Speed–accuracy trade-offs during foraging decisions in the acellular slime mould *Physarum polycephalum*

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Speed–accuracy trade-offs (SATs) are thought to be a fundamental feature of biological information processing, yet most evidence of SATs comes from animals. Here, we examine SATs in the foraging decisions of an acellular, amoeboid organism: the slime mould *Physarum polycephalum*. Slime moulds were given a simple discrimination task: selecting the highest-quality food item from a set of three options. We investigated the effect of two stressors, light exposure and hunger, on the speed and accuracy of decision-making. We also examined the effect of task difficulty. When given a difficult discrimination task, stressed individuals tend to make faster decisions than non-stressed individuals. This effect was reversed in plasmodia given easy discrimination tasks, where stressed individuals made slower decisions than non-stressed individuals. We found evidence of SATs, such that individuals who made fast decisions were more likely to make costly errors by selecting the worst possible food option. Our results suggest that SATs occur in a wider range of taxa than previously considered.

Keywords: speed–accuracy trade-offs; slime mould; *Physarum*; decision-making; decentralized behaviour

1. INTRODUCTION

Making decisions is difficult; making the correct decision is an even harder task, particularly when under pressure. In a perfect world, a decision-maker would have instant access to complete information about every available option. In reality, collecting information takes time and decision-makers are often time-constrained. A decision-maker may opt to make a fast decision by collecting less information, but they do so at the expense of decision accuracy. Conversely, a decision-maker might choose to collect as much information as possible, resulting in a highly accurate, but very slow decision. This relationship between speed and accuracy has been termed the speed–accuracy trade-off (SAT; e.g. [1,2]), and it is a common feature of human decision-making [3].

Not only are SATs common in human decision-making, but recent evidence suggests that they may also have important ecological implications in non-human animals. Speed–accuracy trade-offs are central to many animal decisions, such as mate choice, predator avoidance and foraging [4], with the cost of making a mistake varying from choosing a suboptimal food patch or mate to being eaten by a cryptic predator. Speed–accuracy trade-offs can occur for several reasons. Time-constrained organisms might sample fewer alternatives, and so have incomplete information about the true availability of options. These types of errors are not primarily owing to constraints of the individual's information-processing system, and are instead owing to a lack of complete information. One of the more intriguing forms of SATs occur when an individual has access to information, yet lacks the time to use the information properly. These 'errors of

judgement' (*sensu* [5]) give us insight into how organisms use and process information when time is limited.

A large body of research investigating SATs in humans has resulted in detailed theoretical and neurophysiological models of SATs (e.g. [6,7]; see [3,8,9] for reviews). The ubiquity of SATs in human and animals, combined with the wealth of theoretical evidence, demonstrates that SATs are probably an inherent property of information processing. However, most studies to date have focused on SATs in animals, all of which process information in a centralized manner via the brain. By contrast, many of the most abundant and ecologically significant organisms on Earth, such as the mycelial networks of fungi, function as distributed networks without specialized centres: these organisms process information in a fully decentralized manner. Recent work suggests that slime moulds, which are highly decentralized organisms, are capable of surprisingly sophisticated decision-making and problem-solving [10–17]. Parallels have also been drawn between insect colonies (which use decentralized information processing) and primate brains [18]. Slime moulds provide interesting alternatives to brains and insect colonies with which to test the constraints of information processing.

