

Chapter 4

Modelling the Biological Behaviour of *Physarum*

“Then, suddenly, something happened to it. It did not explode. Nor was there any sound. Rather, it seemed to slit open, as if it had been burst into instantaneous bloom by a vast number of white cilia which rayed out in all directions. The instinctive reaction was to jump back from the window away from it. We did.”

(John Wyndham, 1953)

4.1 Introduction

This chapter presents results reproducing a range of biological patterning observed in *Physarum* using the virtual plasmodium model. We demonstrate the initial formation of protoplasmic networks, and the growth and adaptation under differing nutrient concentration and substrate conditions. We conclude by suggesting how the model may provide clues as to the generation of apparently ‘intelligent’ behaviour of the plasmodium.

4.2 Initial Network Formation from Solid Plasmodial Sheet

In an environment with high nutrient concentration an explant of *Physarum* grows outwards radially to form a uniform sheet-like plasmodium behind the growth front. As the growth front moves forwards there is a breaking of symmetry as protoplasm is transported to different regions of the plasmodium, forming a protoplasmic network which becomes sparse over time (Fig. 4.1).

In the virtual plasmodium the mutual attraction between the particles and the chemoattractant they deposit on forward movement results in cohesion of the collective. The uniform structure of the virtual sheet is preserved, despite this uniform pattern being composed of dynamically moving particles. To demonstrate the formation of transport networks from a uniform sheet we

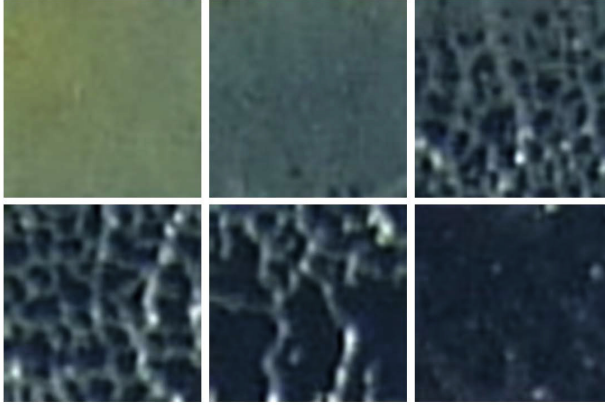


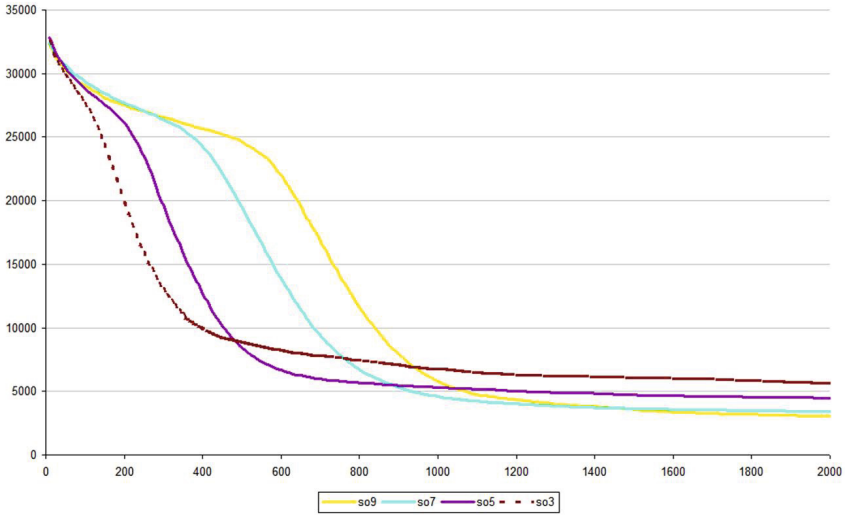
Fig. 4.1 Symmetry breaking in *Physarum* plasmodium to form protoplasmic network (Images courtesy of Andrew Adamatzky)

begin with the simplest case of an idealised hypothetical sheet, a square patch of particles with periodic boundary conditions. When randomly selected particles were removed from the sheet lacunae began to form and grow and the remaining particles self-assembled into networks (Fig. 4.2). When using larger sensor scales the sheet proved more resilient to breakup and the lacunae were more scarce and grew more slowly over time. Smaller sensor scales resulted in less cohesion and a much more rapid breakdown of symmetry was observed with greater initial fragmentation of the sheet.

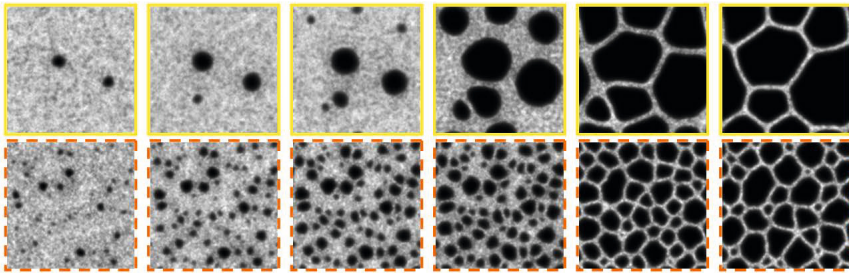
4.3 Morphological Adaptation of Pre-existing Plasmodia

Initial research into the network adaptation of *Physarum* concentrated on the morphological adaptation of fully grown plasmodia to the placement of nutrients within the environment. When the plasmodium occupies a T shaped piece of agar in which only two branches contain nutrient sources, the protoplasmic network in the branch without nutrients eventually collapses, leaving only the connection between the nutrients. The virtual plasmodium also removes redundant paths, by withdrawing pseudopodia from dead-ends. In Fig. 4.3 a, the virtual plasmodium is initialised in the same configuration as the real plasmodium. The smaller branches in the tube network collapse (Fig. 4.3 b-c) and a pseudopodium retracts from the region without nutrients to leave only the connection between the two nutrient sources intact (Fig. 4.3 d-e).

The selection of a shorter path is also reproduced in the virtual plasmodium. In Fig. 4.4a the virtual plasmodium is inoculated to cover an arena with two nutrient sources, at the top and bottom of the arena, linked by two possible paths. Adaptation of the model population is implemented in this



(a)



(b)

Fig. 4.2 Breakdown of model uniform plasmodial sheet to form transport network. (a) Plot of population size at different SO , (b) (top) At SO 9, time: 400, 450, 500, 700, 1000 and 2000 steps, (bottom) At SO 3, time: 100, 150, 200, 250, 1000 and 2000 steps.

case by randomly removing particles with $p=0.0001$, beginning after 2500 steps. As adaptation progresses the collective shrinks during its adaptation, resulting in the selection of the shorter left path and elimination of flux from the longer right path. The flux of particles through each path, and reduction in size of the plasmodium, is shown in Fig. 4.4b and the selection of the shorter path is indicated by the sudden fall in flux through the right channel after 25000 steps. The graph shows three distinct regions of behaviour during the adaptation, as indicated on the graph. Between approximately 2500 and 10500 steps (Stage I) the flux through both regions is roughly equal.

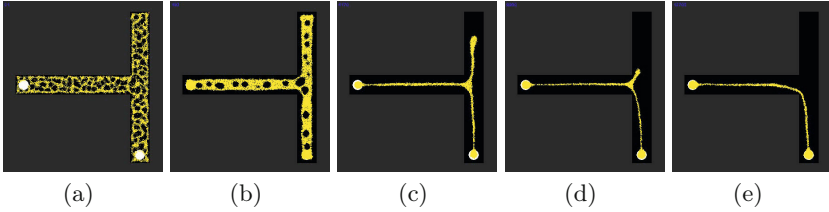


Fig. 4.3 Dead-end removal by the model plasmodium. (a) Virtual plasmodium (particle positions shown) is inoculated in T shape with two nutrient sources (white discs) and initial network forms, (b-e) Network adaptation removes smaller channels and withdraws pseudopodium leaving only nutrient sources connected.

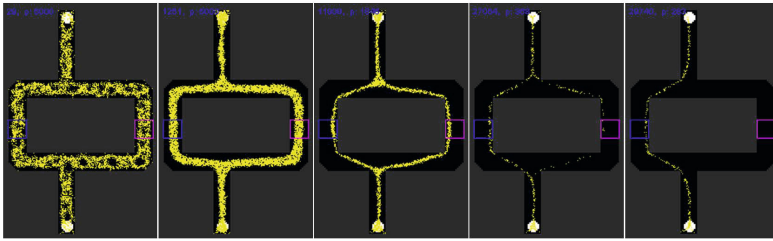
The sharp fall in flux during this time is due to the thickness of the plasmodium in the channels being reduced and flux is equal during this time because the thickness of the plasmodium acts as a buffer or reservoir of particles to reinforce the flux of both channels. During stage II (10500 to 25000 steps) this reservoir of extra material is exhausted and alternation of the levels of flux in the left and right paths is observed as the two paths compete for flux. The shorter left path receives a greater flux of particles as the distance to be traversed is shorter and the bidirectional flux of particles thus reinforces the shorter path. In stage III the flux through the right channel is eliminated as agent particles switch to the left channel.

The selection of a shorter path by path reinforcement reproduces the flux canalisation of the plasmodium tube network. The collective behaviour of the agent population can be interpreted as a auto-catalytic LALI mechanism as it also approximates the foraging behaviour seen in ants [166] which in turn inspired meta-heuristics such as the Ant Colony Optimisation system [69]. Unlike the Ant Colony Optimisation method (which calculates presumed flux based upon path length, in a conventional algorithm), the agent population actually implements the spatial deposition of chemoattractant in the arena.

