



Brainless but Multi-Headed: Decision Making by the Acellular Slime Mould *Physarum polycephalum*

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Abstract

Because of its peculiar biology and the ease with which it can be cultured, the acellular slime mould *Physarum polycephalum* has long been a model organism in a range of disciplines. Due to its macroscopic, syncytial nature, it is no surprise that it has been a favourite amongst cell biologists. Its inclusion in the experimental tool kit of behavioural ecologists is much more recent. These recent studies have certainly paid off. They have shown that, for an organism that lacks a brain or central nervous system, *P. polycephalum* shows rather complex behaviour. For example, it is capable of finding the shortest path through a maze, it can construct networks as efficient as those designed by humans, it can solve computationally difficult puzzles, it makes multi-objective foraging decisions, it balances its nutrient intake and it even behaves irrationally. Are the slime mould's achievements simply "cute", worthy of mentioning in passing but nothing to take too seriously? Or do they hint at the fundamental processes underlying all decision making? We will address this question after reviewing the decision-making abilities of the slime mould.

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Physarum polycephalum

The first paper to describe the life cycle of *P. polycephalum* was published in 1931 by Howard [1]. Prior to Howard's series of papers, publications dealt with the slime mould's rather confusing taxonomy. Although originally classified as a fungus, hence, the name "slime mould", *P. polycephalum* and its relatives currently sit in the paraphyletic kingdom "Protista" that contains a variety of mostly unicellular eukaryotes that do not fit in other kingdoms. *P. polycephalum* is a "true" or "acellular" slime mould. Unlike the "cellular" slime moulds, to whom they are distantly related [2], acellular slime moulds have a syncytial "plasmodium" stage in their life cycles. The plasmodium consists of millions of nuclei lacking any membrane between them and is thus considered to be a single, albeit gigantic, cell. In contrast, cellular slime moulds such as *Dictyostelium discoideum* spend the majority of their life cycles as individual, single-celled amoeba. When conditions become unfavourable, the individual amoeba aggregate to form a multi-cellular "slug"

that crawls a short distance before forming a stalked fruiting body.

The migrating plasmodia of acellular slime moulds typically form an extending fan-like sheet at the front followed by a network of interconnected veins (pseudopodia) through which cytoplasm streams [3]. In nature, plasmodia feed on bacteria and fungi that they engulf and digest. Because of its peculiar morphology, plasmodia can exploit multiple food sources simultaneously by forming networks of veins connecting them (Fig. 1). If food is abundant, plasmodia are capable of extensive vegetative growth and can cover an area exceeding 900 cm² [3]. Under nutritional stress and when exposed to light (light is a stress factor), vegetative growth is arrested and the plasmodium forms sexual structures in which haploid spores are formed (sporangium). The spores germinate to yield microscopic, haploid myxamoebae of different mating types. Myxamoebae feed on bacteria and proliferate by mitotic cell division. When two myxamoebae of different mating types meet, they can fuse to form a binucleate cell. Nuclei within such binucleate cells

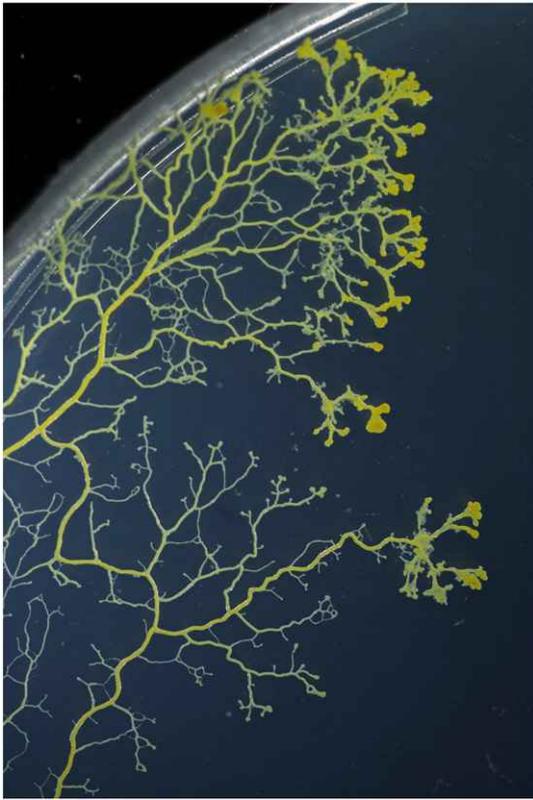


Fig. 1. Close-up of the network the slime mould produces when searching for food. The veins transport cytoplasm through the organism. Photo: Malcolm Ricketts.

fuse to yield diploid zygotes. These diploid zygotes differentiate into plasmodial cells. This differentiation process alters the pattern of mitosis; whilst the nuclei continue to replicate, the cell itself does not divide. The multinucleate zygote develops into a single syncytial plasmodial cell, thus completing the life cycle (Fig. 2).

P. polycephalum As Model Organism

P. polycephalum is easy to culture on moist filter paper or agar and rolled oats (Camp [4] as cited in Haas [5]). It is thus not surprising that the organism has been and still is widely used as model organism. A search on the Web of Science using “*Physarum polycephalum*” yields 2607 articles (as of February 25, 2015) on an eclectic range of topics, such as the effect of injecting snake venom [6] or radiation [7] on *P. polycephalum*, to the development of an algorithm to solve linear transportation problems based on the way it forms connections between food sources [8].

Our current understanding about the way the slime mould moves through its environment and connects food sources is due, in large part, to the pioneering work of Professor Noburo Kamiya and colleagues. Kamiya was the first to study the process of cytoplasmic streaming in detail [9]. He was particularly interested

in being able to measure the forces involved in shuttling cytoplasm back and forth through the organism [9]. We now know that when a vein contacts a food source, biochemical oscillators give rise to propagating waves resulting in increased cytoplasmic streaming through that vein [10]. The higher the rate of cytoplasmic streaming is, the thicker the vein becomes at the expense of veins that do not form a direct link between two parts of the organism. The combination of positive and negative feedbacks allows the organism to connect food sources via the shortest path.

