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Animal behaviour

# Tasting the unexpected: disconfirmation of expectations leads to lower perceived food value in an invertebrate

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To make sensible decisions, both humans and other animals must compare the available options against a reference point—either other options or previous experience. Options of higher quality than the reference are considered good value. However, many perceptible attributes of options are value-neutral, such as flower scent. Nonetheless, such value-neutral differences may be part of an expectation. Can a mismatch between the expectation and experience of value-neutral attributes affect perceived value? Consumer psychology theory and results suggest it can. To test this in a non-human animal, we manipulated a value-neutral aspect of a food source—its taste—while keeping its absolute value—its sweetness—the same. Individual ants (*Lasius niger*) were allowed to drink either lemon- or rosemary-flavoured 1 M sucrose. After three successive visits to the food, we switched the taste in the last, fourth, visit to induce a disconfirmation of expectations. In control trials, ants received the same taste on all four visits. Disconfirmed ants showed lower food acceptance and laid less pheromone on the way back to the nest, even though the molarity of the food was unchanged. As ants recruit nest-mates via pheromone depositions, fewer depositions indicate that the ants valued the food less. Thus, an expectation of value-neutral attributes can influence the perceived value of a resource. Such influences of value-neutral variables on value perception may affect how animals interact with and exploit their environment, and may contribute to phenomena such as flower constancy.

## 1. Introduction

Making decisions can be a complex and difficult task. In the process, humans and other animals often compare the available options against each other [1,2] or against some previous experience [3]. Discrepancies between a reference point and the chosen option can influence and alter behaviour, especially if the decision turns into a loss [1,2,4]. The influence of previous experience on responses to a newly presented stimulus can be reliably demonstrated by negative successive contrast effects: after receiving a poorer reward than previously, many animals, including insects, decrease their performance or food acceptance [3,5].

In theory, contrast effects are a means to up- or downregulate responses to a changing environment or novel situations to increase foraging efficiency [6]. However, unlike negative contrasts, evidence for positive successive contrasts (increase in performance) is inconsistent at best [7]. This asymmetry in losses and gains is in accordance with prospect theory [1,2], which describes decision under risk in humans. It proposes a reference point, relative to which losses or gains are assessed. Importantly, perceived value is more negatively affected by losses than it is positively affected by gains [1,2,4]. Crucially, both prospect

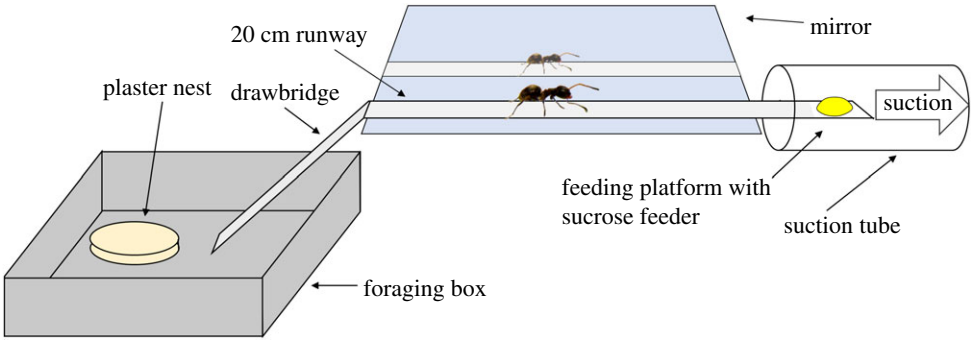


**Figure 1.** Experimental set-up. The ants entered the plastic runway via a movable drawbridge. A flavoured sugar droplet was presented inside a tube with air suction at the end of the runway. Pheromone depositions were counted on the 20 cm runway. Each time the ant passed the runway, the paper overlay was replaced. (Online version in colour.)

theory and successive contrasts do not address situations in which a value-neutral quality of the incentive is altered, for instance when the taste—but not the molarity—of a sucrose solution changes.

Such an effect has been reported in consumer psychology studies investigating effects of expectations on food perception [8]. When expectations and actual quality of a certain food quality (e.g. its taste) diverge, the caused disconfirmation of expectation can affect perception and hedonic ratings of the food. Such an expectancy effect was shown in a classic study [9], where people who expected a sweet drink but got a bitter one rated the drink as being more bitter and thus less pleasant (or less sweet when they expected a bitter drink) than subjects with confirmed expectations, so expectations alone affected perception.