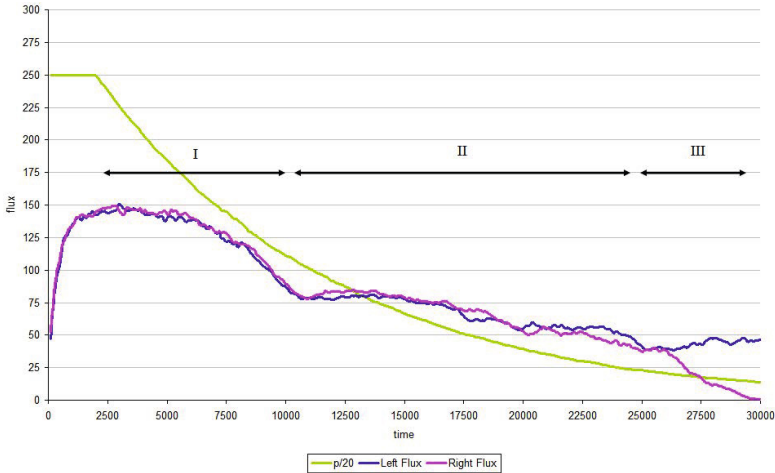
4.4 Growth and Adaptation of Plasmodial Networks

4.4.1 Dendritic Foraging Growth on Nutrient-Poor Substrates

The foraging and minimisation behaviour of the model closely approximates the behaviour of the plasmodium. In Fig. 4.5 we inoculated a *Physarum* plasmodium (cultivated in plastic containers, on paper kitchen towels sprinkled with distilled water and maintained in darkness at temperature 22-25C, except for observation and image recording) by placing it on the circled nutrient oat flake (Asda Smart Price Porridge Oats). Periodically the plasmodium was photographed using Nikon S510 digital camera. After covering the nutrient



(a)



(b)

Fig. 4.4 Selection of shorter path by virtual plasmodium (a) Virtual plasmodium (particle positions shown) is inoculated in arena with two nutrient sources (white discs) connected by two paths. Flux is measured in the two path options (square regions) and composite image shows evolution at 29, 1251, 11908, 27064 and 29740 steps. (b) Graph showing flux in both path options (jagged lines) as the virtual plasmodium shrinks (smooth curve).

source the growth front migrates by streaming to nearby flakes, eventually forming a plasmoidal network spanning the nutrients.

The virtual plasmodium reproduces the network growth behaviour when inoculated at a single nutrient source (Fig. 4.6). The growing particle collective surges towards nearby nutrient sources with pseudopod-like growth, engulfs them (thus suppressing the diffusion of nutrients from that node), and constructs a transport network which approximates the Steiner tree. When the experiment was reproduced without the condition of suppressing diffusion from nodes when engulfed, full network connectivity was not achieved. The population traversed nearby nodes to the inoculation site but did not explore to contact the remaining nodes (see supplementary recording).

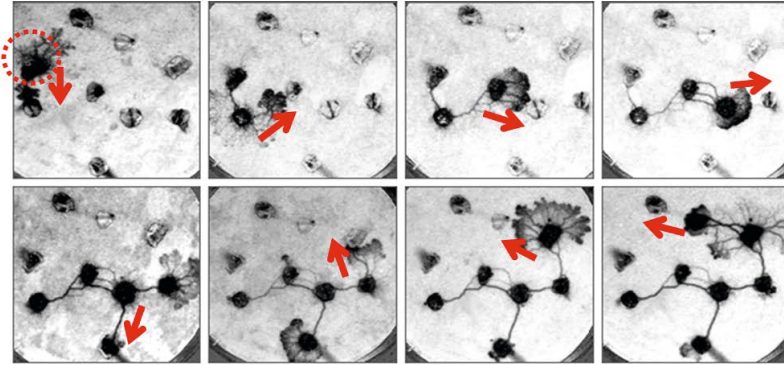


Fig. 4.5 Approximation of spanning tree by *Physarum* in nutrient-poor conditions. Plasmodium is initialised on circled oat flake. Pseudopodia extend from original source towards nearby oat flakes and a protoplasmic tube network connects the nutrient sources. Arrows show current active growth front for clarity.

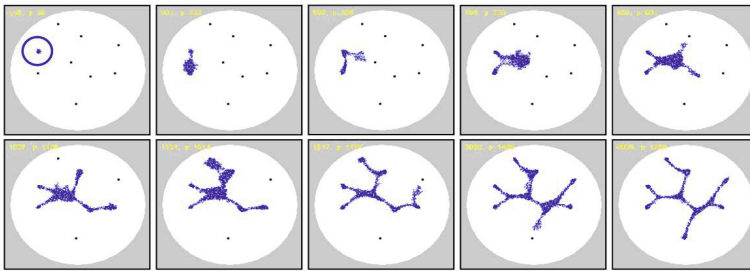


Fig. 4.6 Construction and minimisation of model transport network by pseudopod extension. Nutrient nodes indicated as dots inside circular arena approximating shape of Petri dish. Particles shown as mass of dots. Virtual plasmodium inoculated on left side (circled node). Images show foraging and engulfment of nodes projecting diffusing chemoattractant gradients. Final network configuration approximates the Steiner tree.

4.4.2 *Expansive Radial Growth on Nutrient-Rich Substrates*

The microscopic self-assembly of the particle networks also show effects in the macroscopic patterns and behaviours of the particle population. Fig. 4.7a shows the growth of *Physarum* from an inoculation seed (oat flake) on a nutrient-rich oatmeal agar substrate. The growth approximates circular wave-front propagation with a thick growth front and radial spoke-like veins connecting the source. By tracking outwards from a single vein from the source flake a hierarchical branching pattern can be observed.

Using the growth behaviours in the particle model, a small population was initiated at a central point on a circular source of nutrients. The nutrient-rich substrate was approximated by projecting diffusive stimuli to the environment. The particles moved outwards towards the chemoattractant, consuming the ‘nutrients’ upon contact. The outward movement provided suitable growth stimuli (space availability) and the particle population increased. As the population grew the particle population adapted its size. Overcrowded particles were removed, mimicking decay of the plasmodium and the patterns were morphologically similar to those of *Physarum* (Fig. 4.7). Adjusting the division probability parameter $pDiv$ maintained the hierarchical branching but altered the density of the particle network.

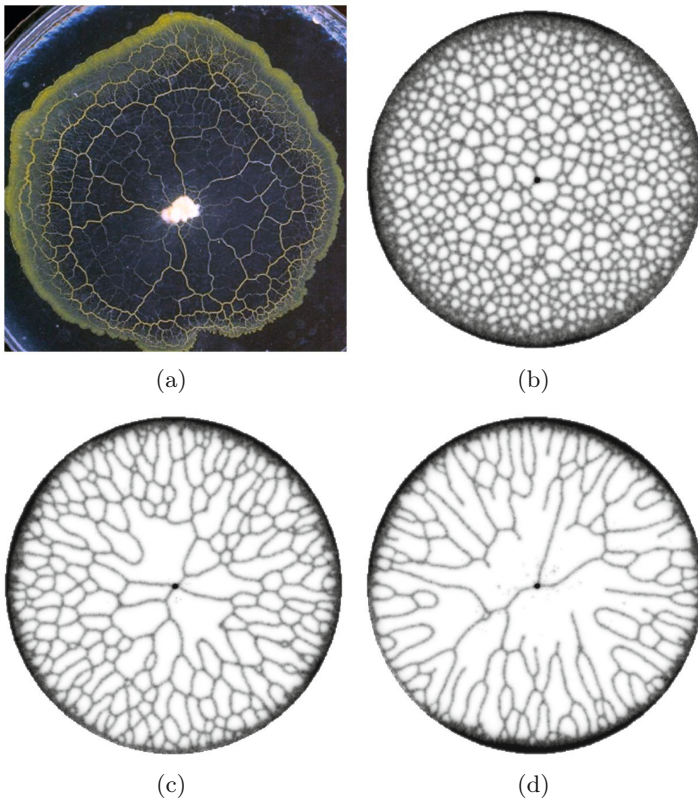


Fig. 4.7 Radial growth of *Physarum* and model on nutrient-rich substrate. (a) Plasmodium of *Physarum* inoculated at oat flake on oatmeal agar (image from [4], courtesy of Andrew Adamatzky). (b-d) Population inoculated at centre of circle. Framework halted when particles encounter border of arena. (b) Growth at $pDiv$ 0.2, (c) 0.08, (d) 0.06.

The emergent transport networks formed by the microscopic interactions of the particle population with their environment reflect not only static pattern morphologies adopted by the *Physarum* plasmodium, but also the long term network adaptation seen in the organism. *Physarum* morphology, evolution and behaviours are strongly affected by the availability, location and concentration of nutrients. The organism appears to behave in a manner which initially optimises (maximises) area exploration and which later adapts its network by optimising (minimising) network distance and network resiliency to damage [9]. The growth and adaptation morphology of *Physarum* strongly depends on the nutrient concentration — high concentration environments generate radial expansive growth whereas low concentration environments result in dendritic growth. Although attempting to characterise the behaviour of such different growth types runs the risk of anthropomorphism, the wave-like (nutrient-rich) behaviours appear more aggressive in terms of the apparent speed of growth and rapid area coverage (see supplementary recordings). The dendritic (nutrient-poor) behaviours appear almost tentative in terms of growth speed and area coverage.