That *P. polycephalum* is indeed able to find the shortest path to connect food sources has been nicely illustrated by Nakagaki *et al.* [11]. They filled a maze with the slime mould and offered the organism two food sources. After 4 h, most plasmodia had made a connection between the two food sources via the shortest path through the maze. Nakagaki and colleagues received the Ig Nobel Prize in cognitive science in 2008 for their work on maze solving slime moulds. The Ig Nobel Prize is awarded annually for “achievements that first make people laugh then make them think”. However, the implications of the slime mould’s ability to find the shortest path are certainly non-trivial. The exact way by which plasmodia form connections between food sources is influenced by a range of factors such as the characteristics of the substrate it moves through [12], the light regime it is subjected to [13] and the presence of physical barriers [11]. This makes *P. polycephalum* a

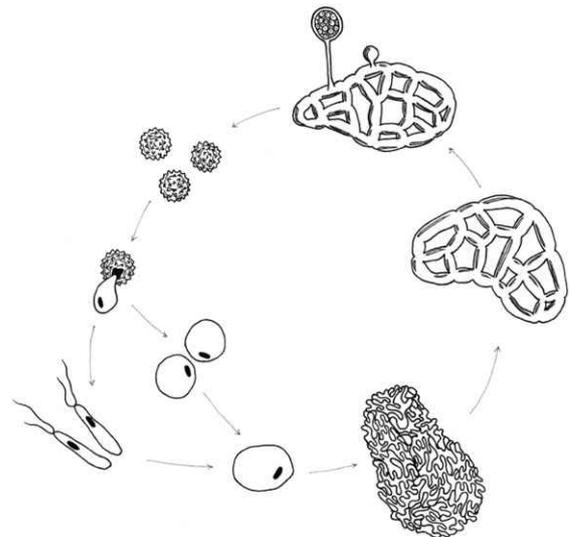


Fig. 2. General life cycle of acellular slime moulds. After a period of vegetative growth, the plasmodium (bottom right corner) converts all its energy into the formation of spores (top right corner). When the spores hatch, they give rise to myxamoebae or flagellated amoebae (middle left). When two that are of opposite mating types meet, they mate to form a zygote (bottom centre). The zygote then grows into a plasmodium. Drawing: Eliza Middleton.

convenient organism to experimentally study the rules underlying network formation in a biological system.

Biological Network Construction

Transport networks are ubiquitous in both social and biological systems. Network performance involves a trade-off amongst cost, transport efficiency and robustness. Biological networks have been fine-tuned by natural selection over millions of years and are likely to yield reasonable solutions to shortest path problems. Moreover, they are constructed without centralised control and may represent a readily scalable solution for growing networks in general.

P. polycephalum is a proven model organism for studying the evolution of an adaptive network in real time [14]. The resulting networks are both efficient and robust. Slime mould networks contain intermediate junctions (Steiner points) that reduce their overall length [15,16]. Tero *et al.* designed a biologically inspired mathematical model [14], the *Physarum* solver [17], which is able to discover the shortest path between many points (stations) in a real-world network system such as the Tokyo subway network. Incidentally, real slime moulds can do the same trick on a map of the system [14].

The *Physarum* solver is based on feedback loops between the thickness of each vein and the rate of internal cytoplasmic flow so that increased rates of cytoplasmic streaming lead to an increase in vein diameter, whereas veins contract when flow rates decline. The *Physarum* solver constructs networks by making some nodes in the network “sources” of flow and others “sinks” whilst keeping the total biomass constant. Increasing the flow rate promotes the construction of redundant connections that increase the robustness of the network. However, redundancy also increases the network’s total cost. How does one construct a network that is both robust enough and with minimal redundancy at a low cost? Many human constructed networks, be they transportation networks, supply chains or routing networks, are susceptible to the risk that the complete network breaks down after one component of the network fails. Biological systems are equally susceptible to failure but have had millions of years of evolution to fine-tune network construction. Researchers are therefore looking for biological systems that are amenable to experimental manipulation so that they can construct a general model of network development, applicable to both biological and artificial networks, based on actual empirical data. The slime mould provides such a biological system.

Network Construction in Dynamic Environments

Constructing a network in a static environment is quite an achievement, but what if the environmental

conditions change making a previously constructed network no longer the best solution? Reid and Beekman used a dynamic version of the well-known Towers of Hanoi problem to study if, and if so how, the slime mould adapts to disruptions in its network [18]. In the Towers of Hanoi problem, n discs of different diameters are stacked upon one of three pegs in order of decreasing diameter from the base. The problem is solved optimally when the stack of discs is transferred to one of the remaining two pegs using the smallest number of possible moves whilst obeying the following rules: only one disc can be moved at a time; only the top disc in a stack can be moved; and a disc can never be stacked upon another of smaller diameter. All possible moves to solve the problem can be mapped on a two-dimensional maze. By connecting this maze to its mirror image, Reid and Beekman formed a maze with a total of 32,678 unique paths between the opposing ends (see Fig. 3, adapted from Reid and Beekman [18]). Only two of these paths are the shortest.

As in the original maze solving study by Nakagaki *et al.* [11], Reid and Beekman first filled the complete Towers of Hanoi maze with slime mould before adding a food source at either end of the maze. As expected, the plasmodia then quickly connected the sources, however, not necessarily following one of the two possible shortest paths (Fig. 4, adapted from Reid and Beekman [18]). They then made the problem dynamic by blocking and opening paths forcing the slime mould to construct a new network. This time the slime mould was more likely to construct a network following the shortest path, probably because the experimental disruption forced the slime mould to build a new solution from scratch.

