

Research



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Phenotypic variability predicts decision accuracy in unicellular organisms

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When deciding between different options, animals including humans face the dilemma that fast decisions tend to be erroneous, whereas accurate decisions tend to be relatively slow. Recently, it has been suggested that differences in the efficacy with which animals make a decision relate closely to individual behavioural differences. In this paper, we tested this hypothesis in a unique unicellular organism, the slime mould *Physarum polycephalum*. We first confirmed that slime moulds differed consistently in their exploratory behaviour from ‘fast’ to ‘slow’ explorers. Second, we showed that slow explorers made more accurate decisions than fast explorers. Third, we demonstrated that slime moulds integrated food cues in time and achieved higher accuracy when sampling time was longer. Lastly, we showed that in a competition context, fast explorers excelled when a single food source was offered, while slow explorers excelled when two food sources varying in quality were offered. Our results revealed that individual differences in accuracy were partly driven by differences in exploratory behaviour. These findings support the hypothesis that decision-making abilities are associated with behavioural types, even in unicellular organisms.

1. Introduction

Individual differences within a species have been reported in a wide range of organisms, including slime moulds, insects, reptiles, birds, fish and mammals (e.g. [1–4]). Most studies of individual differences have focused on boldness, aggressiveness, exploration, sociability and activity. Individual differences in these behaviours have been referred to as variation in ‘fast–slow’ behavioural types (BTs) [5]. Recently, numerous researchers have raised the possibility that organisms might also differ in the way they perceive and process information when making a decision [6,7], and it has been suggested that variation in decision-making ability could be correlated with variation in BTs [5–8]. For instance, slow individuals might be more thorough in how they collect and assess information than fast individuals, who might explore more quickly but less carefully. The idea thus arose that speed–accuracy trade-offs (SATO) in decision-making ability might align with fast–slow BTs [5]. In this paper, we used slime moulds to test this hypothesis.

The ‘true’ slime mould *Physarum polycephalum* is a giant multinucleated unicellular organism that can cover hundreds of square centimetres. As it explores its environment, it constructs a network of intersecting veins in which oscillatory flows of the protoplasm, also called ‘shuttle streaming’, take place [9]. This transport network allows (i) an efficient distribution of chemical signals, oxygen and nutrients, and (ii) cell movement at a speed of a few millimetres per hour [9]. Although slime moulds lack the complex hardware of animals with brains, they live in environments that are no less complex and face the same decision-making challenges: they must search for food, adapt to changing conditions and choose suitable microclimates to grow. *Physarum polycephalum* succeeds in solving these challenges. For instance, it can find the shortest

path through a maze [10], construct efficient transport networks [11], interact with conspecifics [1,12], anticipate periodic events [13], avoid traps [14] and learn to ignore repulsive substances [15,16]. In the context of foraging, slime moulds have been shown to succeed in selecting the best option when offered multiple alternatives [17–19]. For instance, when presented with two environments offering unequal amounts of food items distributed randomly, slime moulds are able to integrate and combine information to focus their foraging activity on the most rewarding environment [19].

In a previous study [1], we investigated behavioural variability in *P. polycephalum* and we identified distinct BTs: ‘slow–regular–social’, ‘fast–regular–social’ and ‘fast–irregular–social’, corresponding to three different strains (JPN, AUS and USA). We showed that the existence of these BTs relies in part on calcium signalling. While feeding, slime moulds extrude calcium in the environment. As calcium is an attractant, its excretion plays a retention role and slows down exploration rate [1]. When comparing the three strains, we demonstrated that AUS slime moulds excreted the highest quantities of calcium and were the most responsive to calcium [1]. These differences in signalling and behaviour yielded to robust differences in speed among strains. These results offer a unique opportunity to test the hypothesis that decision-making abilities in slime moulds align with fast–slow BT.

Decisions often need to be made based on noisy and partial evidence. The most widely used model to describe decision processes in taxa ranging from insects to humans is the drift-diffusion model [20,21]. This model assumes that organisms make decisions by gradually accumulating noisy evidence about each option until reaching one of two decision boundaries (i.e. decision thresholds). The average rate at which evidence accumulates, known as drift rate, strongly depends on the discriminability of the options. Large differences between the options lead to large drift rates, which in turn lead to more rapid evidence accumulation. Accordingly, responses in an easy task are predicted to be both faster and more accurate than responses to a difficult task, and decisions between similar options should take the longest time [20,21]. Drift-diffusion models have been successful in accounting for the SATO observed under a wide variety of circumstances but mostly when a single alternative was rewarded [20,21].

When studying decision abilities in a foraging context, organisms are often presented with various food sources and feed on the one that they choose. In situations where food options are hard to distinguish or similar, a correct choice would yield only a minor or no increase in reward over the incorrect choice. In other words, the benefit of spending time to make the correct decision decreases, as the food sources get closer together in value. However, drift-diffusion models, being driven only by the difference in food value, predict the decision to be unaffected by the absolute value of the food sources offered. Hence, Pirrone *et al.* [22–24] argued that rather than seeking to maximize accuracy and being trapped in deadlocks over difficult decisions, organisms should maximize the relative benefits from their decisions and optimize value instead of accuracy. Following this rationale, when presented with two equal food sources, as the quality of these food sources increases, decision time should decrease.