Intriguingly, indications that food scent alone can influence value perception in invertebrates were reported by Lindauer 70 years ago [10]. By using the number of waggle dances of honeybees as proxy for perceived food attractiveness, he found that adding a scent to a previously unscented food source led to an initial decrease in waggle dances compared to a control group, but then rose to be higher than the control group after extended foraging.

In our study, we specifically test whether invertebrate value perception is distorted by disconfirmed expectations. Instead of a downshift in sucrose solutions, which directly affects energetic gain, we manipulate taste—a value-neutral attribute in respect of energy content.

## 2. Methods overview

For a detailed description of experimental and statistical methods, see electronic supplementary material, document ESM1.

In brief, an ant was allowed to make three return visits to a drop of 1 M sucrose solution at the end of a runway (figure 1). The drop was flavoured with either lemon or rosemary, odours which were equally attractive to the ants in a pilot study (see electronic supplementary material, table S1). On the fourth visit, we presented either the same flavour as before (confirmation) or the opposite flavour (disconfirmation). On all visits, we scored food acceptance (1, full acceptance; 0, partial acceptance or rejection) and pheromone deposition on the 20 cm runway from the food to the nest. Ants deposit more pheromone for higher quality (= sweeter) food sources [11]. Thus, the intensity of pheromone deposition reflects perceived value. Using innate behaviours such as acceptance or pheromone deposition provides feedback without the need for pretraining [12]. Data were analysed using generalized linear mixed-effect models (GLMMs) [13]. In total, 327 ants from eight colonies were analysed (electronic supplementary material, table S2). All scoring was performed blind to treatment.

## 3. Results

We found that disconfirmed ants showed significantly lower food acceptance than ants which found the expected taste (binomial GLMM, $z = -4.124$, $p < 0.0001$; figure 2*a*). Likewise, disconfirmed ants deposited significantly less pheromone when returning to the nest than ants which encountered the expected food taste (quasi-Poisson GLMM, $t = -3.102$, $p < 0.0026$; figure 2*b*).

Comparing the final and initial visits, we found a significantly lower food acceptance on the final visit in both confirmation and disconfirmation treatments ($z = -5.118$, $p < 0.001$, and $z = -5.171$, $p < 0.0001$, respectively). This was caused by an overall drop in food acceptance after the initial visit. Nonetheless, disconfirmed ants showed another significant drop in food acceptance on the fourth visit (see above, electronic supplementary material, figure S1). However, disconfirmed ants showed no significant difference in pheromone depositions between the first and fourth visit ($t = -1.684$, $p = 0.0942$), while confirmed ants deposited significantly more pheromone on the fourth visit ($t = 4.648$, $p > 0.0001$; electronic supplementary material, figure S4*b*).

No significant differences were found between tastes, nor was the interaction between treatment and food taste significant (electronic supplementary material, S1, figures S5 and S6).

## 4. Discussion

Our results demonstrate a negative effect of disconfirmed expectations on value perception in invertebrates, which has only been fully demonstrated in humans so far [8,9]. Although it has been reported that the addition of scent to sucrose can affect the number of waggle dances in honeybees (a proxy for food value), that study only compared dances between unscented and scented food [10] and the reported results might be mediated by scent preferences, or simply the presence versus absence of a scent. In our study,