Slime Mould “Memory”

Why would the slime mould be better at finding the shortest path after its original solution had been destroyed? Most likely because it uses its external memory to avoid areas it has been before, similar to using one’s footprints to determine where one has been before. As it moves through its environment, *P. polycephalum* leaves behind a thick mat of non-living, translucent, extracellular slime (Fig. 5). When given a choice between an area that contains this extracellular slime and an area that does not, the slime mould prefers to move into the area devoid of extracellular slime [19]. After the slime mould’s initial solution was disrupted, it would construct a new connection between the two food sources, avoiding routes constructed in the first phase of the experiment. Because it most often did not utilise the shortest path in the first stage of the experiment, the slime mould was more likely to construct a new network using the shortest path after the experimental disruption.

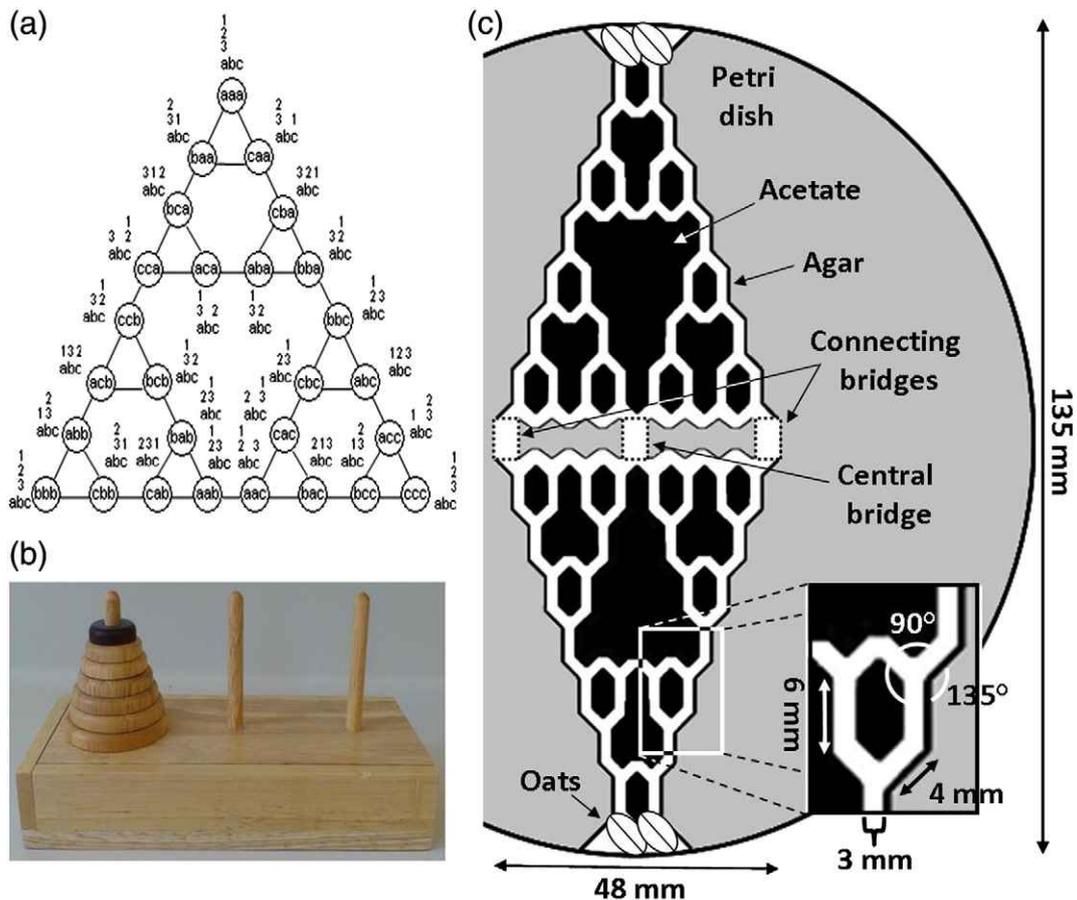


Fig. 3. (a) Graph of the three-disc version of the Towers of Hanoi puzzle (b) (note that the figure shows the puzzle with seven discs). “1”, “2” and “3” represent discs of increasing size and their positions on the rods “a”, “b” and “c”. The graph’s nodes signify the distributions of the discs whereas the branches represent the moves of the discs. (c) Illustrates the experimental setup. Two Towers of Hanoi graphs were joined end to end to form a maze. This maze was then filled with the slime mould. Once the maze was filled such that the slime mould had spread throughout the maze, food was offered at both ends of the maze. The slime mould then constructed a network of veins to connect the two food sources. The maze could be modified by removing or adding connecting bridges. Reproduced with permission from Ref. [18].

By using the presence of extracellular slime to avoid areas previously explored, the slime mould is capable of solving the U-shaped trap problem [20], a classic test of autonomous navigational ability commonly used in robotics [21,22]. The robot needs to navigate around a U-shaped obstacle that it can only achieve by using an external spatial memory. When the slime mould is able to use the presence of extracellular slime to avoid areas it has been before, it avoids getting stuck in the U-shaped trap. If, on the other hand, it cannot utilise its external spatial memory, it is unable to avoid the obstacle [20]. The avoidance of extracellular slime is not absolute; plasmodia will readily crawl across extracellular slime if they detect the presence of food. The slime mould thus uses a hierarchy of rules: avoid extracellular slime unless food can be detected. Slime moulds can also distinguish between extracellular slime deposited by members of their own species and members of other slime mould species [19].