In this paper, using a battery of experimental tests, we describe the relationship between BT (slow versus fast) and decision-making abilities in slime moulds. In the first experiment, slime moulds were required to explore a homogeneous environment and we verified that there are inherent differences in speed between strains. In the second experiment, slime moulds were offered a single food source. In this situation, as individuals were rewarded only on making a correct choice, the assumption was that they should optimize their accuracy. In the third experiment, slime moulds faced a choice between two equal food sources. Since making either decision was correct, individuals were expected to optimize value. In the fourth experiment, slime moulds were presented with food sources varying in quality. As individuals were rewarded by the quality of the food source they selected, they could either optimize accuracy or value depending on the reward offered for an incorrect choice. In the fifth and sixth experiment, slime moulds were offered a food source placed closer or beforehand to render the information relative to the food source within easy reach. Here, individuals were expected to make both fast and accurate decisions. In the last experiment, slime moulds were placed in a competitive environment and we tested which decision-making strategies (slow/accurate or fast/inaccurate) were most successful.

2. Methods

(a) Species and rearing conditions

Physarum polycephalum is an acellular slime mould that inhabits shady, cool and humid organic substrates. In the presence of chemical stimuli in the environment, *P. polycephalum* shows directional movements (i.e. chemotaxis) [9]. We used three different strains of *P. polycephalum*: AUS (Southern Biological, Victoria, Australia), JPN (Hakodate University, Japan) and USA (Carolina Biological, South Carolina, USA). Experiments were initiated with a total of 10 sclerotia per strain, which are encysted resting stages. We cultivated the slime moulds on a 10% oat medium (powdered oat in a 1% agar solution) in Petri dishes (diameter 140 mm). All the experiments were conducted in the dark at 25°C temperature and 70% humidity. Pictures were taken every 5 min for 24 h with a digital Canon 60D camera.

(b) Experiments

(i) Experiment 1: homogeneous environment

We began by monitoring the exploration movement evoked in slime moulds in the absence of food in the environment to confirm the existence of slow and fast BTs [1]. We placed one slime mould in a circular arena (figure 1). The arena consisted of 90 mm diameter Petri dish filled with plain 1% agar. Once the agar had set, we punched one hole (diameter 1.3 cm) in the centre of the arena (figure 1*a*). The hole was filled with a circular slime mould (diameter 1.3 cm). We recorded the time taken by the slime mould to extend a first pseudopod in the arena. We also measured the latency to reach a maximum distance from the centre of 3 cm and the surface of the slime mould. The mean expansion rate was computed as the surface divided by the latency to reach a maximum distance of 3 cm. We replicated each experiment 40 times with each strain.

(ii) Experiment 2: one food source

We presented the slime moulds with a choice between a rewarded and an unrewarded option to investigate if BTs observed in the first experiment align with SATO. The arena

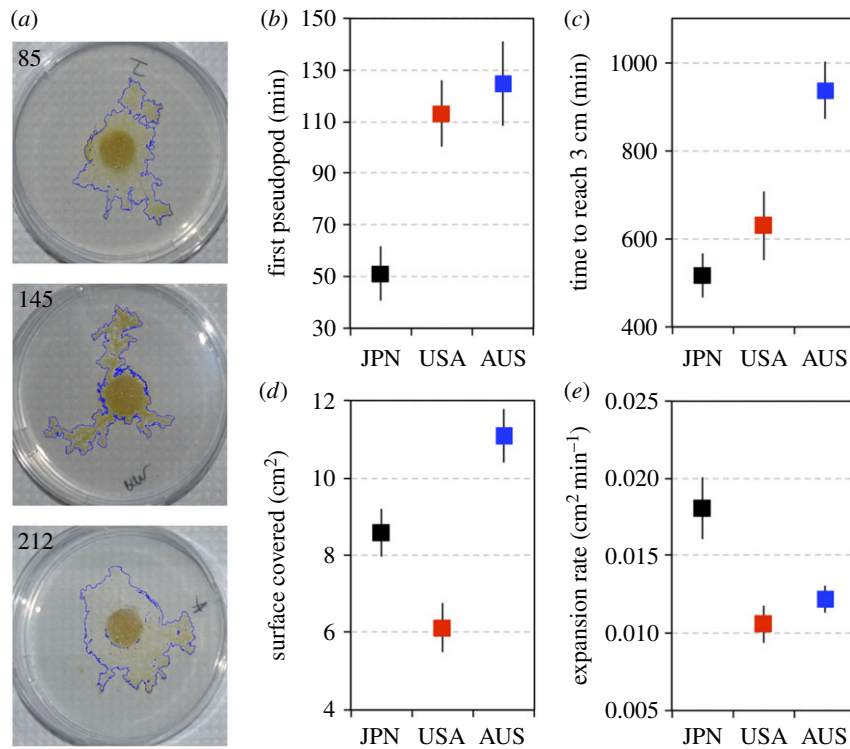


Figure 1. Experiment 1, homogeneous environment. (a) Photographs showing AUS, JPN and USA slime moulds that reach a distance of 3 cm from the centre of the arena (diameter 90 mm). (b) Time to extend a first pseudopod to explore the arena. (c) Latency to reach a distance of 3 cm. (d) Mean surface covered by the slime moulds when the maximum distance from the centre of the arena was 3 cm. (e) Mean expansion rate (computed as the surface divided by the latency to reach a maximum distance of 3 cm). The blue, red and black squares represent AUS, USA and JPN slime moulds, respectively. $n = 40$ replicates for each strain. Error bars are the 95% confidence intervals.