Here, we investigate the speed and accuracy of decision-making in the acellular slime mould *Physarum polycephalum* (Supergroup: Amoebozoa), with emphasis on the effects of task difficulty, time pressure and hunger. *Physarum polycephalum* is an acellular, multinucleate amoeboid organism that forages as a mass of flowing pseudopods. The active life stage of the slime mould, known as the plasmodium, is organized as one or more actively moving search fronts, followed by a network of veins. In nature, slime moulds actively move around searching for bacteria or fungi, which they
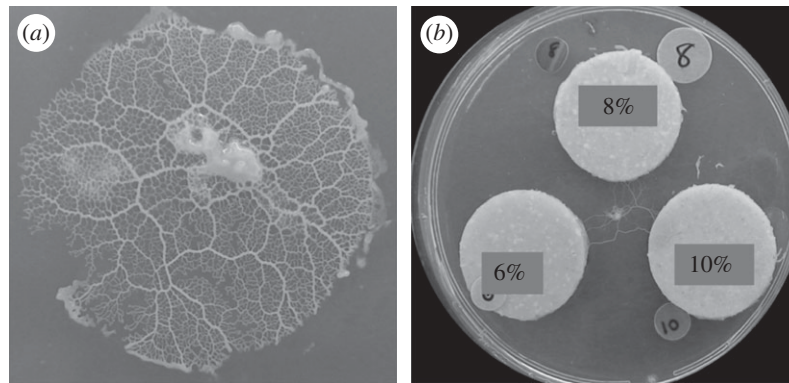
Figure 1. Experimental set-up. (*a*) Slime mould plasmodium after the 12 h acclimation process. (*b*) The experimental arena. Each food disc is labelled with its percentage oatmeal content. Veins linking the plasmodia to the food sources are visible (plasmodium is in the centre).

subsequently engulf. Slime moulds can achieve speeds up to 5 cm h^{-1} [19].

In humans, SATs can be investigated by asking participants to emphasize either decision speed or decision accuracy. For example, humans asked to make a decision quickly usually do so by sacrificing decision accuracy [3,9]. Since it is not possible to give clear instructions to most non-human animals, the emphasis on speed or accuracy must be manipulated in other ways. Decision speed can be emphasized by placing individuals into harsh or unpleasant environments. For example, ant colonies choosing between several potential nest sites made slow but accurate decisions when in benign environments, and fast but inaccurate decisions when placed into harsh environments [5]. Hunger is known to affect the selectivity of animals and could therefore affect SATs by shifting emphasis to either speed or accuracy. For example, Perry [20] found that starved predatory snails were less selective than satiated snails, but whether the decreased selectivity resulted in faster decision times is not known. To test for SATs in *P. polycephalum*, we used light exposure and hunger as stressors. Because *P. polycephalum* is photophobic, exposure to light creates a hostile environment. We predicted that plasmodia making decisions under stress would emphasize decision speed at the expense of decision accuracy. We also examined the effect of task difficulty on SATs. In humans and animals, SATs tend to occur when decisions are difficult, because subjects can solve easy discrimination tasks with high accuracy over all reasonable time ranges (reviewed in [4]). Here, we examine whether this holds true in a slime mould.

2. METHODS

(a) *Culture techniques*

Our original *P. polycephalum* culture was obtained from Southern Biological Supplies (Nunawading, Australia). We cultured *P. polycephalum* plasmodia in 30 × 20 cm rectangular plastic tubs containing 1.5 per cent agar. Cultures were maintained at 24°C in the dark. We reared cultures on flakes of rolled oats (Coles brand, Australia), which were liberally sprinkled across the surface of the agar daily. We sub-cultured plasmodia into new tubs every 2 days.

(b) *General procedures*

To test decision speed and accuracy, we presented *P. polycephalum* plasmodia with a simple discrimination task: selecting the food source with the highest nutrient concentration from a set of food options. Food discs consisted of varying amounts of finely ground oatmeal (Soland Health Foods, Arana Hills, Australia) mixed with 1.5 per cent liquid agar. The oatmeal–agar mixture was poured into a plastic tub and allowed to set. Individual food discs were punched out using a circular 28 mm diameter cutter, resulting in equally sized food discs.

Our choice arena consisted of an 8.5 cm diameter Petri dish filled with 1.5 per cent agar. Circles of 20 mm diameter were cut into transparency film and placed on top of the agar, resulting in a circle of agar surrounded by dry transparency film. Plasmodial fragments were severed from the main cell before being placed in the centre of the circle. Because *P. polycephalum* is multi-nucleate, fragments severed from the main cell become fully functional, separate individuals within minutes [21]. We allowed plasmodia to acclimate in the dark for 12 h. Since plasmodia prefer the moist agar environment to the dry transparency film, the plasmodia symmetrically filled the circle, resulting in a circular amoeba (figure 1*a*). This procedure was necessary to ensure that all plasmodia were equally acclimated when the experiment started. To start an experiment, the plastic film was removed, and the food options were placed so that they were touching the edges of the circular plasmodium. Note that sample sizes in experiments are uneven because slime moulds sometimes failed to form circular plasmodia during the acclimatization phase; these were not used in the experiments.