It is easy to see how even a brainless organism can make use of cues left behind in the environment, but what about an intracellular memory that allows the organism to anticipate periodic events? Saigusa *et al.* placed a small plasmodium of *P. polycephalum* in a narrow lane and let it move through the lane under optimal culture conditions (warm and humid) [23]. After the plasmodium had moved through the lane for a few hours, the experimenters changed the ambient conditions to cool and dry, conditions unfavourable to slime moulds. These unfavourable conditions were maintained for 10 min after which conditions became favourable again. Each plasmodium was subjected to unfavourable conditions three times at various intervals (ranging from 30 to 90 min). After exposure to unfavourable conditions, the slime mould reduced their locomotive speed at the time when the next unfavourable episode would have occurred. Thus, the plasmodium “remembered” when the next bout of cold and dryness was about to take

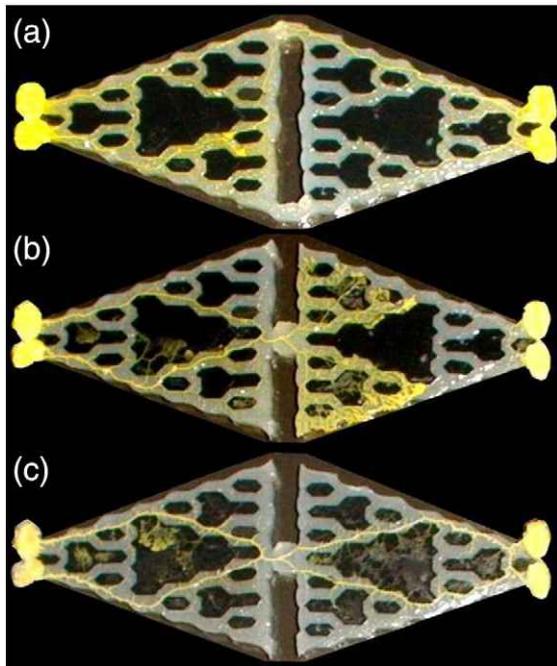


Fig. 4. Example of a solution to the Towers of Hanoi problem outlined in Fig. 3. (a) The solution the slime mould had found to connect two food sources. (b) Now the two outermost connecting bridges have been removed and a new, central, connecting bridge is added. The slime mould needs to construct a new solution. (c) The slime mould's new solution. Reproduced with permission from Ref. [18].

place. The authors and others [24,25] argue that the slime mould's ability to anticipate periodic events hints at the cellular origins of primitive intelligence.

What could the possible mechanism be? Pershin *et al.* suggest the following [24]: the interior of the slime mould contains a gel–sol solution. The gel is present in the ectoplasm and is more gelatinous than the less viscous sol in the endoplasm. As a result, the sol flows through the gel in a way similar to water moving through a sponge. The viscosity of the



Fig. 5. Extracellular slime left behind by the slime mould. Photo: Malcolm Ricketts.

gel–sol solution changes as the pressure changes. As the plasmodium moves, the actin–myosin fibres in the ectoplasm contract both radially and longitudinally and this creates a pressure gradient pushing the endoplasm in the direction of movement. When the pressure gradient increases beyond a certain point, the gel can break down into sol, resulting in new low-viscosity channels. If the external temperature and humidity change, the flow of the sol changes in a non-linear fashion. Returning to the initial conditions after a change induced by environmental conditions takes time and depends on the number and shape of the newly formed, low-viscosity channels. Such mechanism is similar to that underlying the function of memory-resistance behaviour of certain electronic devices. Using a mathematical model, Pershin *et al.* showed that, if the flow of sol indeed depends on the history and state of the system, memory-resistance behaviour, or memristor, can indeed explain the slime mould's behaviour under Saigusa *et al.*'s [23] experimental conditions [24].

***P. polycephalum* As Intelligent Decision Maker**

All organisms need to make decisions about where to forage, what to forage for, how long to exploit existing patches and when it is time to move on again. How individuals make foraging decision based on the costs and benefits associated with foraging became known as optimal foraging theory [26]. One of the best-known experimental studies on optimal foraging is probably Kacelnik's study on load carrying in starlings [27]. By applying the marginal value theorem [28], Kacelnik determined the costs and benefits of carrying an extra prey item (in the form of leatherjackets) back to the nest and the time necessary to travel to the nest. With each extra prey item to carry, the starling's efficiency at collecting further prey items diminishes until a point is reached at which it is more efficient to return to the nest and offload. Similar approaches have been successfully used to predict an individual's behaviour depending on risks associated with foraging [29], how to choose between preys that differ in handling time and energy yield [30] and when to leave a patch [31], to name but a few examples.

In recent years, studies have shown that the slime mould too is capable of making foraging decisions based on optimality theory. When given a choice between food sources that differ in quality (concentration of oatmeal), *P. polycephalum* is capable of choosing the source highest in concentration [32]. When one food source is placed in an environment that is dangerous to the slime mould (in this case, in the light, which is damaging to the cell), plasmodia trade off risk against food quality such that the food needs to be 5 times higher in

concentration before the slime mould will forage in the light [32].

The slime mould's aversion to light can also be exploited to investigate if the organism trades off risk against speed when making foraging decisions. Give the slime mould the following simple task: select the highest-quality food source out of three options. With the variation of the relative difference in food quality, the discrimination task can be made more or less difficult. When the experimental setup is placed in the dark, the organism does not need to make a decision quickly. If, however, the slime mould is exposed to light whilst making a choice, it should make a faster decision to avoid light damage. The effect of light did not affect the slime mould's ability to select the best food source compared with slime moulds that made decisions in the dark. However, the experiments did show that the faster the decision is, the less likely the plasmodium was to select the best food source. Slime moulds clearly trade off speed against accuracy when deciding which food source to select [33]. Moreover, as in all other organisms in which speed–accuracy trade-offs have been studied, the more difficult the discrimination task is, the more likely the speed of decision making compromises the accuracy of the decision [33–36].