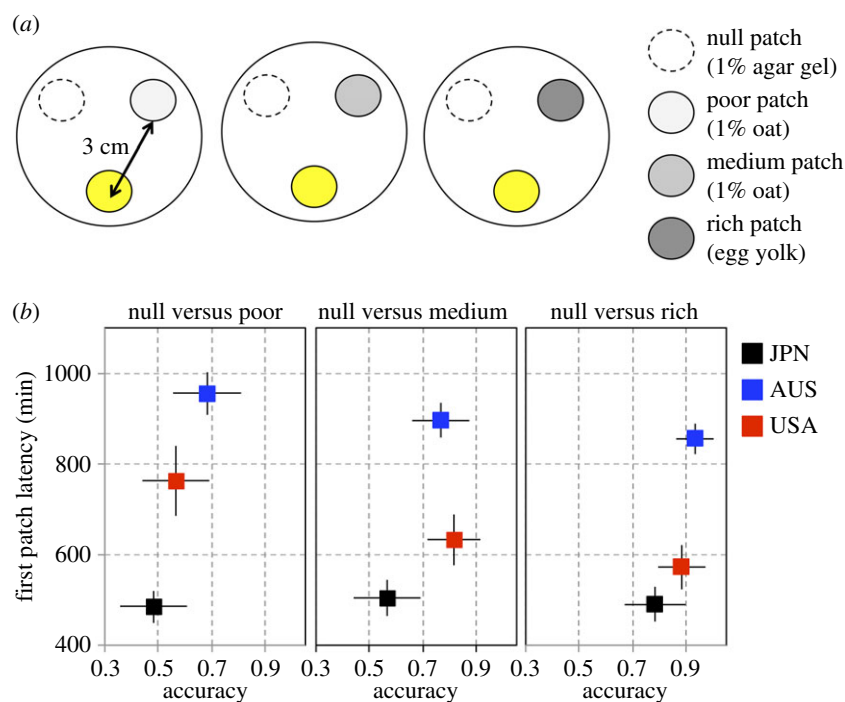


Figure 2. Experiment 2, one food source. (a) A slime mould, a null patch and a food patch (poor patch, medium patch or rich patch) were placed in an arena filled with plain 1% agar (diameter 90 mm). Each experiment lasted for 24 h. (b) Speed and accuracy of AUS, USA and JPN slime moulds when a single food patch was offered. The y-coordinate is the average time taken by slime moulds to reach either one of the two patches (first patch latency). The x-coordinate is the proportion of slime moulds that reached the best patch first (accuracy). Error bars are the 95% confidence intervals. Each binary choice was repeated 60 times with each strain.

consisted of 90 mm diameter Petri dish filled with plain 1% agar. Once the agar had set, we punched three holes in a triangular configuration (diameter 1.3 cm) (figure 2a). The first hole was filled with a slime mould (diameter 1.3 cm), the second one with a food patch (diameter 1.3 cm) and the last one with plain 1% agar gel (null

patch, diameter 1.3 cm). The experiment started when we introduced the slime mould in the arena. We used three different food patches varying in nutritional value: 1% w/v powdered oat (poor patch), 10% w/v powdered oat (medium patch) and 10% w/v powdered oat mixed with 10% w/v egg yolk (rich patch) [12]. We know

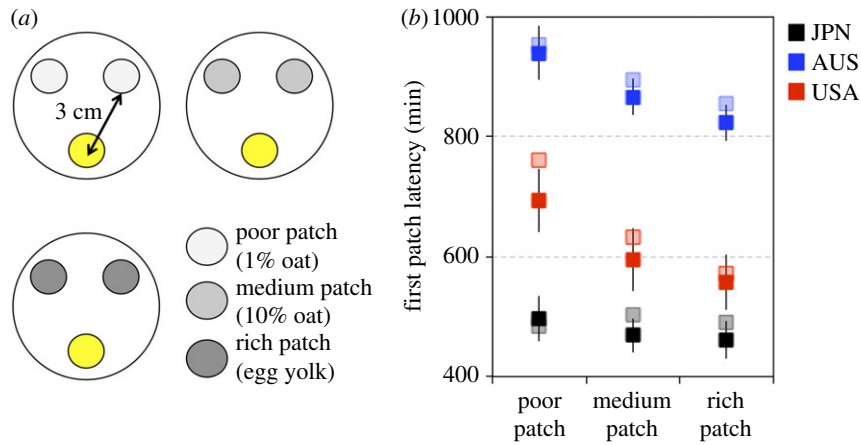


Figure 3. Experiment 3, two equal food sources. (a) A slime mould and two equal food patches (poor patches, medium patches or rich patches) were placed in an arena filled with plain 1% agar (diameter 90 mm). Each experiment lasted for 24 h. (b) Average time taken by the slime moulds to reach either one of the two patches (first patch latency). For purposes of comparison, the data obtained when the food patches were offered against a null patch (figure 2) were added (water colour squares). Error bars are the 95% confidence intervals. Each binary choice was repeated 60 times with each strain.

that slime mould growth depends mostly on protein concentration [17]. Therefore, based on protein concentrations in oat and egg yolk, the nutritional value of the medium patch (1.7% w/v) was half the one of the rich patch (3.3% w/v) and 10 times the one of the poor patch (0.17% w/v). Thus, the choices offered to the slime moulds ranged from easy (rich patch versus null patch) to difficult (poor patch versus null patch). We tested if increasing difficulty led to an increase in the mean speed and a decrease in accuracy (drift-diffusion models prediction).

(iii) Experiment 3: two equal food sources

Here, slime moulds were presented with a choice between two equal food sources. We used the same experimental set-up as in experiment 2. One hole was filled with a slime mould, while the two other holes in the arena were filled with two poor, two medium or two rich patches (figure 3a). In this experiment, any decision made by the slime moulds was considered as correct so we investigated if slime moulds took slow (drift-diffusion models prediction) or quick decisions (value-based models prediction).

(iv) Experiment 4: two different food sources

We presented the slime moulds with a choice between two food sources varying in quality using the same experimental set-up as in experiment 2 (figure 4a). Here, slime moulds were rewarded by the quality of the food source they chose. One hole in the arena was filled with a medium patch and the other hole was either filled with a poor patch or a rich patch. In both choices, the differences in value between the food patches (i.e. protein content) were comparable (0.17 versus 1.7%, $\text{diff} = 1.53$; 1.7 versus 3.3%, $\text{diff} = 1.6$), but the reward for the incorrect decision varied (0.17 or 1.7%). Thus, we investigated if accuracy and speed varied according to the reward offered for an incorrect decision.

