by using a specific radial geometry of network paths when engaging in foraging.

Artificial intelligence systems could benefit by focusing on the information processing of simple organisms, with highly complex behavior.

REFERENCES

Adamatzky, A., de Lacy Costellob, B., Melhuisha, C., and Ratcliffeb, N., (2004) Experimental implementation of mobile robot taxis with onboard Belousov–Zhabotinsky chemical medium, *Materials Science and Engineering, C*, **24**(4), 541-548.

Allen, R.G., and Venkatraj, V.S., (1992) Oxidants and Antioxidants in Development and Differentiation, *Journal of Nutrition*, **122**(3),_Suppl, March, 631-635.

Ball, P., (2008) Cellular memory hints at the origins of intelligence, *Nature*, **451**, 7177, 385.

Blackstone, N.W., (2001) Redox state, reactive oxygen species and adaptive growth in colonial hydroids, *J. Exp Biol*, **204**, 1845-1853.

Blackstone, N.W., (2006) Multicellular redox regulation: integrating organismal biology and redox chemistry, *Bioessays*, **28**(1), 72-77.

Durham, A.C.H., Ridgway, E.B., (1976) Control of chemotaxis in Physarum Polycephalum, *The Journal of Cell Biology*, **69**, 218-223.

Hickey, D.S., and Noriega, L.A., (2008) Relationship between structure and information processing in Physarum polycephalum, *Int. J. Modelling, Identification and Control*, (in press).

Maulik, N., (2002) Redox Signalling of Angiogenesis, *Antioxidants & Redox Signaling,* **4**(5), 805-815.

Nakagaki, T., (2001) Smart behavior of true slime mold in a labyrinth, *Res. Microbiol.*, **152**, 767–770.

Nakagaki, T., Kobayashi, R., Nishiura Y., Ueda T., (2004) Obtaining multiple separate food sources: behavioural intelligence in the Physarum plasmodium, *Proc Biol Sci*, **271**(1554), 2305-2310.

Nakagaki, T., Yamada, H., and Tóth Á., (2000) Intelligence: Maze-solving by an amoeboid organism, *Nature*, **407**, 470.

Ridgway, E.B., and Durham, A.C., (1976) Oscillations of calcium ion concentrations in Physarum polycephalum, *J Cell Biol*, **69**(1), 223-226.

Steinbock, O., Tóth, A., Showalter, K., (1995) Navigating Complex Labyrinths: Optimal Paths from Chemical Waves, *Science*, **267**(5199), 868 – 871.

Takamatsu, A., Tanaka, R., Yamada, H., Nakagaki, T., Fujii, T., and Endo I., (2001) Spatiotemporal Symmetry in Rings of Coupled Biological Oscillators of Physarum Plasmodial Slime Mold, *Physical Review Letters*, **87**(7), 1-4.

Tero A. Kobayashi R. Nakagaki T. (2007) A mathematical model for adaptive transport network in path finding by true slime mold, *J. Theoretical Biology*, **244**, 553-564.

Yu, B.P, (1993) *Free Radicals in Aging*, pp 20-22, CRC Press Inc, Boca Raton, FL.