Slime moulds also adjust their search pattern depending on the quality of the food source they are exploiting. When the food source is of high quality, *P. polycephalum* will perform an area-restricted search [37,38], thus focusing their search effort within the vicinity of the source it has found before. If the source found initially is of low quality, the slime mould will move away from the source before exploring the area for alternative food sources [39]. Such flexible search strategy is adaptive when food is patchily distributed and varies in quality within a patch [39].

A final decision a slime mould plasmodium has to make whilst foraging is when to leave a patch and move to the next one. In the absence of complete information, the best an organism can do to decide when to leave a patch is to use heuristics, or “rules of thumb”, based on the limited information it does have available. *P. polycephalum* uses the number of food items it has engulfed as a rule of thumb such that each encounter with a high-quality food item (the effect is less strong when food items are of lesser quality) decreases the likelihood that the plasmodium leaves the patch [40]. Such incremental departure rules had previously been found in parasitoid wasps [41], bumblebees [42,43] and even humans [44–46].

The Irrational Slime Mould

We humans like to think that we make choices in an economically rational fashion. When deciding which item to purchase, we compare the absolute

values of the items on offer and base our decision on those values. Similarly, we assume that animals use comparable considerations when making foraging decisions. We are all rational beings. Or are we? When choosing between two items based on their absolute value, the addition of a third item that is of lower quality than the two items already present should not make any difference to the original preference. However, humans [47], bees [48,49], birds [49–51] and individual ants [52] all change their preference in the presence of a decoy. The individuals no longer base their choice on the absolute values of the items present. In other words, they behave irrationally in an economical sense.

We used the slime mould to investigate whether the observed violations of rationality indicate that comparative valuation rules are the norm for biological decision makers or if they occur as a consequence of neuron-based decision-making systems [53]. If comparative valuation rules are a consequence of neuron-based decision making, we would not expect the slime mould to behave irrationally. However, we found that the slime mould behaves irrationally when presented with a decoy, just like humans, bees, birds and individual ants [53]. It thus seems that organisms do not use the absolute value of the items to choose from but instead use a comparative valuation process.

Absolute valuation processes require more or less complete information about the organism's environment. In most, if not all, instances, having access to global information is not possible. Even if global information is available, the cognitive load required to process this information is beyond the capacity of most organisms. Therefore, as discussed earlier, organisms use simple behavioural rules, or rules of thumb, to use selected information from the environment to make decisions that are often “good enough” [54].

Nicolis *et al.* argue that the slime mould's irrational behaviour is a side effect of the way by which positive feedback allows the organism to form veins to profitable food sources [55]. Once positive feedback is well under way to one of the food sources, a vein to a food source of higher quality is unlikely to become established. Such effect of initial conditions on the final choice will become stronger as the number of items increases. Therefore, the slime mould makes choices that seem irrational when offered three food items, whereas it is able to select the best food source when only two items are presented.

Kacelnik *et al.* referred to comparative valuation processes as Darwin's “tug of war” [56]. Darwin famously composed a list of reasons in favour and against marrying. Only because the list of items under “Marry” was longer than the number of items

under “Not Marry” did he decide to get married. An alternative way by which one can make decisions is to choose the first item that passes a threshold; decision making now becomes a “horse race” [56]. The positive feedback mechanism governing the slime mould's decision-making process seems to favour a “horse race” scenario. Foraging opportunities for most organisms are likely to occur sequentially instead of simultaneously. Hence, a decision-making process based on a “horse race” heuristic is probably good enough under most natural foraging conditions. The slime mould is no exception. In fact, due to its peculiar biology, a slime mould can exploit multiple food sources simultaneously. Hence, even if it encounters a better option whilst it is already exploiting a food source, it can still divert part of its biomass to exploit both at the same time.

Solving Nutritional Challenges

All organisms need to balance their intake of essential nutrients. Of particular importance to many organisms is the relative intake of protein and carbohydrates. The exact requirements, often measured as the ratio of protein to carbohydrates, depend on the specific organism, but so far, all organisms studied to date have a protein-to-carbohydrate ratio that is optimal for growth and development [57]. Most foods contain a mixture of protein and carbohydrates, making balancing the relative intake of the two a non-trivial task. In fact, some researchers argue that it is our inability to correctly balance the intake of carbohydrates and protein that has led to the current obesity crisis [58].

Simpson and Raubenheimer designed an experimental framework that allows one to determine the target intake of an organism: the protein-to-carbohydrate ratio that optimises growth and reproduction [59]. This “geometrical framework” has shown how well organisms can regulate their intake, provided that both nutrients are present at adequate levels in the environment. It is not difficult to envision how animals regulate their nutrient intake. The brain regulates the organism's nutritional requirements at the cellular level via inputs from sensory systems and peripheral organs. Colonies of ants too are capable of regulating their intake of protein and carbohydrates, provided that brood is present in the colony. Adult ants cannot properly digest protein; thus, in the absence of developing brood, colonies accumulate too much protein and die [60]. When brood are present, their requirement for protein regulates the amount of protein and carbohydrates the foraging workers bring back to the colony [60]. In both instances, animals and insect colonies, specialised components regulate the intake of nutrients (brain and peripheral organs in animals, foraging workers and brood in ants). Can a single-celled, brainless organism too regulate its nutritional intake?