(v) Experiment 5: distance

When offered a choice between food sources, if the exploration space was totally homogeneous and no information was accessible then the slime moulds should explore randomly and reach the best option by chance. However, substances from the food source diffuse and produce a chemical field, which can be sensed by the slime moulds from a distance [9,12]. Thus, placing the food source closer to the slime moulds should increase accuracy. To test this hypothesis, slime moulds were offered a

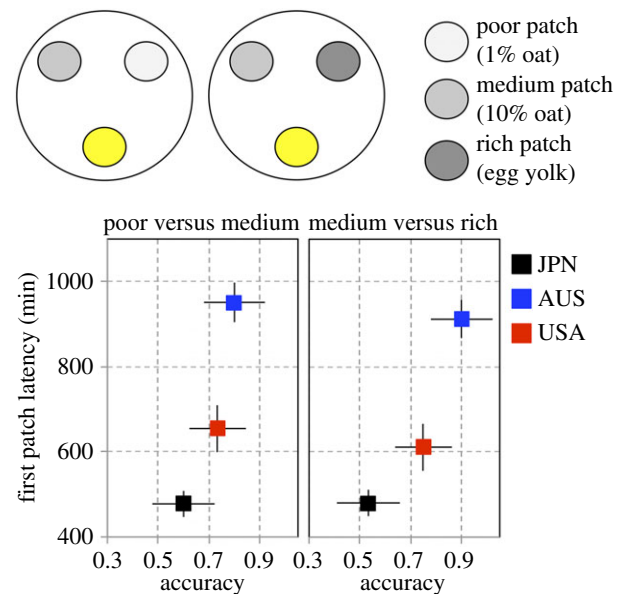


Figure 4. Experiment 4, two different food sources. (a) A slime mould and two different food patches (poor patch, medium patch or rich patch) were placed in an arena filled with plain 1% agar (diameter 90 mm). Each experiment lasted for 24 h. (b) Speed and accuracy of AUS, USA and JPN slime moulds when two different food patches were offered. The y-coordinate is the average time taken by the slime moulds to reach either one of the two patches (first patch latency). The x-coordinate is the proportion of slime moulds that reached the best patch first (accuracy). Error bars are the 95% confidence intervals. Each binary choice was repeated 60 times with each strain.

medium patch placed 1.75 cm away (close patch) against either a null patch placed 3 cm away (null patch) or a medium patch placed 3 cm away (distant patch) (figure 5a).

(vi) Experiment 6: diffusion

To confirm indisputably that slime moulds would be more accurate if we let the food substances diffuse for a longer time, we ran an experiment offering a medium patch placed 24 h prior to the experiment against a null patch or against a medium patch placed at the start of the experiment (figure 6a).

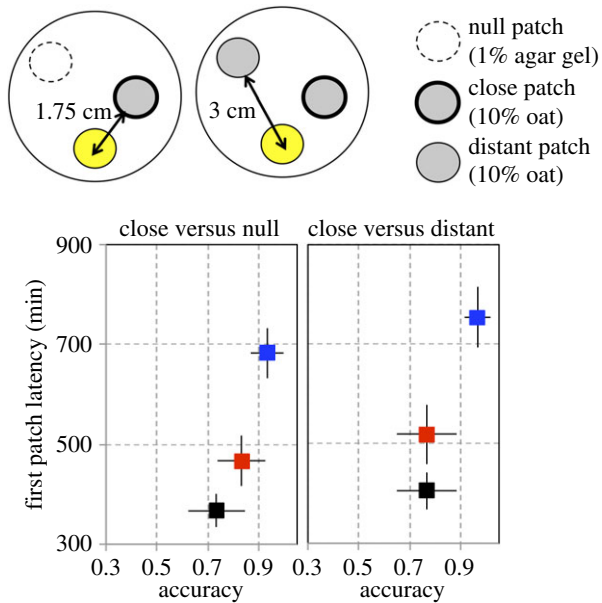


Figure 5. Experiment 5, distance. (a) A slime mould and two patches (null patch, close patch and distant patch) were placed in an arena filled with plain 1% agar (diameter 90 mm). Each experiment lasted for 24 h. (b) Speed and accuracy of AUS, USA and JPN slime moulds when the two patches were placed at different distances. The y -coordinate is the average time taken by the slime moulds to reach either one of the two patches (first patch latency). The x -coordinate is the proportion of slime moulds that reached the close patch first (accuracy). The blue, red and black squares represent AUS, USA and JPN strains, respectively. Error bars are the 95% confidence intervals. Each binary choice was repeated 60 times with each strain.

(vii) Experiment 7: competition

If different BTs are present within a population, we expect that one type excels in one situation, while a second type excels in another situation. Spending time in making a decision or making error can both result in competition. In this last experiment, we tested this hypothesis by presenting two slime moulds from different strains with either a single medium patch or two food patches of different quality (medium patch versus rich patch) (figure 7a). The arena consisted of 145 mm diameter Petri dish filled with plain 1% agar. Once the agar had set, we punched four holes (diameter 1.3 cm) in a diamond shape configuration. Two holes were filled with slime moulds of different strains, the two others holes with either a null, a medium or a rich patch (figure 7a). The slime moulds were distant from one another (5 cm) and interactions were unlikely [1].

(c) Variable measured

We replicated each binary choice 60 times with each strain leading to a total of 2880 slime moulds tested. For each replicate, we measured the time taken by the slime mould to reach either one of the two food patches.