Plasmodia were checked every hour for the first 12 h, and then once again at 24 h. At each check, we recorded whether the plasmodium had completed its decision-making. We considered the decision process to be complete when the plasmodium had moved all of its biomass to a single food option. To examine decision accuracy, we recorded which food patch had been selected. We recorded a decision as being accurate if the plasmodium selected the highest concentration food disc (10% oatmeal).

In discrimination tasks, task 'difficulty' is typically defined as the similarity between the 'target' option and the 'distracter' option (e.g. [22]). We tested the effect of task difficulty on the speed and accuracy of decision-making by presenting plasmodia with either an 'easy' or a 'difficult' discrimination task. 'Easy' discrimination tasks consisted of three food discs containing 10, 6 and 2 per cent oatmeal (a concentration difference of 4 percentage points), and 'difficult' discrimination

tasks containing 10, 8 or 6 per cent oatmeal food discs (a 2 percentage point difference). Food discs were placed so that they were equidistant from one another, and the location of each food disc was randomized to prevent directional biases (figure 1*b*).

(c) Light–stress experiment
We were interested in the effect of light exposure on the speed and accuracy of decision-making in *P. polycephalum*. Plasmodia in the 'light' environment were exposed to 6600 lux of light, while those in the 'dark' environment were shaded from light exposure (43 lux). Light was provided by a fluorescent light mounted 30 cm above the choice arenas. We predicted that light exposure would cause plasmodia to make faster decisions at the expense of accuracy. Each level of light exposure (light/dark) was crossed with each level of task difficulty, resulting in four treatment groups (sample size in brackets): dark–easy (41), dark–difficult (39), light–easy (43) and light–difficult (39). This design allowed us to test for interactions between each light and task setting.

(d) Hunger–stress experiment
We investigated the effect of hunger on the speed and accuracy of decision-making. 'Starved' plasmodia were grown on plain, non-nutritive agar for 24 h prior to the acclimation phase of the experiment, while non-starved plasmodia were allowed ad libitum access to oat flakes. Each level of hunger was crossed with each difficulty level, resulting in four groups (sample size in brackets): starved–easy (28), starved–difficult (26), non-starved–easy (26) and non-starved–difficult (27).

(e) Statistical analyses
We used Cox proportional hazards modelling and likelihood ratio tests to examine the effect of stressors (hunger or light exposure) and task difficulty on the plasmodia's decision times. Although survival modelling has traditionally been used to study the time until failure (i.e. death), it can also be used for any data that describes the 'time until an event' [23]. The advantage of using survival time analysis is that it can accommodate 'censored' data. Censoring occurs when the value of an observation is only partially known, such as when events happen beyond the observation period. Survival modelling allowed us to include data from plasmodia that took longer than 12 h to make a decision. 'Decision time' was included in the model as a dependent variable, with stressor/no-stressor and task difficulty (easy/hard) as independent variables. Because not all experiments were performed on the same day, we controlled for variation in decision speed by including 'day' as a covariate in all models.

To test the effect of stressors and task complexity on decision accuracy, we used a nominal logistic regression model with decision accuracy (defined as choosing the 10% food item) as a dependent variable, and stressor/no-stressor, task difficulty and the interaction between stressor treatment and task difficulty as independent variables.