The short answer is: yes, it can. Dussutour *et al.* first determined what protein-to-carbohydrate ratio the slime mould performs best on by offering plasmodia 35 different diets [61]. In addition to changing the ratio of nutrients, they also looked at the effect of nutrient concentration. Plasmodia grew most densely when the diet contained twice the concentration of protein relative to carbohydrates. When the concentration of carbohydrates was too high, the slime mould died. When the total concentration of nutrients was low, the slime mould expanded its mass so that it covered more of the diet, thus increasing intake. Dussutour *et al.* then set out to test if the slime mould could regulate its intake of carbohydrates and protein such that it reaches its intake target when offered 11 different diets simultaneously none of which alone would be sufficient [61]. They then estimated nutrient intake by assuming that the amount of mass covering a particular diet is proportional to the amount of nutrients extracted from that diet. The results showed that an individual slime mould contacts patches of different nutrient quality in the precise proportions necessary to compose an optimal diet. Because of its peculiar biology, the slime mould can cover more than one diet, thus regulating intake of carbohydrates and protein to reach its target.

The Slime Mould As Model Decision Maker?

The ability of the slime mould to utilise several food sources simultaneously allows it to precisely regulate its nutrient intake by allocating appropriate amounts of biomass to the different diets. In effect, the individual slime mould acts as a brain, using the information obtained from the parts of its body extracting nutrients from different diets to allocate biomass across the diets on offer. Would it therefore be possible to use the slime mould as a model for biological decision making? The beauty of the organism is that it is macroscopic and we can observe its decision-making process by studying the way it constructs connections between food items via veins.

Marshall *et al.* use the following, rather straightforward, definition of decision making [62]: “Decision making is a process in which uncertain information must be processed in order to make a choice between two or more alternatives”. They further assume that a decision is made once one of the options has gathered sufficient evidence, analogous to the horse race scenario of Kacelnik *et al.* [56]. As we have described above, the slime mould certainly meets the criteria of a decision maker. In fact, the slime mould would be an ideal model decision-making system as we know the feedback mechanisms that underlie the formation and disappearance of the veins. Moreover, these processes are readily observable. Previously, colonies of insects, in particular, the honeybee *Apis*

mellifera and the ant *Temnothorax sp.*, have been developed as model systems to study decision making in collective systems [52,63–65]. More so, indeed, these colonies provide a nice analogy to the vertebrate brain (individual insects being equivalent to neurons, their colonies are the complete brain) but we are still using individuals that are rather sophisticated neurologically and which share the same cognitive architecture—brains and neurons—as human and other animals. Slime moulds have a radically different mechanism by which information is processed and might therefore provide insight into how non-neuronal organisms process information.

The rather surprising finding that the slime mould behaves in an economically irrational way, similar to organisms that have a brain, suggests that very different biological systems use the same underlying decision-making processes, irrespective of the actual decision-making apparatus, be they neurons in a brain or oscillators in a slime mould. Decision making in higher organisms such as primates is often studied using the “moving dots experiment”: a subject is shown a screen with dots moving to the left and the right and a decision needs to be made regarding the direction in which the majority of the dots move (described in Marshall *et al.* [62]). Such experiments indeed suggest that decision making is based on thresholds; the same mechanism Nicolis *et al.* [55] argue underlies the slime mould's irrational behaviour. Based on the moving dots experiment and others similar to it, several models describe how the brain makes decisions based on neuronal input. However, observing the firing patterns of live neurons in real time is technically difficult. An organism similar to the slime mould, whose decision-making strategy can be observed in real time, may be the perfect experimental system to look at the mechanisms that underlie decision making at the organismal level. They are a fascinating example of an alternative path to complex decision making that does not rely on neuronal information processing. As such, we suggest that slime moulds be adopted as a model system for the study of biological decision making.

The slime mould's relatively homogenous organisation and macroscopic size means that it will be possible to dissect all levels of its decision-making process, from molecular mechanisms to behavioural programmes. At present, we have an increasingly good understanding of *what* kinds of information processing slime moulds are capable of; what is lacking is a clear understanding of *how* slime moulds accomplish these feats. Understanding slime mould decision making will require input from a range of disciplines including molecular biology, cell biology, mathematics and physics. For example, we suspect that behaviour in slime moulds is driven largely by biochemical oscillators that collectively control the flow of biomass to different regions of the cell. Local oscillation rates increase when the plasmodium

comes into contact with attractive substances and decrease in response to repellent substances [13,66,67]. Each oscillating region can also entrain neighbouring oscillating regions. Our understanding of how biochemical oscillators translate to cellular movement has been greatly enhanced through the contributions of mathematicians and physicists, but more work remains to be performed to understand how oscillations ultimately result in information processing. In contrast to the well-studied cellular signalling pathways of the cellular slime moulds, we know comparatively little about cellular signalling in *P. polycephalum*. For example, how is information propagated within the cell? How are activities coordinated within the cell? Slime moulds have the potential to be one of the first fully characterised biological information processing systems; achieving this aim will require extensive collaboration between many disciplines.

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References

- [1] F.L. Howard, The life history of *Physarum polycephalum*, *Am. J. Bot.* 18 (1931) 116–133.
- [2] A.M. Fiore-Donno, S.I. Nikolaev, M. Nelson, J. Pawlowski, T. Cavalier-Smith, S.F. Baldauf, Deep phylogeny and evolution of slime moulds (Mycetozoa), *Protist* 161 (2010) 55–70.
- [3] D. Kessler, Plasmodial structure and motility, in: H.C. Aldrich, J.W. Daniel (Eds.), *Cell biology of Physarum and Didymium*, Academic Press, Sydney, Australia 1982, pp. 145–196.
- [4] W.G. Camp, A method of cultivating myxomycete plasmodia, *Bull. Torrey Bot. Club* 63 (1936) 205–210.