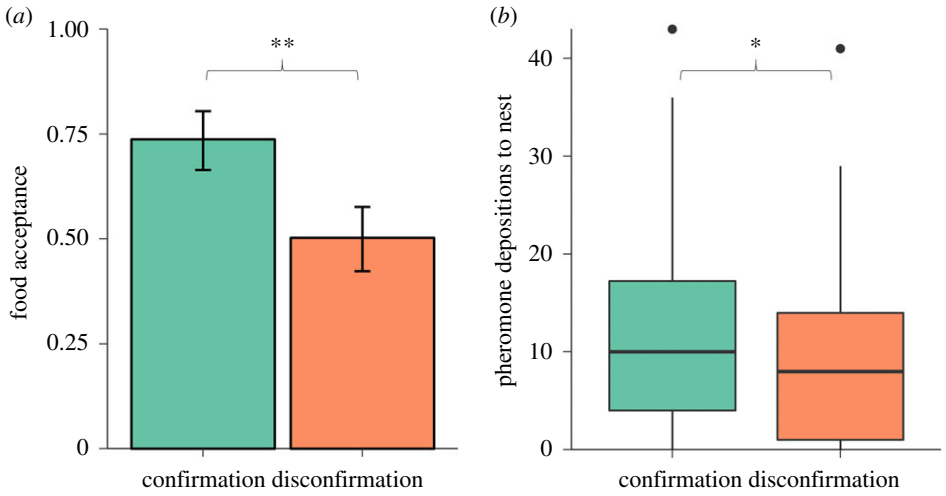


**Figure 2.** (*a*) Food acceptance scores (1, full acceptance; 0, interrupted drinking) on the fourth visit. (*b*) Pheromone depositions to the nest on the fourth visit. Bars depict means, error bars 95% confidence intervals. Horizontal lines are medians, boxes correspond to first and third quartile and whiskers extend to the largest value within 1.5 × inter-quartile range (IQR). Dots represent values outside of the IQR. Confirmation: $n = 164$, disconfirmation: $n = 163$; $*p < 0.01$, $**p < 0.001$. (Online version in colour.)

ants perceived the food as less valuable, even restricting recruitment in spite of food deprivation. Our results resemble results obtained in negative contrast experiments [3,14], even though we did not manipulate the energetic content of the food. Consequently, in energetic terms, the ants reacted irrationally.

Contrast effects are thought to be beneficial for adaptive behaviour in changing environments. Theory suggests that it is beneficial to react to varying food value by up- or down-regulating effort in the face of changing environmental quality [6]. Optimal foraging theories do not offer a viable explanation for the effects of value-neutral attributes on value perception. However, the effect of value-neutral stimuli can be explained in the context of basic learning theory [15], as a cue associated with a reward can gain its own value. In our case, the ants learned the taste to be part of the reward, so taste gained predictive power. When the taste cue was missing, the ants may have experienced this as a loss. Thus, they may have attributed value to a formerly value-neutral quality.

Our findings may offer insights to flower constancy, the tendency to forage on just one type of flower at a given time, often displayed by bees and other pollinators [16]. While this might lead to optimization processes, as each animal learns to handle flowers faster [17], the proximate driver might be that flowers with a different appearance (colour, shape) could be neglected because they are perceived as less valuable. Likewise, ants are known to associate odours with food or other stimuli and to form olfactory memories [18–20]. Associations of food qualities and other cues could thus facilitate site fidelity, a behaviour often described in ants exploiting semi-permanent food sources like honeydew [21].

Attributes of food, like taste, can represent important information about the food location. If route memory and food attributes mismatch, an ant might have made a navigational error. Social insects gather information about the food source via trophallaxis [5,22–24]. The decrease in recruitment in disconfirmed ants may be due to the ant's uncertainty about its location. The reduction in recruitment may thus be ecologically rational.

An alternative explanation of our finding would be that the ants simply 'reset' upon discovery of the unexpected food source and behave as if they encountered an unknown food. Despite a decline, disconfirmed ants show similar deposition rates after manipulation to those in the initial visit (electronic supplementary material, figure S4*b*). However, a 'reset' cannot explain the lower food acceptance on the final, manipulated, visit compared to the first visit (electronic supplementary material, figure S4*a*). Another possibility is that ants exhibit neophobia to new tastes. However, the significantly higher food acceptance in the initial visit suggests that it is not the 'newness', but rather the 'unexpectedness' which is driving the observed behaviour. Nonetheless, neophobia effects could be counteracted by high motivation stemming from starvation, which is indicated by the drop in acceptance after the first visit (electronic supplementary material, figure S1), and thus neophobia as a proximate mechanism cannot be ruled out. Interestingly, neophobia could also well explain similar results in human experiments [25].

Our results show that the foraging behaviour of insects is not only mediated by rational energetic decisions, but also encompasses value-neutral expectations about the food source. Ants, like humans, devalue things with unexpected attributes. The use of pheromone depositions and drinking acceptance as proxies for value perception provides valuable insights how invertebrates perceive value.

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

Data accessibility. Raw data and a data handling protocol containing all data analysis can be accessed as electronic supplementary material.

Authors' contributions. T.J.C. conceived the experiment, F.B.O. collected and analysed the data, F.B.O. and T.J.C. wrote the manuscript. Both authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. The authors declare no competing interests.

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