The same morphological and apparent behavioural effects were observed in the particle model when background environmental conditions were modified. Fig. 4.8 and Fig. 4.9 show the effects of high and low concentrations of nutrient substrates on the morphology and collective behaviours of the particle population. The environment is represented by discrete oat flakes (white circles) and nutrient-rich oatmeal agar medium background (grey background). In both experiments identical geometric configurations were used in the environment (i.e. the placement of simulated oat flakes were identical), but the concentrations of the background substrate were different. In both cases the population grows as the environment is searched for nutrients. After the search is complete both conditions spontaneously undergo network contraction and minimisation until minimal network configurations are achieved. In the high concentration condition (Fig. 4.8) the growth is wave-like and expansive and the final network configuration resembles a relative neighbourhood graph with a number of cycles in the network. The growth in low concentration background conditions (Fig. 4.9) shows dendritic growth patterns and the search of the environment is slower. The final network configuration is also more tree-like with only a small inner cycle.

The cause of the differences in growth and adaptation patterns is the background nutrient concentration. In the high concentration condition, the background presents a stronger stimulus to the periphery of the virtual plasmodium and the ‘pull’ of the environment causes expansive movement outwards and provides space for growth. As nutrients are depleted by the outwardly moving population, the background stimulus moves further outward from the edge of the collective and the outer regions of the population move further towards the nutrients. In the low concentration condition the lower background concentration does not provoke such a strong attraction to the population because the nutrient gradients are approximately the same

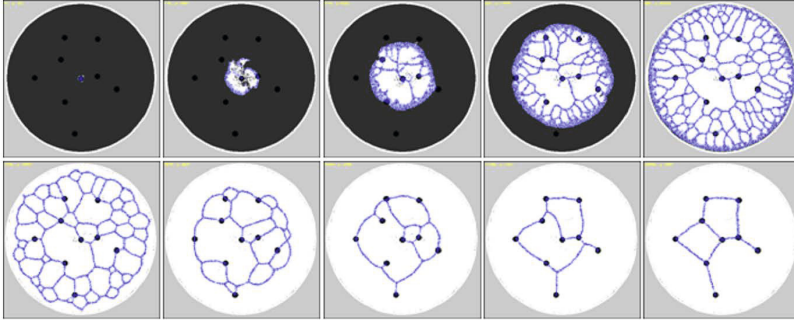


Fig. 4.8 Radial growth and adaptation at high background nutrient concentration. Background nutrient concentration $Proj_d$ 0.01, Population initialised at central node. Images sampled at 11, 110, 213, 327, 487, 1476, 4576, 7004, 11240 and 25000 scheduler steps. Consumed nutrient indicated by white areas.

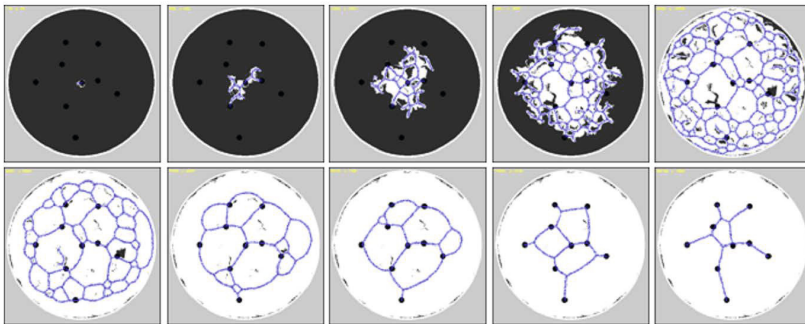


Fig. 4.9 Dendritic growth and adaptation with lower background nutrient concentration. Background nutrient concentration $Proj_d$ 0.001 Consumed nutrient indicated by white areas. Population initialised at central node. Images sampled at 116, 566, 1262, 2361, 3636, 4880, 7448, 9640, 17620 and 36708 scheduler steps.

as the background level of chemoattractant flux. Growth of the population does gradually occur outwards but this is only when significant differences in concentration are created by the local consumption of nutrients by foraging particles. The effect of nutrient concentration on the particle population size can be observed in Fig. 4.10 which indicates the rapid expansion in population size under high concentration conditions (the environmental search is completed at a maximum population size of 21258 at 470 scheduler steps) followed by a rapid initial collapse in population size as network adaptation continues. The low concentration condition shows a slower rise in population size (maximum population of 13574 with search completed in 3440 steps)

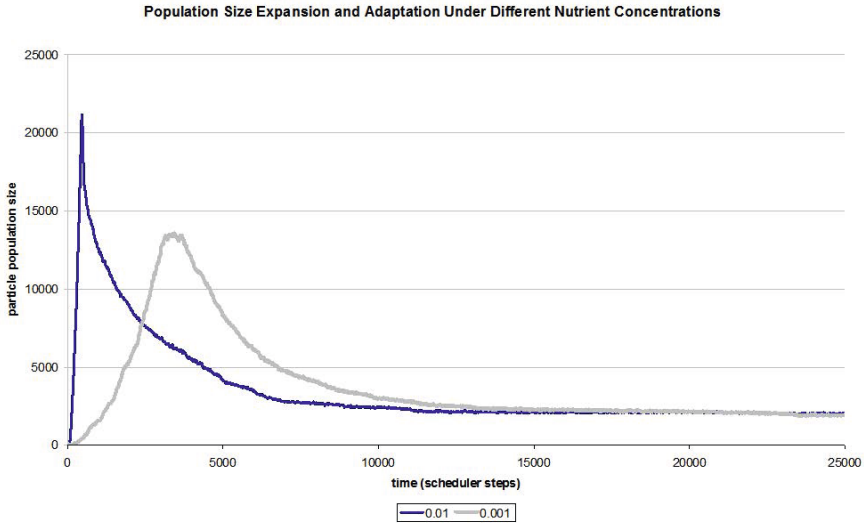


Fig. 4.10 Model population growth and adaptation at different nutrient concentration. Concentration 0.01 indicated by sharp peak in population size, 0.001 indicated by lighter shade and lower peak in population size.

with a slower initial rate of network adaptation. The population sizes of both conditions converge within 15,000 steps although the final network size of the low concentration condition is slightly smaller than the high concentration condition due to the reduced number of cyclic regions in the configuration.

4.4.3 Growth Patterns on Substrates with Varying Nutrient Concentrations

When *Physarum* is inoculated in the middle of an agar dish where one half of the dish is plain agar and the other half is nutrient-rich oatmeal agar, the plasmodium shows preferential growth towards the nutrient-rich side (Fig. 4.11a,b). The growth pattern on the nutrient-rich side is florid and radial, whereas the growth pattern on the plain agar is much smaller and shows a dendritic pattern. The model plasmodium behaves similarly when inoculated in an arena with high concentration nutrient projection on the left and low concentration on the right (Fig. 4.11c), showing much stronger radial growth on the high concentration side and weak growth on the low concentration side.

4.5 Avoidance of Light Hazards and Repellents

Avoidance of light irradiation and chemorepellents was implemented in the model by decreasing the agent sensor values by multiplying by a weighting

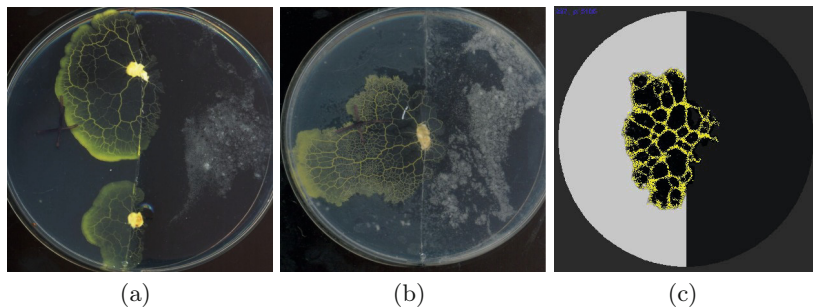


Fig. 4.11 Combination of radial and dendritic growth on dual-concentration substrates. (a) and (b) Plasmodium inoculated at centre line of dish with left side composed of nutrient-rich oatmeal agar and right side plain agar (images courtesy of Andrew Adamatzky), (c) Model plasmodium (particle positions shown) inoculated at centre of dish with left side high concentration and right side low concentration.

factor in areas of the arena exposed to values corresponding to light (L_d , weight factor from 0 to 1, default of 0.2) and repellents (R_d , weight factor from 0 to -1 , default -0.2) respectively. Fig. 4.12 illustrates the response of both fixed and adaptive population sizes to simulated light hazards, in this case vertically placed bars obstructing a straight path between two nutrient sources. For fixed populations the population shifts the bulk of its shape away from illuminated regions (Fig. 4.12, left). In adaptive populations the virtual plasmodium curves around the light obstacles to connect the two nutrient sources at opposite sides of the arena (Fig. 4.12, right), thus reproducing the collision-free path planning by *Physarum* reported in [75].

When growing in an environment containing both nutrients and repellents the *Physarum* growth front extends towards nutrients whilst moving away from repellents. This behaviour was reproduced in the model which avoided the repellent regions (Fig. 4.13, light squares) whilst growing towards and consuming nutrients (dark squares) in the arena.