(d) Statistics

For all experiments, the latencies to reach the first patch or a distance of 3 cm were compared using general linear models (glm), with strain, binary choice and the interaction strain \times binary choice as fixed factors. We conducted generalized linear models (gglm) using a logit-link function to compare accuracy (proportion of slime moulds that reach the best patch first) across strain and experiments. All statistical tests were conducted with SPSS (v. 21.0). Slime mould was not included in the analyses as we used a different slime mould for each replicate.

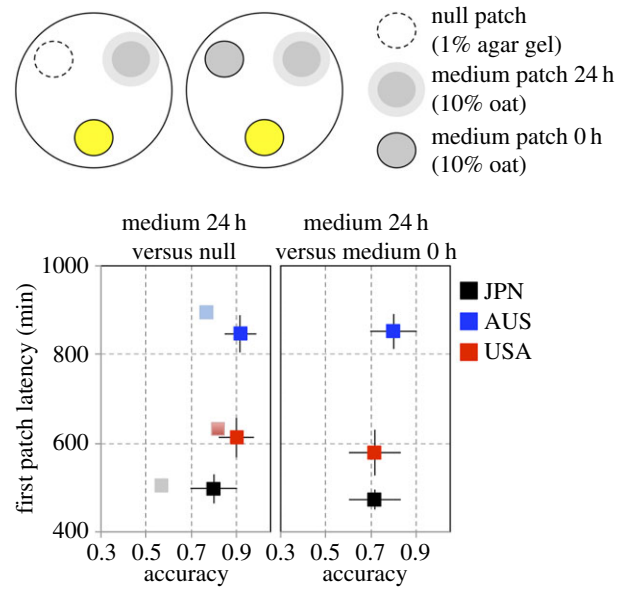


Figure 6. Experiment 6, diffusion. (a) A slime mould and two patches (null patch, medium patch 0 h or medium patch 24 h) were placed in an arena filled with plain 1% agar (diameter 90 mm). Each experiment lasted for 24 h. (b) Speed and accuracy of AUS, USA and JPN slime moulds when one food patch was placed beforehand. The y -coordinate is the average time taken by the slime moulds to reach either one of the two patches (first patch latency). The x -coordinate is the proportion of slime moulds that reached the patch placed beforehand first (accuracy). Error bars are the 95% confidence intervals. For purposes of comparison, the data obtained when the medium patch was offered against a null patch (figure 2) were added (water colour squares). Each binary choice was repeated 60 times with each strain.

3. Results

(a) Experiment 1: homogeneous environment

JPN slime moulds extended their first pseudopod more rapidly than AUS and USA slime moulds, which started exploring at the same time (glm on pseudopod extension, strain effect $F_{1,119} = 32.42$, $p < 0.001$; figure 1b). JPN slime moulds travelled very fast, followed by USA slime moulds and then AUS slime moulds (glm on speed, strain effect $F_{1,119} = 42.50$, $p < 0.001$; figure 1c). AUS slime moulds reached the largest surface for a given distance, while the USA slime moulds expanded the least (glm on surface, strain effect $F_{1,119} = 54.73$, $p < 0.001$; figure 1d). Thus, JPN slime moulds had the highest exploration rate in terms of area covered, followed by the AUS and USA slime moulds, which had similar exploration rates (glm on expansion rate, strain effect $F_{1,119} = 28.56$, $p < 0.001$; figure 1e).

(b) Experiment 2: one food source

In the following experiments, we checked how quickly slime moulds reached a decision (speed) and whether the rewarded patch was contacted first (accuracy).

For all binary choices, JPN slime moulds were consistently faster than USA slime moulds, which in turn were faster than AUS slime moulds (glm on speed, strain effect $F_{2,539} = 235.09$, $p < 0.001$; figure 2b). The time taken by AUS and USA slime moulds to make a decision decreased when the quality of the food patch increased (i.e. the choice difficulty decreased), while for JPN slime moulds, it