We investigated SATs by dividing plasmodia into those that made fast decisions and those that made slow decisions. We defined 'fast' decision-makers as those whose decision speed was in the bottom quartile of decision speeds (5 h in the light-exposure trials, 4 h in the hunger trials); all others were classified as 'slow'. We determined whether there was a relationship between fast decisions and making an accurate choice (the 10% food disc) using a χ^2-test with 'correct choice' as the dependent variable and fast/slow as the independent variable. We also examined whether
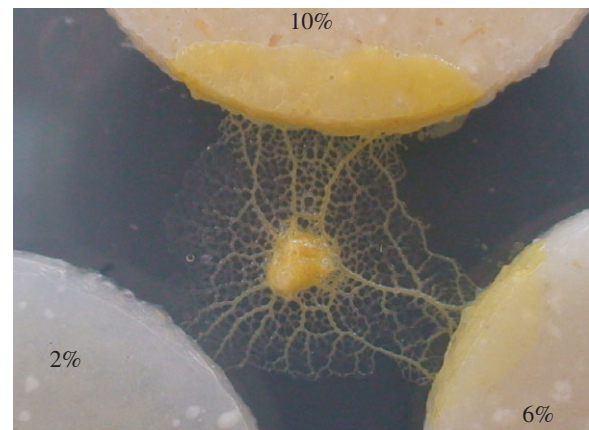
Figure 2. A plasmodium 4.5 h into the decision-making process. Note that search fronts have been extended onto both the 10 per cent and the 6 per cent food disc, but are in the process of being retracted from the 6 per cent disc (as evidenced by the paler colour).

individuals who made fast decisions were more likely to choose the lowest quality food disc (6% food disc in the difficult discrimination task, 2% food disc in the easy discrimination task).

3. RESULTS
Plasmodia typically began extending pseudopods onto the food discs within the first 4 h of the experiment. The plasmodia initially extended pseudopods onto all three options, before eventually retracting pseudopods away from non-preferred food discs. As the decision-making process continued, the network of tubes began to change such that tubes leading to non-preferred food sources became inactive and collapsed (figure 2). The decision-making process continued until all biomass had moved, via the tube network, to a single food source. Twenty-two plasmodia (13.5%) in the light-exposure treatment and one (1%) in the starvation treatment had not selected a single food option after 24 h, and so were classified as 'split decisions' and omitted from the general statistical analysis. These individuals typically had biomass on two of the three food items, with a thin tube connecting the search fronts on each food item.

(a) Decision speed
Plasmodia had a range of decision times, from those that completed a decision in less than 2 h to those that took longer than 12 h. In the light–stress experiments, the interaction between light exposure and task difficulty did not have a significant effect on decision time (Cox proportional hazards model: $p = 0.07$, $\chi^2 = 3.18$, d.f. $= 1$, $n = 135$). Among plasmodia given an easy discrimination task, those exposed to light made decisions more slowly than plasmodia that were shaded. This effect was reversed in the difficult task groups, where plasmodia that were exposed to light made faster decisions than those in the shaded groups (figure 3*a*). 'Day' had a significant influence on decision time (Cox proportional hazards model: $p < 0.01$, $\chi^2 = 8.96$, d.f. $= 2$, $n = 135$).