4.6 Connectivity of Virtual Plasmodium Networks

Baumgarten and Hauser performed image analysis to extract and describe the structure and topology of *Physarum* transport networks [167]. They found that the nodes (junctions) within the plasmodium network had, almost exclusively, degree of connectivity equal to 3. To examine the connectivity of virtual plasmodium networks we adopted a similar approach to that of Baumgarten and Hauser. Transport networks formed by a radially growing virtual plasmodium within a simulated nutrient-rich substrate (Fig. 4.14a) were skeletonised (reduced to single pixel thickness, Fig. 4.14b) using the ImageJ image analysis software [168]. We extended the skeletonisation analysis method of

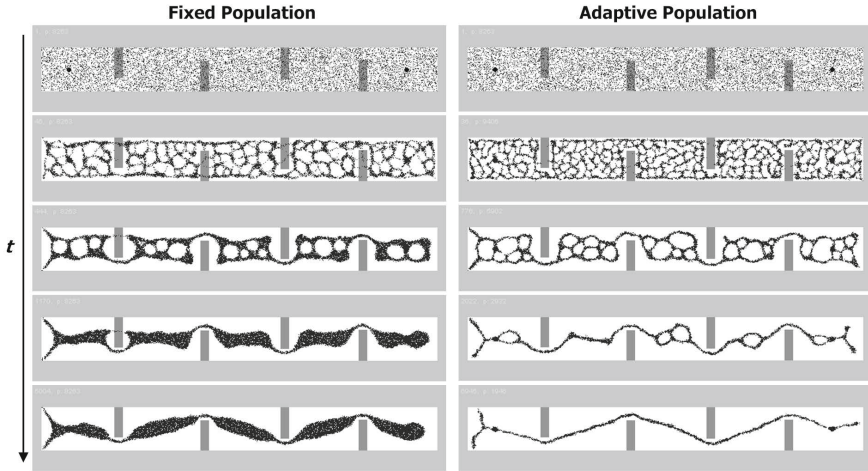


Fig. 4.12 Avoidance of simulated light hazards in fixed and adaptive populations. Population (particle positions shown) is initialised in arena with two nutrient sources at either end interrupted by vertical bars of projected light. Population adapts to avoid migrating onto exposed areas. (left) fixed population, (right) adaptive population.

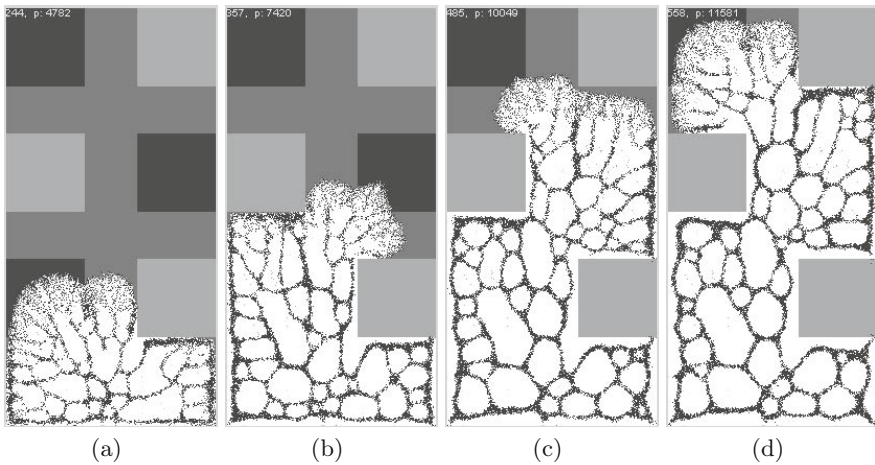


Fig. 4.13 Growth towards attractants and avoidance of repellents in model plasmodium. a-d) Growth of model plasmodium (particle positions shown) on simulated nutrient-rich substrate with high concentration regions indicated by dark grey squares and repellents by light grey squares.

Arganda-Carreras et al. [169] in order to calculate the connectivity information from the skeletonised image data (Fig. 4.14c and d). Analysis of virtual transport networks found that the degree of connectivity matched that found by Baumgarten and Hauser (specifically, a mean degree of 3.02 in a sample of 2069 junctions). The vast majority of junctions were of degree 3 (Fig. 4.15a) and the distribution of angles about these junctions showed that the most common angle was 120° (Fig. 4.15b).

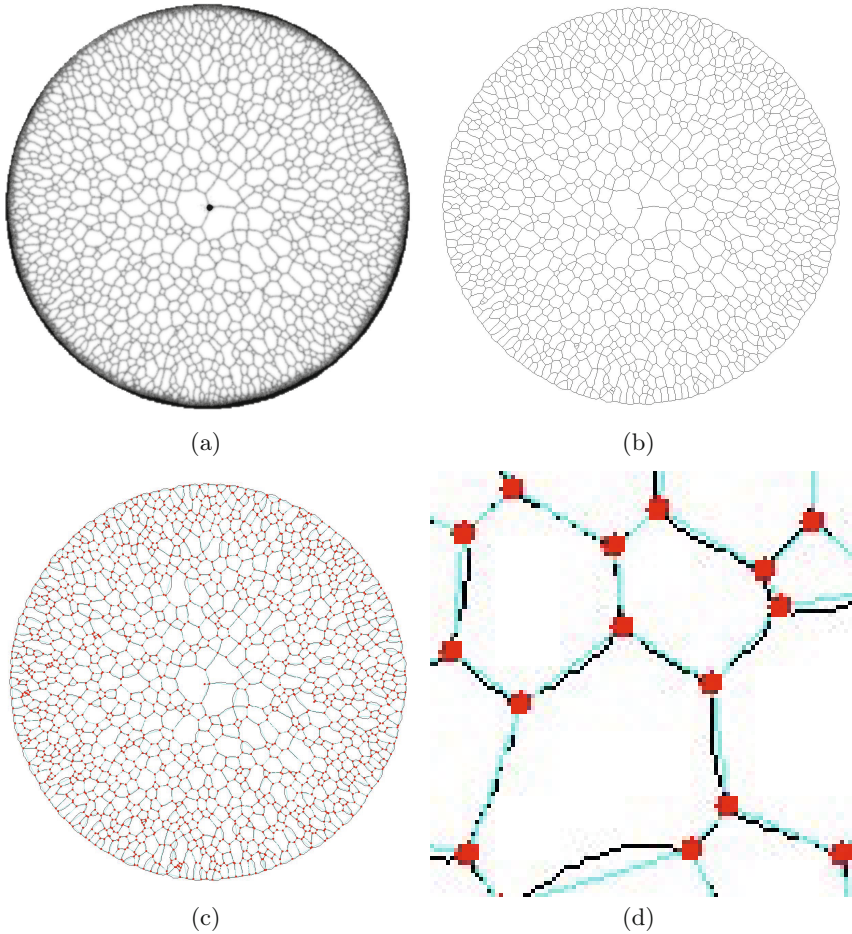
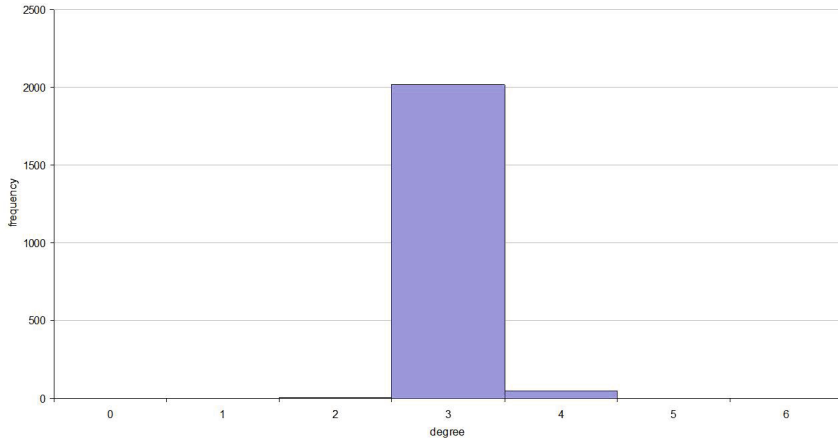
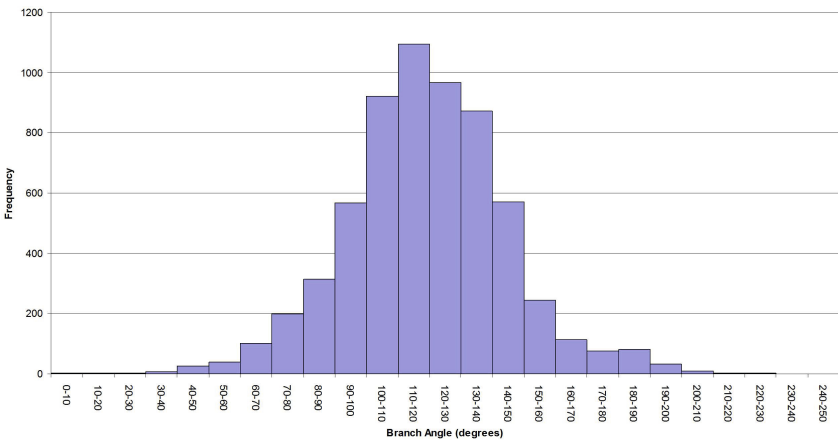


Fig. 4.14 Extraction of junction data from virtual plasmodium network. (a) Emergent transport network formed by growing virtual plasmodium on simulated nutrient-rich substrate, (b) Skeleton extracted from (a), (c) 'logical' junction connectivity calculated from (b), (d) Enlarged section from (c) showing junctions (solid discs), original network paths (dark lines) and 'logical' paths (pale lines).



(a)



(b)

Fig. 4.15 Distribution of degree and angle distribution in virtual plasmodium network. (a) Histogram of junction degree calculated from Fig. 4.14. Number of junctions was 2069 and mean degree was 3.02, (b) Plot of histogram distribution of junction angles showing the most frequent angle of 120° .

4.6.1 Dynamical Evolution of Network Connectivity

Analysis of static snapshots of virtual transport networks does not illustrate the complex evolution of their formation, evolution and minimisation. We developed methods to dynamically track the evolution of connectivity of the networks. A typical example is shown in Fig. 4.16a,b, where a virtual plasmodium is represented by a population of 9600 particles initialised at random

locations in a circular arena containing 100 nutrient nodes. Transport networks spontaneously formed within the ‘plasmodium’. The network became smaller as competing paths merged. The minimisation process was affected by attraction to the nodes which served to constrain the evolution of the network. The majority of the minimisation occurred in the first 2500 steps in both high and low concentration conditions. When high node concentration was used (Fig. 4.16a, projection weight 0.1) the closure of network lacunae was restricted by the attraction of the network to the nodes. At low concentration (Fig. 4.16b, projection weight 0.01) there was less constraining of network adaptation which persisted for a longer time resulting in a shorter overall network (Fig. 4.17a) and larger lacunae (Fig. 4.17b).