- [5] J.N. Haas, Effects of some enzymes injected into the slime mold *Physarum polycephalum*, *J. Cell. Comp. Physiol.* 41 (1953) 171–200.
- [6] H.R. Engel, Effects of the injection of snake venom containing lecithinase A into *Physarum polycephalum*, *J. Cell. Comp. Physiol.* 44 (1954) 203–210.
- [7] S. Warren, O.K. Scott, *Physarum* as a radiation test object, *Proc. Soc. Exp. Biol. Med.* 52 (1943) 149–151.
- [8] C. Gao, C. Yan, Z. Zhang, Y. Hu, S. Mahadevan, Y. Deng, An amoeboid algorithm for solving linear transportation problem, *Phys. A* 398 (2014) 179–186.
- [9] N. Kamiya, The control of protoplasmic streaming, *Science* 92 (1940) 462–463.
- [10] T. Nakagaki, H. Yamada, T. Ueda, Interaction between cell shape and contraction pattern in the *Physarum* plasmodium, *Biophys. Chem.* 84 (2000) 195–204.
- [11] T. Nakagaki, H. Yamada, Á. Tóth, Maze-solving by an amoeboid organism, *Nature* 407 (2000) 470.
- [12] A. Takamatsu, E. Takaba, G. Takizawa, Environment-dependent morphology in plasmodium of true slime mold *Physarum polycephalum* and a network growth model, *J. Theor. Biol.* 256 (2009) 29–44.
- [13] T. Nakagaki, M. Ima, T. Ueda, Y. Nishiura, T. Saigusa, A. Tero, et al., Minimum-risk path finding by an adaptive amoebal network, *Phys. Rev. Lett.* 99 (2007) 068104.
- [14] A. Tero, S. Takagi, T. Saigusa, K. Ito, D.P. Bepper, M.D. Fricker, et al., Rules for biologically inspired adaptive network design, *Science* 327 (2010) 439–442.
- [15] T. Nakagaki, R. Kobayashi, Y. Nishiura, T. Ueda, Obtaining multiple separate food sources: Behavioural intelligence in the *Physarum* plasmodium, *Proc. R. Soc. Lond. B* 271 (2004) 2305–2310.
- [16] T. Nakagaki, H. Yamada, M. Hara, Smart network solutions in an amoeboid organism, *Biophys. Chem.* 107 (2004) 1–5.
- [17] A. Tero, R. Kobayashi, T. Nakagaki, *Physarum* solver: A biological inspired method of road-network navigation, *Phys. A* 363 (2006) 115–119.
- [18] C.R. Reid, M. Beekman, Solving the Towers of Hanoi—How an amoeboid organism efficiently constructs transport networks, *J. Exp. Biol.* 216 (2013) 1546–1551.
- [19] C.R. Reid, M. Beekman, T. Latty, A. Dussutour, Amoeboid organism uses extracellular secretions to make smart foraging decisions, *Behav. Ecol.* 24 (2013) 812–818.
- [20] C.R. Reid, T. Latty, A. Dussutour, M. Beekman, Slime mould uses an external spatial “memory” to navigate in complex environments, *Proc. Natl. Acad. Sci.* 109 (2012) 17490–17494.
- [21] T. Balch, R. Arkin, Avoiding the past: A simple but effective strategy for reactive navigation, *Proc. IEEE Int. Conf. Robotics Aut.* 1–3 (1993) 678–685.
- [22] G.-C. Luh, W.-W. Liu, An immunological approach to mobile robot reactive navigation, *Appl. Soft Comput.* 8 (2008) 30–45.
- [23] T. Saigusa, A. Tero, T. Nakagaki, Y. Kuramoto, Amoebae anticipate periodic events, *Phys. Rev. Lett.* 100 (2008) 018101.
- [24] Y. Pershin, S. La Fontaine, M. Di Ventra, Memristive model of amoeba learning, *Phys. Rev. E* 80 (2009) 021926.
- [25] P. Ball, Cellular memory hints at the origins of intelligence, *Nature* 451 (2008) 385.
- [26] G.H. Pyke, H.R. Pulliam, E.L. Charnov, Optimal foraging: A selective review of theory and tests, *Q. Rev. Biol.* 52 (1977) 137–154.
- [27] A. Kacelnik, Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time, *J. Anim. Ecol.* 53 (1984) 283–299.
- [28] E.L. Charnov, Optimal foraging, the marginal value theorem, *Theor. Popul. Biol.* 9 (1976) 129–136.
- [29] T. Caraco, W.U. Blanckenhorn, G.M. Gregory, J.A. Newman, G.M. Recer, S.M. Zwicker, Risk-sensitivity: Ambient temperature affects foraging choice, *Anim. Behav.* 39 (1990) 338–345.
- [30] R.W. Elner, R.N. Hughes, Energy maximization in the diet of the shore crab, *Carcinus maenas*, *J. Anim. Ecol.* 47 (1978) 103–116.
- [31] S.L. Lima, Downy woodpecker foraging behavior: Efficient sampling in simple stochastic environments, *Ecology* 65 (1984) 166–174.
- [32] T. Latty, M. Beekman, Food quality and the risk of light exposure affect patch-choice decisions in the slime mold *Physarum polycephalum*, *Ecology* 91 (2010) 22–27.
- [33] T. Latty, M. Beekman, Speed-accuracy trade-offs during foraging decisions in the acellular slime mould *Physarum polycephalum*, *Proc. R. Soc. Lond. B* 278 (2011) 539–545.
- [34] R. Bogacz, E.-J. Wagenmakers, B.U. Forstmann, S. Nieuwenhuis, The neural basis of the speed-accuracy tradeoff, *Trends Neurosci.* 33 (2009) 10–16.
- [35] L. Chittka, P. Skorupski, N.E. Raine, Speed-accuracy trade-offs in animal decision making, *Trends Ecol. Evol.* 24 (2009) 400–407.
- [36] J. Palmer, A.C. Huk, M.N. Shadlen, The effect of stimulus strength on the speed and accuracy of a perceptual decision, *J. Vis.* 5 (2005) 376–404.
- [37] P. Kareiva, G. Odell, Swarms of predators exhibit “prey-taxis” if individual predators use area-restricted search, *Am. Nat.* 130 (1987) 233–270.
- [38] S. Benhamou, Efficiency of area-concentrated searching behaviour in a continuous patchy environment, *J. Theor. Biol.* 159 (1992) 67–81.
- [39] T. Latty, M. Beekman, Food quality affects search strategy in the acellular slime mould, *Physarum polycephalum*, *Behav. Ecol.* 20 (2009) 1160–1167.
- [40] T. Latty, M. Beekman, Slime moulds use heuristics based on within-patch experience to decide when to leave, *J. Exp. Biol.* 218 (2015) 1175–1179.
- [41] G. Driessen, C. Bernstein, Patch departure mechanisms and optimal host exploitation in an insect parasitoid, *J. Anim. Ecol.* 68 (1999) 445–459.
- [42] D. Lefebvre, J. Pierre, Y. Outreman, J.-S. Pierre, Patch departure rules in bumblebees: Evidence of a decremental motivational mechanism, *Behav. Ecol. Sociobiol.* 61 (2007) 1707–1715.
- [43] J. Biernaskie, S. Walker, R. Gegear, Bumblebees learn to forage like Bayesians, *Am. Nat.* 174 (2009) 413–423.
- [44] J. Hutchinson, A. Wilke, P.M. Todd, Patch leaving in humans: Can a generalist adapt its rules to dispersal of items across patches? *Anim. Behav.* 75 (2008) 1331–1349.
- [45] A. Wilke, J.M.C. Hutchinson, P.M. Todd, U. Czienskowski, Fishing for the right words: Decision rules for human foraging behaviour in internal search tasks, *Cogn. Sci.* 33 (2009) 497–529.
- [46] P. Louâpre, J.J.M. Alphen van, J.S. Pierre, Humans and insects decide in similar ways, *PLoS One* 5 (2010) e14251.
- [47] A. Tversky, Intransitivity of preferences, *Psychol. Rev.* 76 (1969) 31–48.
- [48] S. Shafir, Intransitivity of preferences in honey bees: Support for “comparative” evaluation of foraging options, *Anim. Behav.* 48 (1994) 55–67.
- [49] S. Shafir, T.A. Waite, B.H. Smith, Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*), *Behav. Ecol. Sociobiol.* 51 (2002) 180–187.