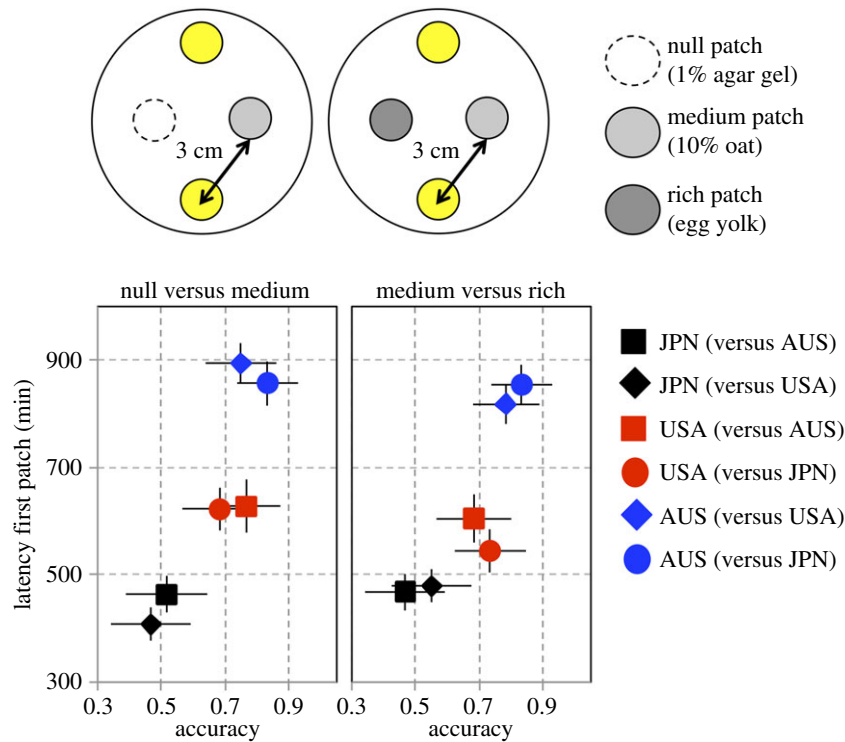


Figure 7. Experiment 7, competition. (a) Two slime moulds (AUS, USA or JPN) and two patches (null patch, medium patch or a rich patch) were placed in an arena filled with plain 1% agar (diameter 145 mm). Each experiment lasted for 24 h. (b) Speed and accuracy of AUS, USA and JPN slime moulds under competitive environment. The y -coordinate is the average time taken by the slime moulds to reach either one of the two patches (first patch latency). The x -coordinate is the proportion of slime moulds that reached the best patch first (accuracy). Square, diamond and circle indicate that the focal slime mould is associated with an AUS, USA or JPN slime mould. Error bars are the 95% confidence intervals. Each binary choice was repeated 60 times with each strain.

remained constant (choice effect $F_{2,539} = 12.58$, $p < 0.001$; interaction strain \times choice $F_{4,539} = 4.74$, $p = 0.001$; figure 2b).

JPN slime moulds were significantly less accurate than AUS and USA slime moulds (gglm on accuracy, strain effect $\chi^2 = 17.44$, $p < 0.001$). In two of the choices, JPN slime moulds chose randomly one of the two patches (choice effect $\chi^2 = 34.24$, $p < 0.001$; strain \times choice $\chi^2 = 3.41$, $p = 0.491$; figure 3b). They were accurate only when offered a rich patch (i.e. when given an easy choice). AUS slime moulds selected the best option most of the time regardless of the choice offered, but their accuracy decreased with choice difficulty. USA slime moulds, although faster than AUS slime moulds, were only slightly less accurate as most of their decisions were correct except when presented with a poor patch (i.e. when given a hard choice).

(c) Experiment 3: two equal food sources

For all binary choices, JPN slime moulds made consistently quicker decision than USA slime moulds, which in turn were quicker than AUS slime moulds (glm on speed, strain effect $F_{2,539} = 289.45$, $p < 0.001$; figure 3b). Decision time decreased when food quality increased for the three slime moulds strains (choice effect $F_{2,539} = 16.92$, $p < 0.001$; interaction strain \times choice $F_{4,539} = 1.77$, $p = 0.134$; figure 3b). Interestingly, slime moulds wasted less time to make a decision in equal-alternatives situations than in single alternative ones (comparison experiments 2 and 3, glm on speed, $F_{2,1079} = 6.97$, $p = 0.008$)

(d) Experiment 4: two different food sources

Again, JPN slime moulds made the quickest decisions while AUS slime moulds made the slowest ones regardless of the

choice offered (glm on speed, strain effect $F_{2,359} = 226.73$, $p < 0.001$; choice effect $F_{1,359} = 2.30$, $p = 0.130$; strain \times choice $F_{2,359} = 0.65$, $p = 0.524$; figure 3b). JPN slime moulds chose randomly one of the two options in both choices, while AUS and USA slime moulds made fewer error and selected often the most rewarding option (gglm on accuracy, strain effect $\chi^2 = 23.10$, $p < 0.001$, choice effect $\chi^2 = 0.65$, $p = 0.419$, strain \times choice $\chi^2 = 2.75$, $p = 0.252$; figure 3b). AUS slime moulds were slightly more accurate than USA slime moulds. For all strains, speed and accuracy did not differ between the two choices (i.e. whether the reward for an incorrect option was low or medium).

(e) Experiment 5: distance

Most slime moulds made correct decisions when the food patch was placed closer. Yet AUS slime moulds still made the fewest errors in both choices (gglm on accuracy, strain effect $\chi^2 = 15.06$, $p = 0.001$, choice effect $\chi^2 = 0.20$, $p = 0.654$; strain \times choice $\chi^2 = 1.68$, $p = 0.432$; figure 5b). Again JPN slime moulds were quicker to decide than USA slime moulds, which were themselves faster than AUS slime moulds (glm on speed, strain effect $F_{2,359} = 105.15$, $p < 0.001$; choice effect $F_{1,359} = 4.53$, $p = 0.034$; strain \times choice $F_{2,359} = 0.08$, $p = 0.927$; figure 5b).

(f) Experiment 6: diffusion

If we placed the food patch 24 h prior to the experiment, all slime moulds were equally accurate and made few errors (gglm on accuracy, strain effect $\chi^2 = 4.44$, $p = 0.109$; figure 6b) even if the difference in speed between the strains remained (glm on speed, strain effect $F_{2,359} = 164.70$, $p <$