To analyse the dynamical changes in connectivity as the network evolution progressed, we analysed the networks every 50 scheduler steps. The network trail images (as per examples in Fig. 4.16a-b) were skeletonised and each skeleton junction point was analysed to assess its degree of connectivity. We implemented the fast skeletonisation method described by Mukundan ([170], and personal communication) to enable the dynamical tracking of junction points (specifically the moving Steiner junction points). The changes in connectivity degree at low and high concentration are shown in Fig. 4.18.

In both conditions there is a steep initial decline in the number of junctions of degree 3, reflecting the initial shrinkage of the transport networks (see supplementary video recordings for a visual illustration). In the high weight condition the evolution is mostly stabilised after 5000 steps with the majority of junctions being of either degree 2 or 3. In the low concentration condition the minimisation (closure of network cycles) continues after 5000 steps with a fall in degree 3 connectivity and a corresponding increase in degrees 1 and 2. The increase in degrees 1 and 2 is visualised pictorially (Fig. 4.16b) as more isolated nodes (degree 1) and the organisation of networks into longer chains of nodes (degree 2) when compared to the high concentration condition (Fig. 4.16a).

4.7 Environmental Factors Affecting Growth and Adaptation

Growth of *Physarum* is dependent on the availability, concentration and placement of nutrient sources in the environment. The plasmodium membrane is sensitive to diffusion gradients and preferentially grows towards nearby sources of nutrients by extending pseudopodia towards the nutrients. Adamatzky found that on nutrient-poor conditions (damp filter paper and oat flake nutrient nodes) the plasmodium initially constructs a spanning tree when inoculated at a single site and constructs networks relating to the upper ranges of the Toussaint hierarchy of proximity graphs when inoculated at multiple sites [80].

To assess the effect of chemoattractant diffusion, nutrient concentration and nutrient placement on the growth in the particle model we inoculated a

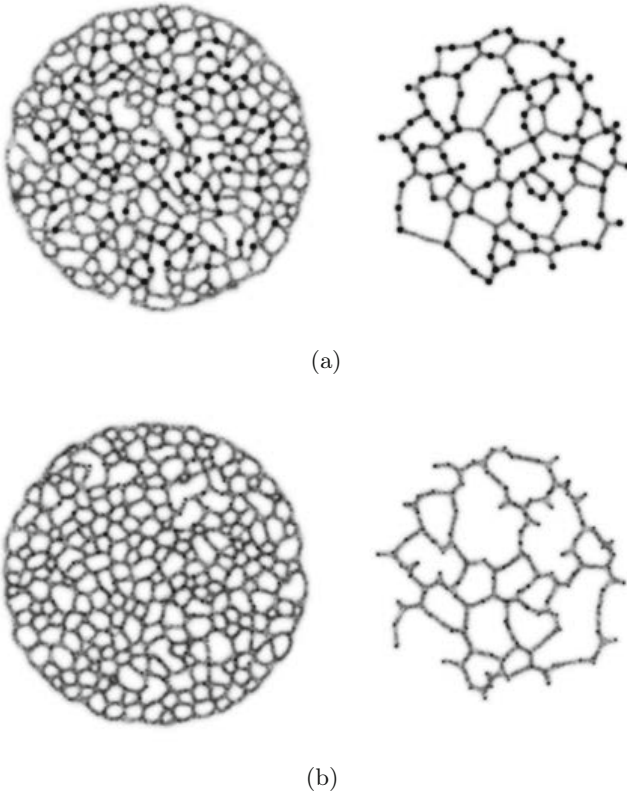
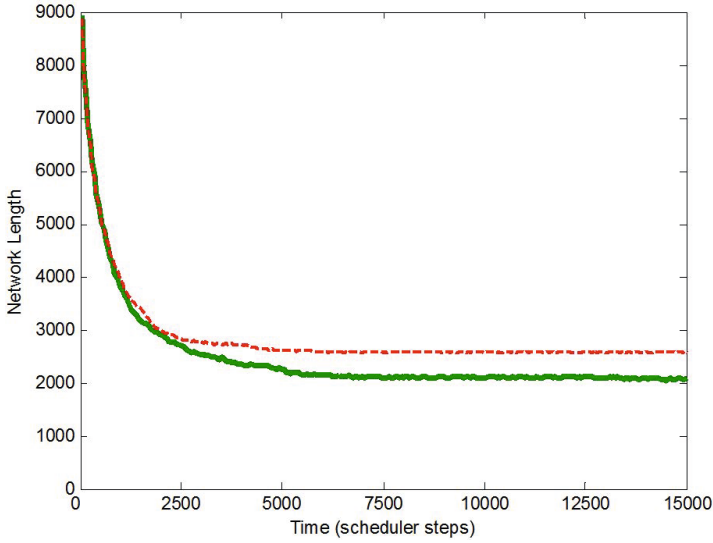
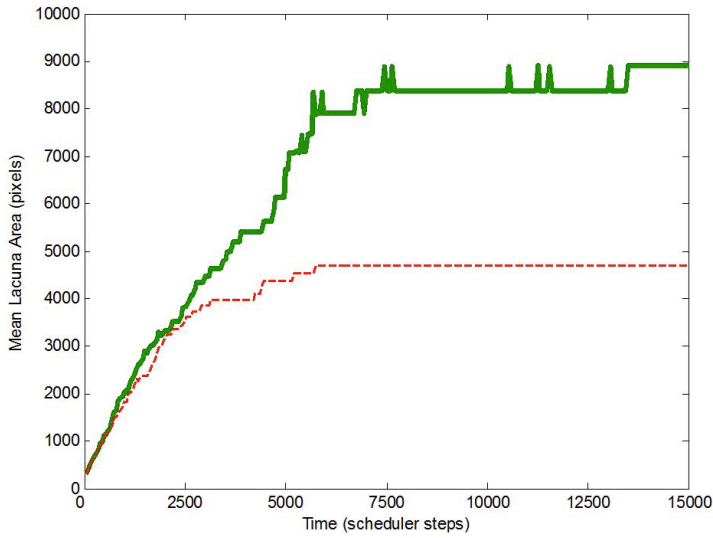


Fig. 4.16 Effect of nutrient concentration on transport network structure in a 100 node network. (a) Initial transport network (left, 102 steps) and final network configuration (right, 14994 steps) at high nutrient concentration. (b) Evolution of network at low nutrient concentration.

small population at a simulated nutrient source. We assumed (as in [80]) that any nutrients covered by the virtual plasmodium would suppress the diffusion of chemoattractant from that source. Fig. 4.19 shows the effects of placing nutrients near the plasmodium. When the diffusing chemoattractant gradient reaches the initial site of population initialisation, the particles closest to the gradient are attracted towards the gradient and move towards it. The movement of the population stimulates flow from the periphery of the collective and a pseudopod-like process emerges and moves towards the source of the gradient. The width of the pseudopodium active region is dependent on the size of the chemoattractant gradient. When the nutrient source is reached the engulfment by the particles suppresses the diffusion from the node and the connection is stabilised and minimised. The adaptation also occurs when stimuli are removed from the environment by retracting the pseudopodium

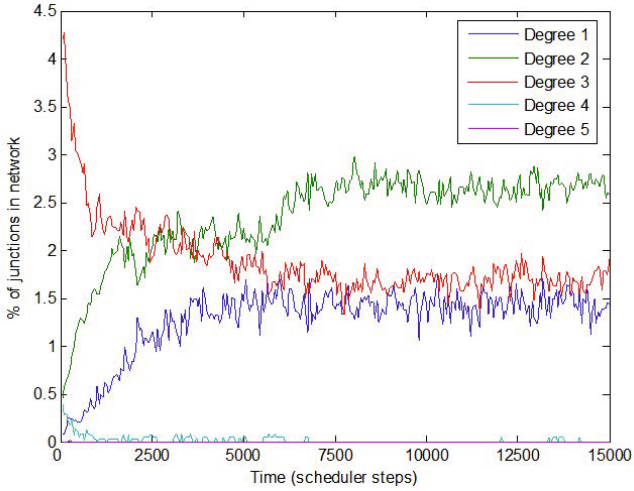


(a)

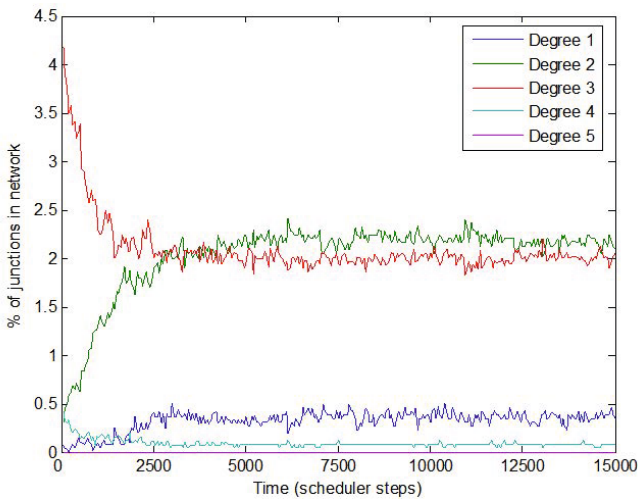


(b)

Fig. 4.17 Effect of nutrient concentration on transport network connectivity in a 100 node network. (a) Evolution of transport network length at nutrient concentration 0.1 (dashed) and 0.01 (solid), (b) Evolution of mean lacuna size at nutrient weights 0.1 (dashed) and 0.01 (solid).



