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Animal behaviour

Individual ant workers show self-control

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Often, the first option is not the best. Self-control can allow humans and animals to improve resource intake under such conditions. Self-control in animals is often investigated using intertemporal choice tasks—choosing a smaller reward immediately or a larger reward after a delay. However, intertemporal choice tasks may underestimate self-control, as test subjects may not fully understand the task. Vertebrates show much greater apparent self-control in more natural foraging contexts and spatial discounting tasks than in intertemporal choice tasks. However, little is still known about self-control in invertebrates. Here, we investigate self-control in the black garden ant *Lasius niger*. We confront individual workers with a spatial discounting task, offering high-quality reward far from the nest and poor-quality reward closer to the nest. Most ants (69%) successfully ignored the closer, poorer reward in favour of the further, better one. However, when both the far and the close rewards were of the same quality, most ants (83%) chose the closer feeder, indicating that the ants were indeed exercising self-control, as opposed to a fixation on an already known food source.

1. Introduction

Self-control—the ability to choose a large delayed reward over a small immediate one—is an important feature of human behaviour [1]. A lack of self-control, also called impulsivity, is said to be a central factor in many human problems, such as failures at school, depression and criminal tendencies [2].

Research on apes, monkeys and ravens suggests that they, like humans, can show good self-control [3–5]. However, many other animal species, such as pigeons and rats, were shown to have poor self-control unless they had received extensive training before testing [6,7]. Many of these experiments were carried out using laboratory protocols which may have had little ecological meaning for the animals tested. In pigeons, for example, self-control was often examined using intertemporal choice tasks [8], in which subjects must choose between an immediate small and a larger reward later. Hayden [9] suggests that animals which were shown to behave impulsively in such intertemporal choice tasks did not understand the task of waiting for a better reward, and may have been attempting to maximize food intake per unit time [10]. To prevent animals from choosing the smaller reward in order to proceed to the next trial faster, a post-reward delay, equalizing the length of both small and large reward trials, is often added after small rewards. Nonetheless, animals may still not understand the task unaided. Pearson *et al.* [11] tested monkeys in an intertemporal choice task, adding visual cues to show the length of delays. Monkeys with access to such cues showed less impulsivity than those which had no information about delay times. These results suggest that many experiments testing self-control in animals may overestimate impulsivity [9].

Spatial discounting tasks may be a more ecologically appropriate test of self-control in animals. Here, an animal must choose between a small reward nearby and a larger reward further away [12]. For example, Cheng *et al.* [13] trained honeybees to find a small reward (10 μl syrup) at the entrance of a box and a larger (ad libitum) reward 15 cm further away. After extensive

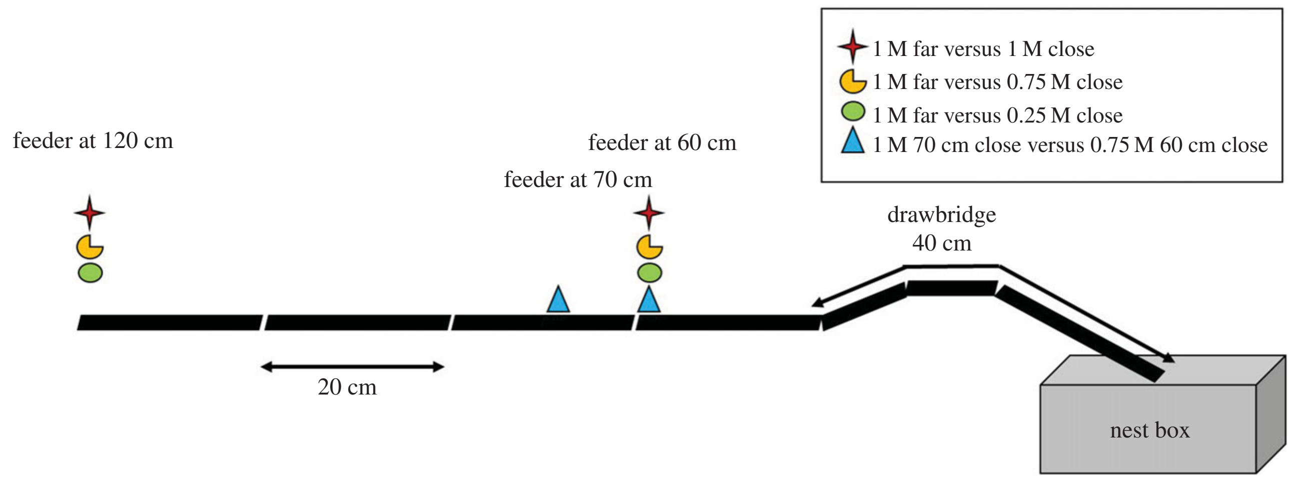

Figure 1. Experimental set-up for the four possible treatments. Each unbroken segment is 20 cm long and covered with paper stripes, which can be replaced with pheromone-free paper stripes. The sucrose droplets were located at 120 or 70 cm (1 M) and 60 cm (1, 0.75 or 0.25 M) from the nest, depending on treatment. (Online version in colour.)

training on both feeders, the bees were offered both simultaneously. Most bees preferred the larger reward and thus showed self-control in a foraging context. A similar temporal discounting task, where bees had to wait 5 s for sweeter food, showed similar results. However, this study of self-control in invertebrates is not without drawbacks. The sample sizes were as low as five individuals for some treatments, and data were expressly excluded to emphasize self-control, making it difficult to draw firm conclusions.