In the hunger–stress experiment, the interaction between starvation treatment and task difficulty also had a significant effect on decision time (Cox proportional
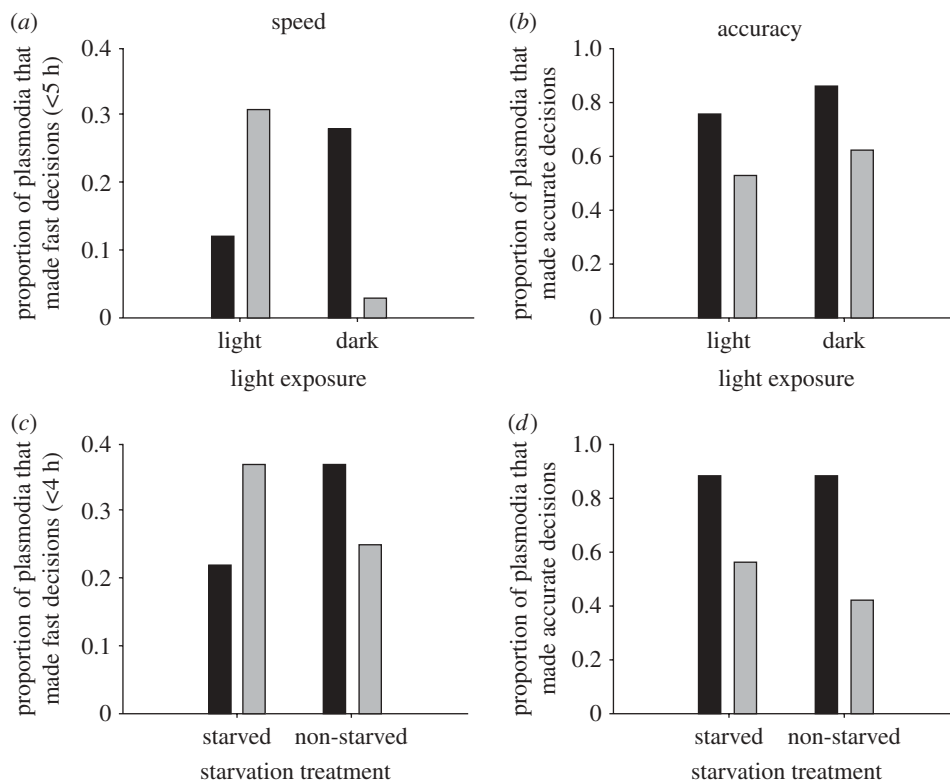
Figure 3. Shows the effect of stressors on the speed and accuracy of decision-making in *P. polycephalum*. (*a,c*) The effect of each experimental stressor ((*a*) light exposure, (*c*) starvation) on decision speed. When plasmodia were exposed to a stressor, either via light exposure or through starvation, easy discrimination tasks (black bars) were completed more slowly than difficult discrimination tasks (grey bars). When plasmodia were not stressed (dark and non-starved), easy discrimination tasks were completed faster than difficult discrimination tasks. (*b,d*) The effect of each stressor ((*b*) light, (*d*) starvation) on decision accuracy. A decision was considered accurate if the plasmodia selected the food disc with the highest nutrient concentration. Plasmodia were less accurate when presented with difficult discrimination tasks than when presented with easy discrimination tasks.

hazards regression model: $p = 0.048$, $\chi^2 = 3.88$, d.f. = 1, $n = 102$). In the easy task group, starved plasmodia made slower decisions than non-starved plasmodia; among plasmodia given a difficult discrimination task, starved plasmodia made faster decisions than did non-starved ones (figure 3*c*). Day also had a significant effect on decision speed (Cox proportional hazards model: $p = 0.018$, $\chi^2 = 5.5$, d.f. = 1, $n = 102$).

(b) Accuracy
We tested whether plasmodia accurately selected the highest quality food item in each choice set using a binomial test. The null hypothesis was that the slime moulds would select each food disc with equal probability (0.33). Plasmodia presented with easy discrimination tasks had a significant preference for the 10 per cent food discs ($p < 0.001$, $\chi^2 = 19.5$, $n = 125$). About 79.2 per cent of plasmodia in the easy discrimination task group chose the 10 per cent food disc, 18.4 per cent chose the 6 per cent food disc and 2.4 per cent chose the 2 per cent food disc. Plasmodia presented with the difficult discrimination task were also significantly more likely to select the 10 per cent food disc ($p = <0.001$, $\chi^2 = 19.5$, $n = 108$), with 53.7 per cent selecting the 10 per cent food disc, 31.5 per cent selecting the 8 per cent food disc and 14.8 per cent selecting the 6 per cent food disc.

In the light–stress experiments, the probability of selecting the 10 per cent oatmeal food disc was not

significantly influenced by light exposure (figure 3*b*; $p = 0.25$, $\chi^2 = 0.25$, $n = 134$). Task difficulty had a significant effect on the probability of choosing the 10 per cent food disc, such that plasmodia presented with an easy discrimination task were more likely to choose the 10 per cent food disc than were those given a difficult discrimination task (figure 3*b*; $p = 0.0029$, $\chi^2 = 8.84$, $n = 134$). The interaction between task difficulty and light exposure was not significant ($p = 0.74$, $\chi^2 = 0.10$, $n = 134$). Day did not have a significant effect on decision accuracy ($p = 0.17$, $\chi^2 = 3.47$, $n = 134$).