(a)



(b)

Fig. 4.18 Dynamical evolution of junction degree connectivity at different nutrient concentrations. Plot of the percentage of junction connectivity in the network showing changes in each degree of connectivity as network minimisation progressed. (a) Evolution at nutrient weight 0.01, (b) Evolution at weight 0.1.

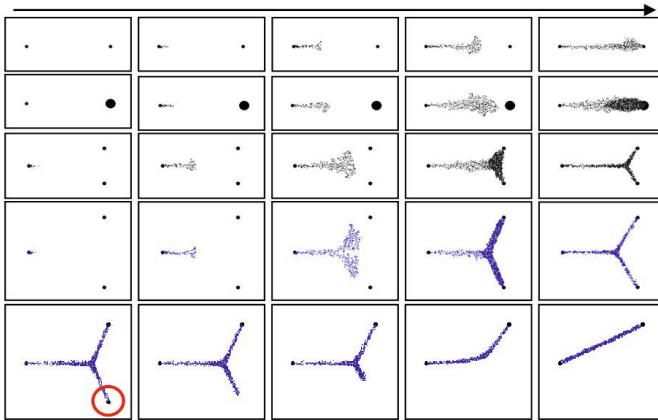


Fig. 4.19 Pseudopodium extension and evolution in model plasmodium: Discovery, pseudopod extension, tube network formation, pseudopod retraction and network adaptation in particle model. Population initialised on left, time progresses in arrowed direction. Nutrient source on right projects chemoattractant into the diffusing gradient field. Pseudopod extension observed as particles multiply. Network minimisation continues once all nodes have been located.

from the deleted source and adapting the network shape in response (bottom row, deleted node is circled).

4.7.1 Nutrient Distance

As the growing population discovers new nutrient sources the transport network automatically adapts its shape in response to the new nutrient sources. Fig. 4.20 shows the network adaptation as information about the nutrient locations arrives at different times due to their increasing distance. The network adapts in response to the changing environment and minimises the distance when all the nutrients are located.

The example in Fig. 4.20 illustrates one mechanism of how stimuli from the environment (diffusion of chemoattractants and differences in the gradient arrival time at the plasmodium) can shape the behaviour of the particle collective. The effect of the environmental conditions on *Physarum* itself was studied by Nakagaki who found that the plasmodium adapted its size and tube network to favour both larger nutrient sources (in terms of surface area) and nutrient sources of higher nutrient concentration [11]. Latty and Beekman demonstrated the effect of nutrient quality on search strategy in *Physarum* when foraging for nutrients and exploiting a nutrient patch [12]. They found that the plasmodium persisted longer at high quality patches of nutrients in

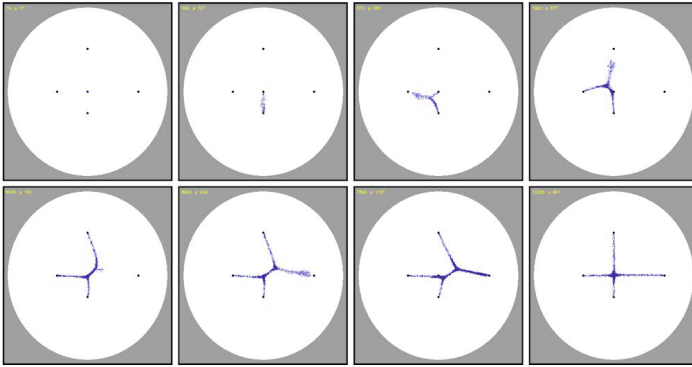


Fig. 4.20 The effect of distance on nutrient discovery and network adaptation. Inoculation of particle population at central node. Closest nutrient source is 50 pixels away. Distances to other nodes are 75, 100 and 125 pixels. Transport network shape adapts as new nutrient sources are discovered. Final image shows optimised transport network when foraging is complete.

order to ‘mine’ the high quality nutrients (an intensive search of the area near the nutrient patch). Lower quality patches resulted in shorter time spent in the region and a more extensive foraging of the environment.

4.7.2 Nutrient Size and Concentration

The effect of nutrient size was studied by inoculating a small population at the centre of a circular arena surrounded by four nutrient sources at identical distances (Fig. 4.21). Each image in the figure shows the concentration gradients (left side of each image) and the particle positions (right side). When nutrient sources were the same size and concentration the particle collective grew by extending pseudopodia towards the nutrients at the same time (Fig. 4.21, left column). When the pseudopodia reached the nutrients the engulfment suppressed the projection of nutrients into the arena and reduced the concentration gradients. When the nutrients were at different concentrations the pseudopodia were preferentially extended in the direction of the strongest nutrients first (Fig. 4.21, middle column). Pseudopodia were only extended to the remaining nutrients (in decreasing order of concentration) when the gradient of the previous nutrient block was suppressed by engulfment. When all sources had been located network adaptation took place (Fig. 4.21, middle column). When the nutrients varied in size only, the concentration gradients from the larger nutrient blocks were larger and pseudopodia were extended to the larger nutrients first. After all nutrients had been discovered the network adapted again to cover the regions of the nutrients but the mass of the population was shifted towards the position of the largest nutrient block (Fig. 4.21, right column, bottom image).

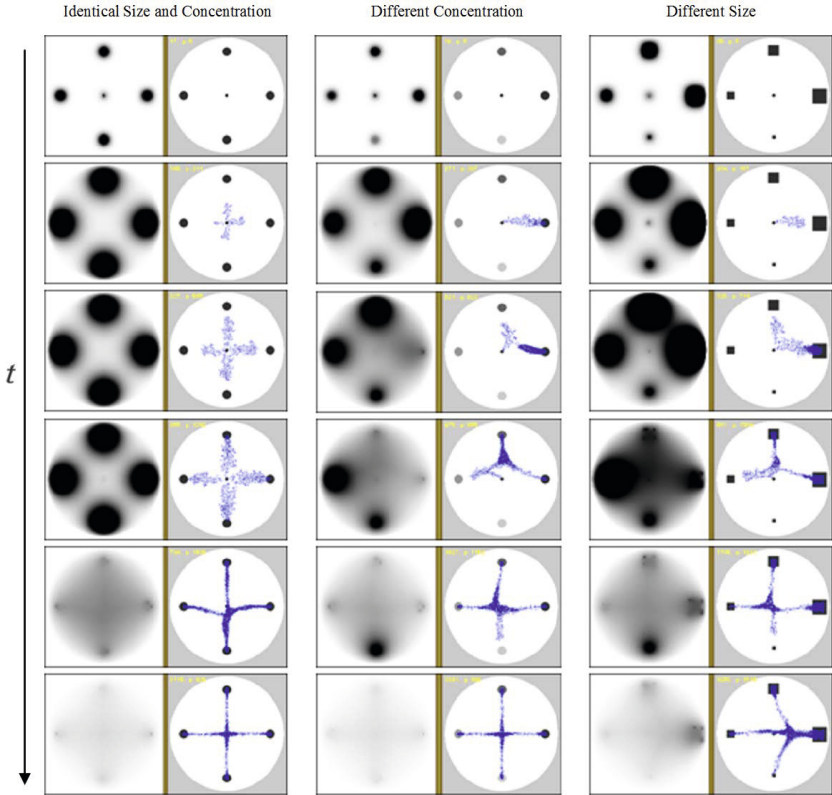


Fig. 4.21 The effect of nutrient size and concentration on network foraging behaviour. Evolution proceeds from top to bottom. Left of each image shows diffusion gradients, right side shows nutrients and particle positions, Left: All nutrients are of equal size and concentration, Middle: Nutrients are of equal size but different concentration, Right: Nutrients are of equal concentration but different size.

4.7.3 Effects of Environmental Noise on Network Adaptation

Plasmodia of *Physarum* live in complex, noisy environments. To assess the response of the virtual plasmodium to noise a noisy environment was implemented by modulating the configuration of an experimental arena with increasing levels of Gaussian noise (Fig. 4.22a-c). The noise contamination presented an extra source of information to the agent particles in addition to the nutrient stimuli nodes. A fixed population was initialised in the arena and formed minimising networks for 20,000 steps. A record of occupancy for every cell in the arena was incremented every time a cell became newly occupied. In the noise free arena the population minimised to a spanning tree structure

(Fig. 4.23a). At increasing noise levels the networks structure contained more cyclic connections (Fig. 4.23c,e) as the noise stimuli caused the population to continue to explore the arena. The plots of cumulative distribution frequencies of occupancy levels indicate that when noise was not present the majority of cells in the lattice were occupied less frequently (during the initial period of network formation and minimisation, Fig. 4.23b). As noise increased the increase in foraging resulted in greater occupancy in more of the lattice sites (indicated by a less steep curve, Fig. 4.23d,f).

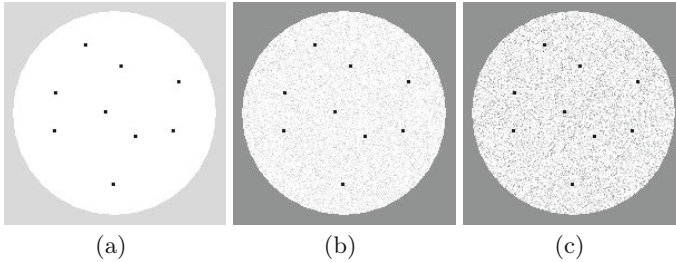


Fig. 4.22 Representation of noise contamination on environment arena. (a) Source data points, (b) Contamination with Gaussian noise $\sigma = 10$, (c) Contamination with $\sigma = 20$ (b and c enhanced by gamma correction for visibility).