- [50] M. Bateson, Context-dependent foraging choices in risk-sensitive starlings, *Anim. Behav.* 64 (2002) 251–260.
- [51] M. Bateson, S.D. Healy, T.A. Hurly, Irrational choices in hummingbird foraging behaviour, *Anim. Behav.* 63 (2002) 587–596.
- [52] T. Sasaki, S.C. Pratt, Emergence of group rationality from irrational individuals, *Behav. Ecol.* 22 (2011) 276–281.
- [53] T. Latty, M. Beekman, Irrational decision-making in an amoeboid organism: Transitivity and context-dependent preferences, *Proc. R. Soc. Lond. B* 278 (2011) 307–312.
- [54] J.M.C. Hutchinson, G. Gigerenzer, Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet, *Behav. Process.* 69 (2005) 97–124.
- [55] S.C. Nicolis, N. Zabzina, T. Latty, D.J.T. Sumpter, Collective irrationality and positive feedback, *PLoS One* 6 (2011) e18901.
- [56] A. Kacelnik, M. Vasconcelos, T. Monteiro, J. Aw, Darwin's "tug-of-war" vs. starlings' "horse-racing": How adaptations for sequential encounters drive simultaneous choice, *Behav. Ecol. Sociobiol.* 65 (2011) 547–558.
- [57] D. Raubenheimer, S.J. Simpson, Integrative models of nutrient balancing: Application to insects and vertebrates, *Nutr. Res. Rev.* 10 (1997) 151–179.
- [58] S.J. Simpson, D. Raubenheimer, *The nature of nutrition: A unifying framework from animal adaptation to human obesity*, Princeton University Press, 2012.
- [59] S.J. Simpson, D. Raubenheimer, A multi-level analysis of feeding behaviour: The geometry of nutritional decisions, *Philos. Trans. R. Soc. Lond.* 342 (1993) 381–402.
- [60] A. Dussutour, S.J. Simpson, Communal nutrition in ants, *Curr. Biol.* 19 (2009) 740–744.
- [61] A. Dussutour, T. Latty, M. Beekman, S.J. Simpson, Amoeboid organism solves complex nutritional challenges, *Proc. Natl. Acad. Sci.* 107 (2010) 4607–4611.
- [62] J.A.R. Marshall, R. Bogacz, A. Dornhaus, R. Planqué, T. Kovacs, N.R. Franks, On optimal decision-making in brains and social insect colonies, *J. R. Soc. Interface* 6 (2009) 1065–1074.
- [63] P.K. Visscher, Group decision making in nest-site selection among social insects, *Annu. Rev. Entomol.* 52 (2007) 255–275.
- [64] T.D. Seeley, *Honeybee Democracy*, Princeton University Press, Princeton, 2010.
- [65] T. Sasaki, B. Granovskiy, R.P. Mann, D.J.T. Sumpter, S.C. Pratt, Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy, *Proc. Natl. Acad. Sci.* 110 (2013) 13769–13773.
- [66] A.C. Durham, E.B. Ridgway, Control of chemotaxis in *Physarum polycephalum*, *J. Cell Biol.* 69 (1976) 218–223.
- [67] R. Kobayashi, A. Tero, T. Nakagaki, Mathematical model for rhythmic protoplasmic movement in the true slime mold, *J. Math. Biol.* 53 (2006) 273–286.