In the hunger–stress experiments, starvation had a significant influence on the probability of making an accurate choice such that starved plasmodia selected the 10 per cent food disc more often than did non-starved plasmodia (figure 3*d*; $p = 0.036$, $\chi^2 = 4.30$, $n = 99$). Task difficulty also had a significant effect on decision accuracy, with plasmodia given easy discrimination tasks being more likely to make an accurate decision than plasmodia given a difficult discrimination task ($p = 0.02$, $\chi^2 = 9.49$, $n = 99$). The interaction between task difficulty and starvation was not significant ($p = 0.97$, $\chi^2 = 0.001$, $n = 99$). Day did not have a significant effect on decision accuracy ($p = 0.87$, $\chi^2 = 0.02$, $n = 99$).

(c) Speed–accuracy trade-offs
In the light–stress experiment, the probability of selecting the best quality food item was not significantly influenced by decision speed. This was true for plasmodia given easy
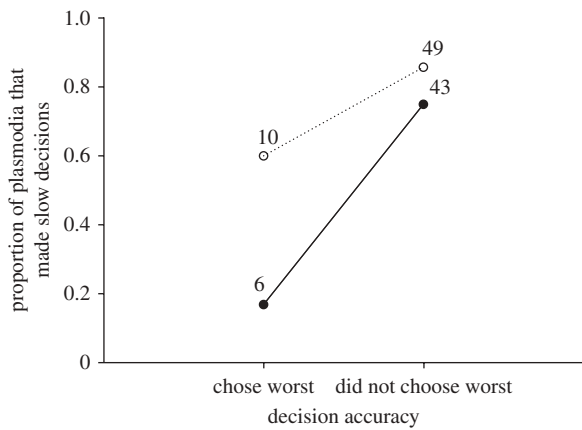
Figure 4. Speed–accuracy trade-offs in hunger (filled circles with solid lines) and light-exposure (open circles with dotted lines) experiments. Results are from the 'difficult' task groups only. Plasmodia were scored as making a 'slow' decision if they took longer than the bottom quartile of fastest times (>5 h for the light-exposure experiments, >4 h for the hunger experiments). The numbers indicate the total sample size for each group.

discrimination tasks ($p = 0.47$, $\chi^2 = 0.56$, $n = 75$) and for those given difficult discrimination tasks ($p = 0.37$, $\chi^2 = 0.81$, $n = 59$). When presented with a difficult discrimination task, plasmodia that made fast decisions were not significantly more likely to chose the worst possible option ($p = 0.07$, $\chi^2 = 3.62$, $n = 59$), although 64 per cent of fast plasmodia selected the worst possible choice, compared with only 12 per cent of slow plasmodia (figure 4). No analysis of decision time and probability to choose the worst food item was possible in the easy choice set, as no plasmodia selected the worst option.

In the hunger–stress experiment, slow plasmodia were not significantly more likely to choose the 10 per cent food disc in either the easy ($p = 0.82$, $\chi^2 = 0.05$, $n = 50$) or the difficult discrimination tasks ($p = 0.47$, $\chi^2 = 0.5$, $n = 49$). In the easy discrimination task, decision speed did not have a significant effect on whether plasmodia selected the worst quality food disc ($p = 0.89$, $\chi^2 = 0.02$, $n = 50$). When presented with difficult discrimination tasks, plasmodia that made fast decisions were significantly more likely to choose the worst quality food item (figure 4: $p = 0.005$, $\chi^2 = 7.59$, $n = 49$).

4. DISCUSSION
In the hunger–stress experiment, plasmodia given a difficult discrimination task experienced SATs. Interestingly, there was no effect of decision speed on choosing the highest quality food item; rather, plasmodia that made fast decisions were more likely to choose the worst possible food item. We detected the same trend among plasmodia given difficult tasks in the light–stress experiments, although we did not detect a statistically significant SAT. The fact that we found evidence of SATs only in our difficult discrimination task group is consistent with the general finding that SATs tend to manifest when tasks are difficult [3,4,24]. Our results show that SATs can occur even in simple, acellular

organisms. Further, SATs in slime moulds apparently have some of the same features (such as being exacerbated by task difficulty) as do SATs in neurobiologically sophisticated organisms.