Another study about self-control in insects investigated collective rather than individual behaviour [14]. *Temnothorax albipennis* colonies were induced to abandon their nest and choose a new one. Colonies were given the choice between a far good nest and a closer poor one. Ant colonies collectively chose the far, good nest in almost all trials, even when it was more than nine times further away, showing 'collective' self-control. However, because the collective behaviour of social insect groups emerges in complex ways from the task performance of individual workers [15], the behaviour of individuals cannot be inferred from behaviour of colonies. In the same species, colonies chose bad nests when tandem running was used, but predominantly chose the best option without tandem running [16]. Effects like these make a comparison of individual and colony behaviour difficult. More broadly, the average behaviour of animals is a poor representation of the behaviour of individuals [17].

Here, we investigate whether hungry *Lasius niger* foragers can ignore a food source they would normally exploit, if they are aware of a higher-quality food source elsewhere. Ant workers can learn the location of a feeder very rapidly [18] and can learn to associate neutral cues with food [19], which makes it easy to conduct spatial discounting experiments without excessive training.

2. Material and methods

(a) General methods

An ant foraged at a feeder (1 M sucrose) located either at the end of a 120 cm runway or at 70 cm distance from the nest (figure 1). After the ants' return from its first (training) visit, but before its second (testing) visit, an additional, closer sucrose droplet of varying molarity (1, 0.75 or 0.25 M depending on treatment) was introduced at 60 cm from the nest. We then observed whether the ant drank at the near feeder (scored 0), the original feeder (scored 1) or at both feeders (scored 0.5) during the testing visit.

(b) Treatments

We conducted four main treatments, which varied in the location of the first feeder (1 M at 120 or 70 cm) and the molarity of the second feeder (1, 0.75 or 0.25 M at 60 cm). In the first treatment, the initial feeder (1 M) was placed at 120 cm from the nest, while the second feeder (0.25 M), which was introduced on the ants' second visit, was located at half the distance of the original feeder (60 cm). The second treatment was identical to the first treatment, except that the new feeder offered 1 M sucrose. In the third treatment, it provided 0.75 M sucrose. In treatment 4, which served as a last control treatment, the first (1 M) feeder was placed 70 cm from the nest and the second feeder (0.75 M) was placed 60 cm from the nest.

Finally, we repeated the '1 M far versus 0.25 M close' and '1 M far versus 1 M close' treatments, but allowed the ants to visit the far feeder twice before presenting the near feeder. For detailed methods, see electronic supplementary material, S1.

3. Results

During the testing visits, 69% of ants successfully rejected a close, low-quality (0.25 M) food source at 60 cm when a higher-quality (1 M) food source was available at 120 cm (figure 2, significantly different from random choice ($p = 0.02$, Fisher's exact test)). By contrast, when the food sources were of equal quality (1 M), only 10% of ants rejected the closer food source while 82% chose the close food source. However, most ants (86%) failed to reject the closer food source when it was of only marginally lower quality (0.75 M) than the 1 M food source at 120 cm. Even when the farther, better food source was only 10 cm further than the close food source, most ants (66%) failed to reject the slightly poorer, slightly closer food source. In this treatment, there were also more choices (24%) for both feeders compared with the other three treatments (electronic supplementary material, table S3 for pairwise comparisons). There were significantly more ants rejecting the closer feeder in the 1 versus 0.25 M than in the other three treatments (ordered linear regression, $Z < 7.21$, $p < 0.001$, see electronic