4.7.4 Consumption of Nutrients

The suppression of nutrient concentration gradients represents a complex non-linear and dynamical environment as the nutrient gradients are in constant flux. In real world systems the complexity is compounded by the consumption of nutrients. The effects of such complex interactions between spatial position, concentration and consumption are shown in Fig. 4.24. The examples show an initial inoculation site at the bottom centre of a circular arena. Above the inoculation site are three nutrient sources of identical size but potentially different concentration (pixel intensity 255 or 50). In Fig. 4.24i all three nutrients are identical and the pseudopodium grows towards the closest source and extends further pseudopodia as the middle nutrient is consumed and gradients from the outer nutrients reach the collective. A similar situation occurs in Fig. 4.24ii but the migration from the central nutrient is delayed because the nutrient is of higher concentration than the outer nodes and its consumption takes longer. In Fig. 4.24iii both outer nutrients are of higher concentration and, although the collective initially grows towards the closer central node, the mass of the collective extends towards the outer nodes as the gradient is stronger. In example Fig. 4.24iv the growth of the collective towards the central nutrient node is waylaid by the stronger attraction towards the left node. Extension towards the rightmost node only occurs after the majority of the left node has been consumed. Finally, in Fig. 4.24v the

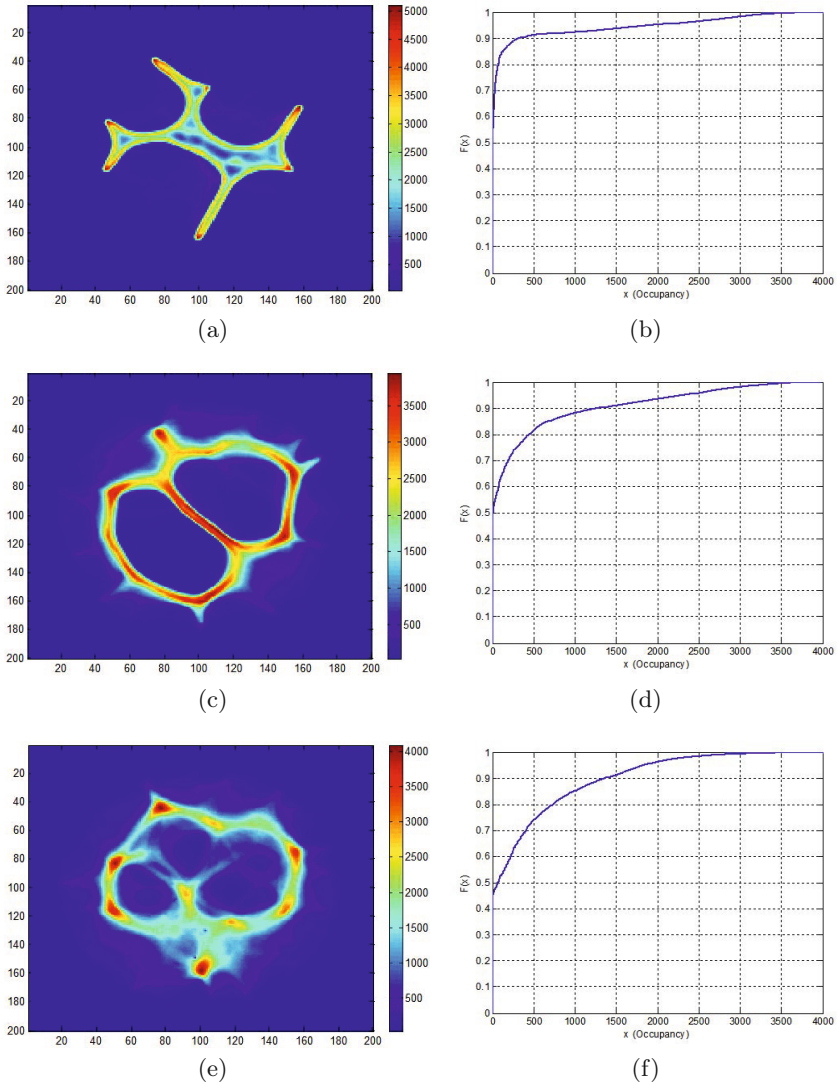


Fig. 4.23 Effect of environmental noise on network adaptation. (a,c,e) Plot of occupancy frequency over 20,000 scheduler steps, (b,d,f) Plot of cumulative distribution frequency indicating occupancy of sites on image at different noise contamination levels.

collective grows towards the (closest) central node and then to the leftmost node which is equal in concentration. Growth towards the node on the right only occurs when the other nodes are mostly depleted.

4.7.5 *Effect of Physical Substrate Properties on Growth Patterns*

Growth patterns in collective organisms may be affected by the physical properties of the growth substrate. In bacterial colonies the hardness of the growth medium affects the locomotion of individuals and the resulting colony patterns with bacteria, in general, favouring less rigid growth media [108]. *Physarum* also exhibits different locomotion behaviours depending on the properties of the substrate. Takamatsu found that *Physarum* propagates a longer distance and with straighter protoplasmic tubes when the medium hardness increases [124]. Qualitative physical differences in substrates also affect foraging behaviours, possibly by affecting the adhesion of the plasmodium and its slime capsule to the substrate as it moves. Fig. 4.25 illustrates the effect of different substrate medium types on foraging behaviours. Growth on crushed oat flakes on damp filter paper results in aggressive non-uniform growth (Fig. 4.25a), possibly because the uneven surface presents an irregular interface at the periphery of the plasmodium. A relatively smooth nutrient-rich agar medium results in more uniform wave-like expansive growth (Fig. 4.25b).

A similar effect can be elicited in the particle model by a difference in growth behaviour. Non-uniform conditions may be simulated by having new particles select random directions from the particle which spawned them. This results in characteristically ‘aggressive’ foraging behaviours (Fig. 4.26a) with the random direction of new particles creating a writing growth margin. The periphery of the collective shows travelling waves of activity as particles are created and destroyed. The aggressive foraging activity continues long after the nutrients have been consumed and the collective finally shrinks to its minimum size.

Uniform media may be simulated by providing newly created particles with the same direction as the particles which spawned them (supported by the observation that *Physarum* plasmodia often exhibit a characteristic directional persistence to their movement). This results in uniform expansive growth behaviour (Fig. 4.26b). The lack of foraging activity at the growth margin results in a more cohesive population which shrinks when the majority of nutrients have been consumed. A side-effect of the cohesive behaviours is the fact that the shrunken population migrates towards small residues of unconsumed nutrients and extends outwards to engulf and consume them.

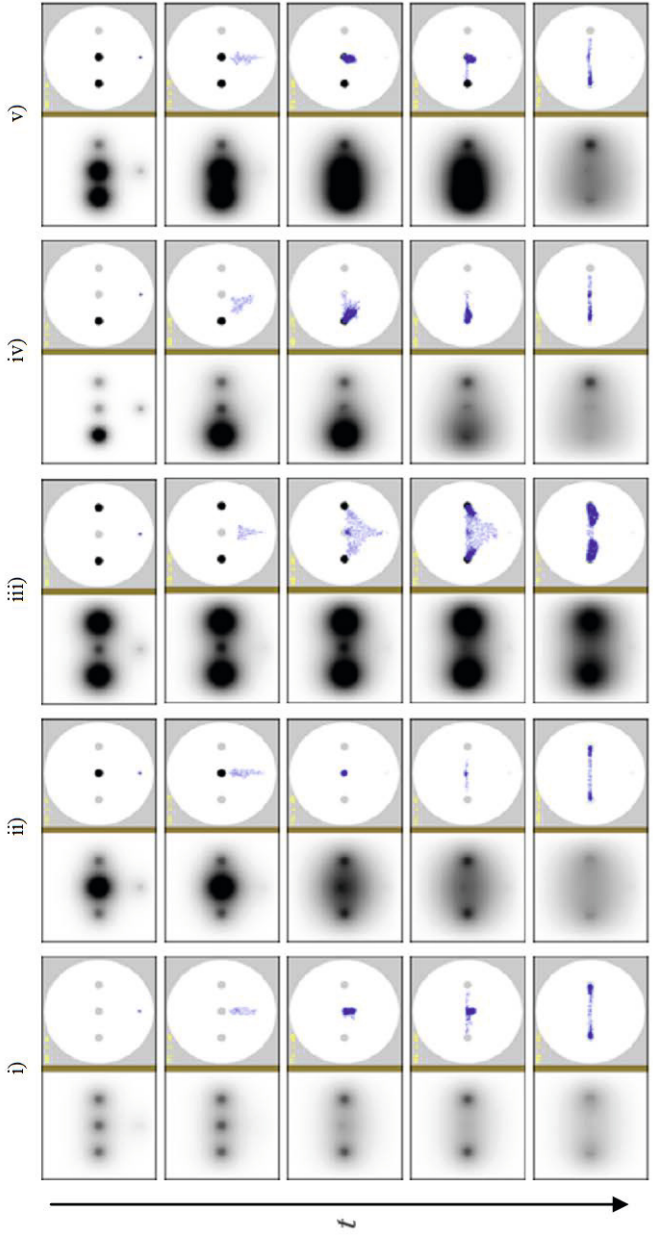
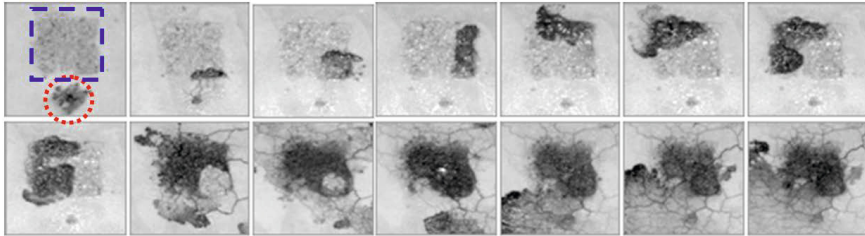
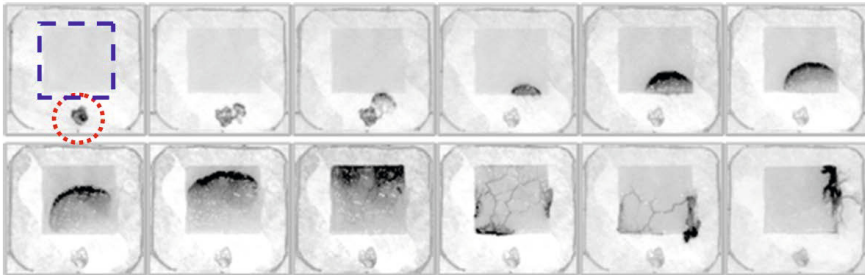


Fig. 4.24 Effect of nutrient concentration and consumption on foraging behaviour. Time evolution proceeds left to right in direction of arrowed t . Left of each image shows diffusion gradients, right side shows nutrients and particle positions.