Given the radically different information-processing system of slime moulds, why and how do SATs manifest? speed–accuracy trade-offs have been modelled using a large number of models (reviewed in [9]). While they differ in the specifics, most models make three assumptions: (i) evidence favouring each alternative is integrated over time; (ii) the accumulation process is subject to noise; and (iii) the decision is made when sufficient evidence has accumulated favouring one alternative over the other [9]. Although designed to examine decision-making in neuron-based information-processing systems, these models could theoretically be applied to any system where information is collected over time. Indeed, Marshall *et al.* [18] recently developed a framework for examining optimal decision-making and SATs in primate brains and insect colonies. All three systems can be modelled as interacting populations that accumulate evidence favouring options up to some threshold [18]. A decision is made when accumulated evidence exceeds this threshold. In slime moulds, biomass is moved via tubes; when a pseudopod comes into contact with a profitable food source, these tubes can widen, resulting in even greater flow. We speculate that the process of competing biomass flows to different food items may be functionally analogous to the build-up of evidence thought to occur in animal brains when choosing between two or more options. The 'competition' between choices and the build-up of evidence (in the form of neurons firing, insects recruiting conspecifics or plasmodial biomass accumulating) may underlie SATs in diverse biological systems.

We expected that stressors such as light exposure and hunger would have a consistent effect on decision speed regardless of task difficulty; instead, stressors had opposing effects depending on whether the task was easy or difficult. When the task was easy, starvation resulted in slower decisions. However, when the task was difficult, starvation caused plasmodia to make faster decisions. We observed the same, albeit non-significant, trend in our light–stress experiments. Despite their fundamentally different natures, both stressors seem to have a similar effect on decision speed. One possible explanation for this perhaps counterintuitive result is that plasmodia adjust the relative weight of decision speed or decision accuracy in order to minimize their probability of making costly mistakes. Food concentrations in the difficult choice set (6%, 8% and 10% oatmeal food discs) were selected because they are perceptually difficult to discriminate; however, the cost of making a mistake was low, as all food discs contained a relatively high concentration of oatmeal. Food discs in the easy set (2%, 6% and 10% oatmeal food discs) were easily distinguishable from one another, but the cost of making a mistake was much higher owing to the larger difference in food concentration. When stress was applied to plasmodia in the difficult discrimination task, the relatively low cost of making an error could have caused individuals to emphasize speed over accuracy. Conversely, since the cost of making a mistake is much higher in the easy discrimination tasks, plasmodia under stress might have

emphasized accuracy to the detriment of speed. Although the ability to use adjustable decision-making strategies might seem unlikely in an organism that lacks a brain, slime moulds are known to be capable of a broad range of complex and flexible behaviours, such as finding the shortest path through a maze [15], using adjustable search strategies to locate food [11], making trade-offs between risk and food quality [12], and anticipating periodic events [16]. Further, the ability to use adjustable SATs has been demonstrated in house-hunting ants, which also use a decentralized decision-making system [5].

Why do individuals sometimes emphasize speed over accuracy, given that this strategy can cause individuals to make mistakes? When solving a difficult decision is time-consuming and the cost of errors is low, then the best strategy for an organism may be to make a quick, but potentially inaccurate, decision [4]. For example, bees that are fast but inaccurate collect nectar at a higher rate than those that are accurate but slow [25]. For slime moulds exposed to light, making fast but inaccurate decisions when the choice set is difficult (and the cost of errors is low), could be optimal in that it decreases the plasmodium's exposure to the damaging effects of light by quickly providing access to shaded, safe feeding areas. A similar rationale can be applied to starved plasmodia, where a fast decision allows faster access to important nutrients.

Our results have implications for a number of ecologically significant taxa. Fungi, in particular, are organizationally similar to slime moulds in that they also use a highly decentralized decision-making process. Fungi form an extremely important component of soil ecosystems and play an important role in decomposition and nutrient cycling. Although the ecological role of slime moulds is less clear, they are known to be bacterial and fungal predators, and probably play an important role in modulating decomposition [26]. Among animals, SATs play an important role in a broad variety of behaviours including mate choice, predator–prey interactions and foraging [4]. Our results suggest that SATs may also be present among important members of the soil community, potentially indicating a much broader impact of SATs than previously assumed. Moreover, our results suggest that SATs may be an important feature of information processing in a wide variety of organisms, regardless of their cognitive complexity.

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