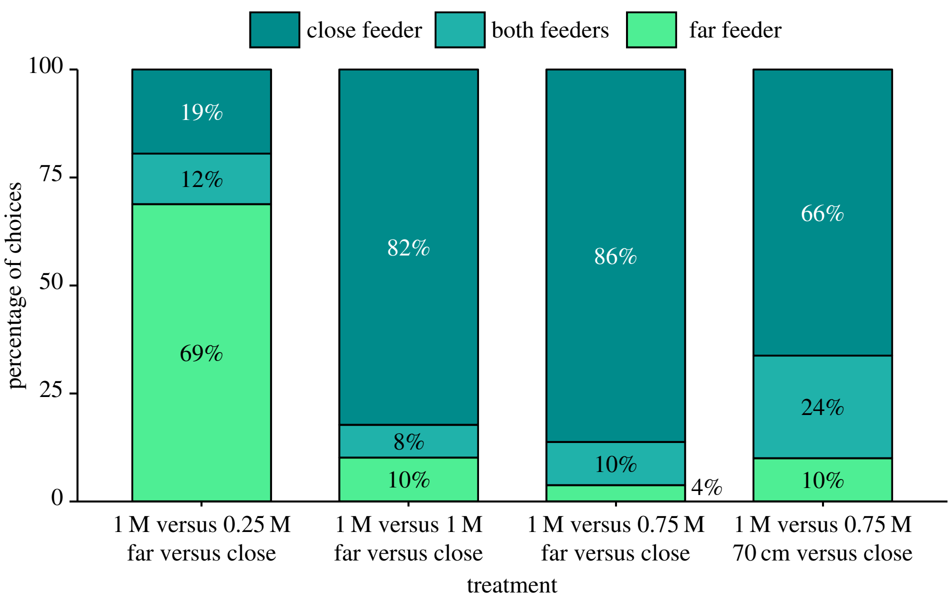

Figure 2. Proportions of decisions made for the different feeders for all treatments. The close feeder was located 60 cm from the nest, and the far-away feeder was located either 120 or 70 cm (for treatment 1 M at 70 cm versus 0.75 M) from the nest. Treatment is named as molarity of the far-away feeder versus molarity of the close feeder. Sample sizes are as follows: 1 versus 0.25 M: $n = 77$; 1 versus 1 M: $n = 79$; 1 versus 0.75 M: $n = 80$; 1 M at 70 cm versus 0.75 M: $n = 80$. Decisions in 1 versus 0.25 M significantly differed from the other treatments. Decisions in 0.75 versus 1 M close significantly differed from 0.75 versus 1 M. The other treatments were not significantly different from each other. (Online version in colour.)

supplementary material, table S1 for pairwise comparisons). Additionally, ants in the 0.75 versus 1 M at 70 cm treatment were significantly less likely to choose the closer feeder than those in the 0.75 versus 1 M treatment ($Z = -2.8$, $p < 0.01$). Finally, there was no significant difference in the proportion of choices between the 1 versus 1 M and 1 versus 0.75 M ($Z = -1.53$, $p > 0.05$) treatments, but a strong tendency between the 1 versus 1 M and 1 versus 0.75 M at 70 cm treatments ($Z = -1.96$, $p = 0.0503$).

With two training visits before testing, significantly more ants (97%) successfully rejected the poorer feeder in the 1 M far versus 0.25 M close treatment compared with ants which received only one training visit ($Z = 2.399$, $p < 0.05$; electronic supplementary material, figure S2). Ants (83%) which were confronted with 1 M far versus 1 M close chose the closer feeder when receiving two training visits. However, there is no significant difference between one and two training visits for this treatment. All data are provided in electronic supplementary material, S2 [20].

4. Discussion

Self-control is the ability to choose a large delayed reward over a small immediate [1]. Here, we showed that individual *L. niger* workers can avoid consuming a low-quality reward earlier in order to exploit a known higher-quality food source later, but can successfully choose a closer food source if its quality is identical to the farther food source. This demonstrates that individual ants exhibit good self-control. Trophallactic interactions in the nest inform ants about food in the environment [21]. Such self-control abilities might allow foragers to concentrate their foraging only on above-average resources.

Ants failed to reject slightly poorer food even if the higher-quality food source was very close. This strongly suggests that the foragers could not tell these food sources apart. This may be due to an inability to sense the molarity difference, a failure in distinguishing both food sources as different locations or, because they only made one visit to the good food source, due to a poor representation of the good food source in their memory. However, because there were more mixed choices when the food sources were close to each other, this may also be an explicit, rational choice for both feeders: the ants may have noticed a difference in quality or distance and attempted to maximize food intake per time, or exploit both food sources.

It seems counterintuitive that individual ants should show good self-control, while many vertebrates have been found to be impulsive. However, the conclusion of impulsivity from many vertebrate studies based on intertemporal choice may be spurious. Vertebrates show a higher degree of self-control when tested in more natural foraging contexts [22].

Most animals try to maximize the food intake per unit time. For this reason, it may be misleading to describe animals as impulsive when they do not show self-control in an intertemporal choice task. Self-control experiments in animals should be performed with regard to the ecology of the studied animals. In unstable environments or environments which suffer from high predation risks, it may be advantageous to show impulsivity. Animals exploiting predictable environments may show good self-control. By testing ants in an ecologically sensible spatial discounting test, we demonstrated impressive self-control abilities in individual ant workers.

Ethics. All animal treatment guidelines applicable to ants under German law have been followed.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material and are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.5181v [20].

Author contributions. S.W. performed the experiments and analysed the data. T.J.C. designed and coordinated the study. S.W. and T.J.C. wrote the manuscript and interpreted the data. All authors gave final approval for publication and agree to be held accountable for the content therein.

Competing interests. The authors declare no competing interests.

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