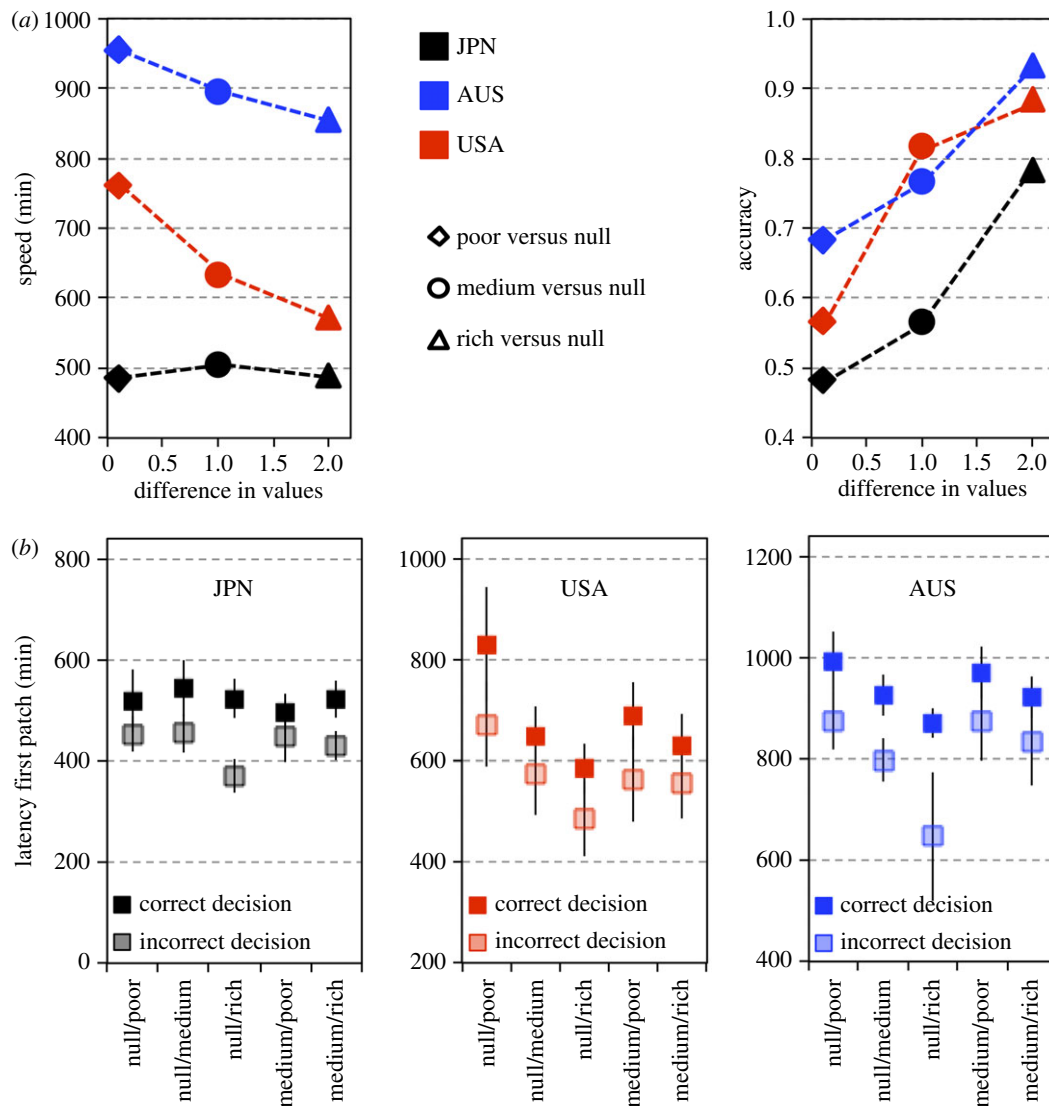


Figure 8. (a) Relation between choice difficulty (differences in values between the two patches), speed and accuracy for the three strains when only a single alternative was rewarded. (b) Speed and accuracy as a function of the choice offered. The y-coordinate is the average time to reach a patch. The x-coordinate is the choice offered. The blue, red and black symbols represent AUS, USA and JPN strains, respectively. Plain and faded colours indicate correct and incorrect decisions, respectively. Error bars are the 95% confidence intervals.

0.001; choice effect $F_{1,359} = 1.13$, $p = 0.288$; strain \times choice $F_{2,359} = 0.53$, $p = 0.590$; figure 6b). The accuracy was higher when the medium patch placed 24 h prior to the experiment was offered against a null patch than against a medium patch placed at the start of the experiment (choice effect $\chi^2 = 9.67$, $p = 0.002$; strain \times choice $\chi^2 = 1.56$, $p = 0.458$).

(g) Experiment 7: competition

When presented with a single food patch, JPN slime moulds that selected first the unrewarded patch moved quickly to the rewarded patch afterwards. Thus, despite being less accurate (gglm on accuracy, strain effect $\chi^2 = 22.01$, $p < 0.001$; association effect $\chi^2 = 1.34$, $p = 0.512$; association \times strain $\chi^2 = 0.34$, $p = 0.562$; figure 7b), JPN slime moulds reached the food patch before its opponents (83.4%, $p < 0.001$, and 70%, $p = 0.001$, for the association JPN/AUS and JPN/USA, respectively). USA slime moulds, being as accurate as AUS ones but faster (glm on speed, strain effect $F_{2,359} = 165.31$, $p < 0.001$; association effect $F_{1,359} = 1.19$, $p = 0.305$; strain \times association $F_{2,359} = 3.24$, $p = 0.073$; figure 7b) monopolized the food patch most often when opposed to AUS slime moulds (68.3%, $p = 0.003$).

When two food patches of different qualities were available, USA slime moulds being more accurate than JPN slime moulds (gglm on accuracy, strain effect $\chi^2 = 18.10$, $p < 0.001$; association effect $\chi^2 = 1.94$, $p = 0.378$; association \times strain $\chi^2 = 1.04$, $p = 0.307$), and faster than AUS slime moulds (glm on speed, strain effect $F_{2,359} = 132.46$, $p < 0.001$; association effect $F_{1,359} = 0.82$, $p = 0.443$; strain \times association $F_{2,359} = 5.26$, $p = 0.022$; figure 7b) monopolized the best food patch most often (60%, $p = 0.031$, and 63.3%, $p = 0.012$ when competing with an AUS slime moulds and JPN slime moulds, respectively). Interestingly when opposed to JPN slime moulds, AUS slime moulds, despite being the slowest, were able to exploit the most rewarding option in 56.6% of the cases ($p = 0.061$) as JPN slime moulds settled on the first option selected regardless of its quality.