(a)



(b)

Fig. 4.25 Growth patterns of *Physarum* on different substrates. (a) *Physarum* (dashed circle) inoculated on oat flake at the bottom of the arena migrates towards square area (dashed square) composed of crushed oat flakes. Exploration of environment and consumption of nutrients continues in an ‘aggressive’ manner. (b) *Physarum* (dashed circle) inoculated on oat flake at the bottom of the arena migrates towards square area (dashed square) composed of nutrient-rich oat-meal agar. Exploration of environment and consumption of nutrients continues as a progressive wave-like expansion.

4.8 Summary: Environmental Mediation of Behavioural Complexity

We have reproduced some of the biological pattern formation behaviours of *Physarum* using the virtual plasmodium model. The model demonstrates the formation of transport networks from a solid ‘sheet’ of material, network adaptation of pre-existing plasmodia, selection of shortest path, hazard and repellent avoidance, and network adaptation. A complex foraging ability is observed, capable of distinguishing between the closest, strongest, and largest sources of nutrients in uniform and noisy environments.

It must be stressed that the computational model is an idealised representation of the relationship between the organism and its environment. In real-life the environmental conditions, and thus the gradients, would be far less stable and this may be partially responsible for the relative unpredictability of the behaviour of the plasmodium. The adaptation response (changes in

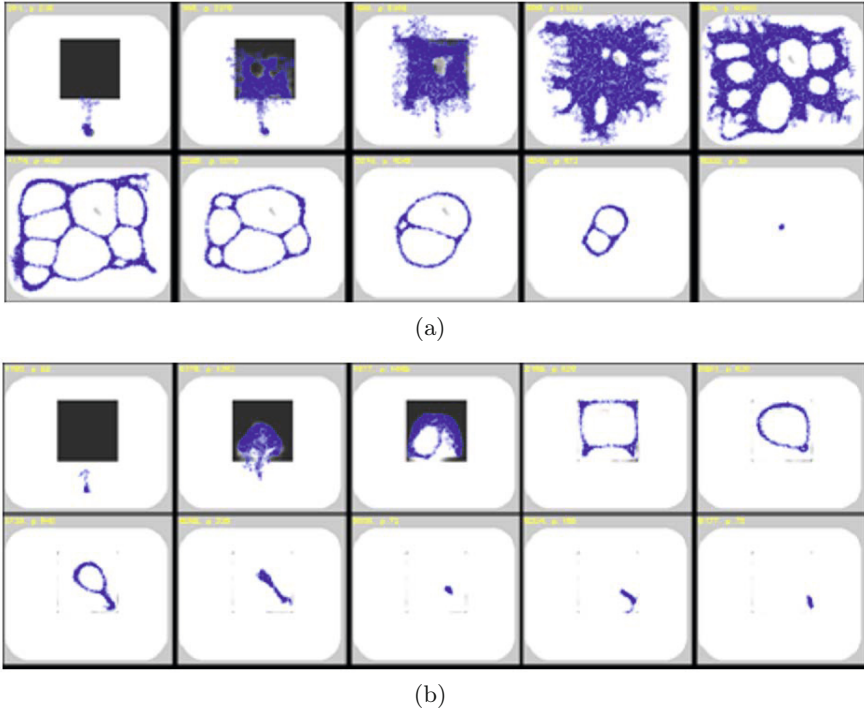


Fig. 4.26 Variations of growth patterns in model via differing growth parameters. (a) Model growth behaviour with random directional selection shows ‘aggressive’ foraging growth. Foraging continues for some time after nutrients have been consumed, (b) Model growth behaviour with identical directional selection (new particle takes direction of previous particle) shows expansive growth and rapid minimisation after majority of nutrients have been consumed. Note that the shrunken collective moves about the arena and consumes remaining nutrients.

morphology) of the particle transport networks in response to environmental changes is also much greater than observed in *Physarum*. This is because the adhesion of the plasmodium to the substrate by the slime capsule (and remnants of old protoplasmic tubes) is not seen in the model transport networks which thus adopts a more idealised minimisation of network length than seen in the organism. The mechanism for population growth and adaptation is also obviously a great simplification of what must occur in the organism, yet is still implemented using constraints which must apply to the organism, i.e. under local, distributed conditions. Despite the idealised relationship between the model, organism and environment the model captures essential emergent behaviours of the plasmodium using only very simple, local and distributed sensory and motor interactions, which is also the case with *Physarum* itself.

Although we have presented a general scheme of an environmentally mediated mechanism for complex morphological behaviours, such a mechanism obviously requires a cellular basis which is not represented in this simulated approximation and is thus out of scope for this model. The cellular mechanism must provide a means of responding to environmental stimuli which come into contact with the plasmodium (sensory behaviours) and a means of generating and directing movement towards (or away from, in hazardous cases) the stimuli. In the particle approximation forward biased movement is intrinsic to the particle specification and the question of how it is generated is not considered.

Nakagaki's seminal experiment exploring complex behaviours in *Physarum* by its ability to solve maze problems [70] provokes questions about the nature of intelligence because *Physarum* does not possess any conventional nervous system or specialised tissue deemed to be necessary for intelligent behaviours to emerge. One possible response is to dismiss the tasks and state that some problems do not actually require intelligence in the first instance. Indeed it is actually possible to perform similar path planning tasks using only physical systems such as chemical reaction-diffusion media [72, 171], or chemotactic oil droplets [71]. However, merely dismissing the task as not requiring intelligence in some way appears to 'move the goalposts' of the definition of intelligence. Would these tasks still be deemed to require intelligence had it not been demonstrated that such a simple organism could solve them?

If we cannot look to the components of *Physarum* itself for clues about its complex behaviours, perhaps some of its abilities can be explained by its complex interactions with the environment. Stigmergic communication has been suggested as a mechanism to encode information about previous actions by individuals in a population [172] and the environment may be considered as an external storage medium. The location and quantity of such stimuli (for example ant corpses or pheromone trails) may be subject to alteration by physical forces such as evaporation or diffusion. In the above examples of maze solving using physical systems, the schemes also make use of the pre-processing of the system by physical forces in the environment, typically diffusion processes. The 'solutions' to the maze are actually methods of displaying the shortest path which has already been computed (in effect, back-tracking to the origin of the gradient).

In the results demonstrated in this chapter, the role of the environment, in particular the diffusion of simulated nutrient gradients, is also critical in invoking an adaptive response from the particle collective. The complex response of the collective is a dynamic interplay between the effect of nutrient gradients at the periphery of the collective (stimulating movement towards the gradient and thus multiplication of the particles) and the changes in gradient concentration caused by engulfment and consumption of the nutrients by the collective. We have shown that such a simple interaction can generate a complex range of *Physarum*-like patterning and foraging behaviours under different environmental conditions.

Optimality in foraging is critical to the survival of organisms and a balance must be found between the cost of searching for new nutrients and the exploitation of the nutrients at the current location. From the results obtained in this chapter we suggest that two-way interactions between the organism and the environment, mediated by the dynamic adjustment of concentration gradients, may provide a suitable mechanism for the complexity of foraging, growth and adaptation behaviours observed in *Physarum*. The mechanism may also provide insights into the apparent intelligence of this simple organism. How can the plasmodium find the optimal (closest, strongest, largest) nutrient sources and exploit and connect nutrient patches efficiently when it does not have the nervous system which would allow it to make informed decisions about such tasks? In higher organisms the foraging behaviour is selected by the organism itself. That is, the organism decides upon, or computes, the foraging choice, which is then executed. In simpler organisms which do not have a nervous system, such as *Physarum*, the environment may be responsible for a greater part of this computation, i.e. for inducing the behaviour in the organism.

Note, however, that *Physarum* is not merely a passive substance reacting to pre-processing by external conditions, nor indeed is there a final static problem solution; the organism morphology reflects, and contributes towards, a continuing adaptive response to current environmental conditions. The modification of nutrient concentration gradients by their engulfment and consumption is in itself a complex modulation of the ‘signal’ which encodes information about the environment.

If *Physarum* does utilise the complex processing of concentration gradients by the environment does this support the view that the organism is not intelligent? Or is the opposite true: perhaps it could instead be viewed as a highly efficient outsourcing of processing which enables a computationally ‘lean’ organism to contribute towards and exploit a highly desirable and efficient search strategy? The adoption of such a mechanism which could exploit natural processing in the environment would prove highly desirable in artificial computing schemes such as distributed robotics which are necessarily limited in computational abilities and power consumption. Examples of how the multi-agent virtual material approach may be used to reproduce the computational abilities of *Physarum* are described in the following chapters.