4. Discussion

Studying decision-making in slime moulds in a foraging context, we showed that differences in BT were correlated with decision-making abilities. We characterized three distinguishable categories: slime moulds that explored and

moved fast (JPN), slime moulds that explored slowly but moved fast (USA), and slime moulds that explored and moved slowly (AUS). Thus, we confirmed the existence of distinct BTs in slime moulds [1]. We find that JPN slime moulds were the quickest to decide but the least accurate, whereas AUS slime moulds were the slowest and the most accurate. These results suggest a trade-off between accuracy and speed (i.e. pareto effect). Interestingly, however, USA slime moulds had an accuracy comparable to that of the AUS slime moulds, while making decisions more quickly. Similar results have been found in other distributed systems such as social insects, in which changing the magnitude of a quorum threshold allows for improved accuracy when choosing a nest site at only a small or no cost in terms of speed (e.g. [25–30]).

Evidence of SATO was found when considering task difficulty (figure 8a). There is an extensive literature demonstrating that animals make faster decision and less errors when task difficulty decreases [25]. Here, we showed a similar pattern in slime moulds. Accuracy increased when the differences between the two patches increased in all strains and speed was negatively correlated with task difficulty in AUS and USA slime moulds (figure 8a). Our results imply that longer exploration times are required to obtain sufficient information to solve harder tasks. Thus, slime moulds (like animals) might ponder difficult decisions longer than they do easy ones [18,25].

However, some of our results contradict accuracy-based decision and diverge from drift-diffusion model predictions. First, slime moulds presented with two equal food sources made decisions more quickly than slime moulds presented with a single food source. Second, they were on average faster in making decisions as the value (i.e. quality) of the two food sources increased. Thus, although the differences between the food sources were equal to zero in all choices offered, as the overall value of the food sources offered increased, decisions were made faster. This result cannot be explained by drift-diffusion models, which are driven only by the difference in option values [20,21]. Instead, our results indicate that in order to avoid decision deadlocks over difficult decisions, slime moulds might maximize value over accuracy, as suggested by Pirrone *et al.* [21–24].

However, following value-based model predictions [21–24], if slime moulds were optimizing only value, they would be expected to sacrifice negligible accuracy with fast and potentially inaccurate decisions when the incorrect decisions were rewarded satisfactorily and the difference in item values remained constant. Yet when slime moulds were offered two food sources varying in quality, we did not observe a decrease in accuracy or an increase in speed when the incorrect decision was rewarded by a medium patch instead of a poor patch. In this situation, slime moulds again maximized accuracy over value. Thus, how can we reconcile our findings obtained with two equal food sources with drift-diffusion models predictions? Our results would require the models' decision boundaries (i.e. decision thresholds) to collapse over time to allow quicker decisions [31,32]. However, to date, no empirical studies have provided strong empirical evidence for collapsing decision-making boundaries. Still, we need to be cautious in interpreting our results as more replicates with more conditions would be needed to provide compelling evidence of collapsing boundaries.

We might expect SATO to occur both among and within strains [18]. Here, in our experiment, we find empirical support for the presence of within-strain correlations in decision time and accuracy regardless of the task difficulty (figure 8b). The quicker response led to wrong decisions in all strains tested and for all tasks offered. In many paradigms, incorrect responses are predicted to be reliably faster than correct responses, but only when decisions are easy and individuals are hurrying. By contrast, when decisions are difficult and cautious, incorrect responses are expected to be slower on average than correct responses [32]. We did not observe such an effect in our experiment (figure 8b). However, in most drift-diffusion models, the mean drift rate is assumed to be constant (i.e. linear), while in our experiment, as the slime mould is exploring, the information relative to the food source (i.e. chemical cues) gets richer and richer, and we can expect information accumulation to increase non-linearly. Further experiments would be required to confirm this assumption.

We have shown that individual variation in decision-making abilities in slime moulds was related to between-individual variation in behaviour. Yet decision-making is central to the ability of all organisms to survive and has ecological and evolutionary consequences [25,33]. Decision-making in slime moulds is achieved by their ability to use chemotaxis [9]. Our data showed that shortening the distance between the slime mould and the food source or placing the food source one day before the slime mould reduced the number of errors and led to comparable decision-making abilities in all strains. This result precludes the possibility that detection thresholds for food cues might be altered in JPN slime moulds and simply suggests that JPN slime moulds moved before collecting enough information to make an accurate decision. The fact that JPN slime moulds were able to find the rich patch but not the medium patch when a single food source was offered suggests that yolk cues diffused through the agar quicker than oat cues [12]. As AUS and USA slime moulds started to explore later than JPN slime moulds, oat cues had time to diffuse enabling slime moulds to gather enough information to make an accurate decision. AUS slime moulds, by spreading multiple migration fronts over a wide area [1,34] and by integrating information between these fronts [19], were the most accurate.

Gathering more information improved accuracy, but at the cost of speed. Thus, what would be the right thing to do? We revealed that depending on the environment, one BT excelled at the expense of others. When a single food source was present being fast was the best strategy to monopolize a food source. By contrast, when multiple food sources of varying quality were present, being accurate was the best approach. Slime mould abundance appears to be maximum in temperate forest, while it decreases in Mediterranean forests, woodlands, scrub and tropical forest [35]. Thus, we can expect competition pressure to be the highest for slime moulds inhabiting temperate climates. Following our results, under competitive conditions, sacrificing accuracy to speed might be the best solution to guarantee any reward, a strategy observed especially in the JPN slime moulds. Our results feature a previously unreported relation between BTs and SATO in a unicellular organism, and establish slime moulds as a promising model to test fundamental behavioural ecology theories.

Data accessibility. Data available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.760fs1j> [36].

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