

Journal of Comparative Psychology

Greater Effort Increases Perceived Value in an Invertebrate

Tomer J. Czaczkes, Birgit Brandstetter, Isabella di Stefano, and Jürgen Heinze

Online First Publication, March 5, 2018. <http://dx.doi.org/10.1037/com0000109>

CITATION

Czaczkes, T. J., Brandstetter, B., di Stefano, I., & Heinze, J. (2018, March 5). Greater Effort Increases Perceived Value in an Invertebrate. *Journal of Comparative Psychology*. Advance online publication. <http://dx.doi.org/10.1037/com0000109>

Greater Effort Increases Perceived Value in an Invertebrate

Tomer J. Czaczkes and Birgit Brandstetter
Universität Regensburg

Isabella di Stefano
Universität Regensburg and University of Sussex

Jürgen Heinze
Universität Regensburg

Expending effort is generally considered to be undesirable. However, both humans and vertebrates will work for a reward they could also get for free. Moreover, cues associated with high-effort rewards are preferred to low-effort associated cues. Many explanations for these counterintuitive findings have been suggested, including cognitive dissonance (self-justification) or a greater contrast in state (e.g., energy or frustration level) before and after an effort-linked reward. Here, we test whether effort expenditure also increases perceived value in ants, using both classical cue-association methods and pheromone deposition, which correlates with perceived value. In 2 separate experimental setups, we show that pheromone deposition is higher toward the reward that requires more effort: 47% more pheromone deposition was performed for rewards reached via a vertical runway (high effort) compared with ones reached via a horizontal runway (low effort), and deposition rates were 28% higher on rough (high effort) versus smooth (low effort) runways. Using traditional cue-association methods, 63% of ants trained on different surface roughness, and 70% of ants trained on different runway elevations, preferred the high-effort related cues on a Y maze. Finally, pheromone deposition to feeders requiring memorization of one path bifurcation was up to 29% higher than to an identical feeder requiring no learning. Our results suggest that effort affects value perception in ants. This effect may stem from a cognitive process, which monitors the change in a generalized hedonic state before and after reward.

Keywords: within-trial contrast, state-dependent learning, cognitive dissonance, effort justification, pheromone deposition

Supplemental materials: <http://dx.doi.org/10.1037/com0000109.supp>

Traditional economic and evolutionary ecology theories assume that work or effort is something negative, which should be minimized. However, behavioral economists have demonstrated regular deviations by humans from economically rational behavior: Resources are plowed into loss-making ventures due to the resources already invested in them (the sunk cost or Concorde fallacy; Arkes & Blumer, 1985). You might watch an outdoor football game when it is raining, as you have already paid for the ticket, but had the game been free, you would not have gone. People will also work for a reward even if it is offered for free, a phenomenon known as contrafreeloading. They will press a bar for

a treat even when a bowl of free treats is placed beside them (Singh & Query, 1971; Tarte, 1981). People place higher value on gains they had to work hard or use their skills for than on rewards gained with little or no effort (Hernandez-Lallemand et al., 2014; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). They thus enjoy such gains more and feel the subsequent loss of such gains more sharply (Hernandez-Lallemand et al., 2014).

Much as in economic theory, traditional theories of foraging behavior have assumed that animals attempt to maximize efficiency by minimizing effort (Charnov, 1976; Stephens & Krebs, 1986). However, several animals, overwhelmingly vertebrates,

Tomer J. Czaczkes and Birgit Brandstetter, Animal Comparative Economics Laboratory, Institute of Zoology, Universität Regensburg; Isabella di Stefano, Animal Comparative Economics Laboratory, Institute of Zoology, Universität Regensburg, and Department of Evolution, Behaviour and Ecology, School of Life Sciences, University of Sussex; Jürgen Heinze, Chair of Zoology and Evolutionary Biology, Institute of Zoology, Universität Regensburg.

Tomer J. Czaczkes conceived and designed the study, analyzed the results, and wrote the article. Birgit Brandstetter collected the data for Experiments 1 and 3. Isabella di Stefano collected the data for Experiment 2. Jürgen Heinze improved the article and suggested the necessity for S1

(online supplemental materials). All authors gave final approval for publication.

Tomer J. Czaczkes was supported by a DFG Emmy Noether group leader grant (grant number CZ 237/1-1). We thank Alex Kacelnik, Thomas Zentall, and Katja Rex for helpful comments on previous versions of this article. Thanks to Stephanie Wendt and Felix Oberhauser for collecting the data presented in the S1 (online supplemental materials).

Correspondence concerning this article should be addressed to Tomer J. Czaczkes, Animal Comparative Economics Laboratory, Institute of Zoology, Universität Regensburg, Universitätsstrasse 31, 93053 Regensburg, Germany. E-mail: tomer.czaczkes@ur.de

have also been found to display contrafreeloading (starlings: Bean, Mason, & Bateson, 1999; rats: Jensen, Leung, & Hess, 1970; macaques: Ogura, 2011; pigeons: Podlesnik & Jimenez-Gomez, 2016), overvalue effort-related rewards (starlings: Aw, Vasconcelos, & Kacelnik, 2011; pigeons: Clement, Feltus, Kaiser, & Zentall, 2000; mice: Johnson & Gallagher, 2011; starlings: Kacelnik & Marsh, 2002; mice: Lydall, Gilmour, & Dwyer, 2010; locusts: Pompilio, Kacelnik, & Behmer, 2006; Zentall, 2015), and arguably make sunk cost errors (for a review, Magalhães & Geoffrey White, 2016). Strangely, the addition of mildly unpleasant stimuli, such as a lack of reward where one was expected, can also increase preference for an option under some circumstances (pigeons: Friedrich, Clement, & Zentall, 2005; Zentall, 2013).

The reason why effort, and negative stimuli, can increase the perceived value of a resource is debated, with the explanation often depending on the background of the researcher. Economists might explain sunk cost effects in terms of loss aversion and the desire to avoid wastefulness (Arkes & Blumer, 1985; Kahneman & Tversky, 1979; Thaler, 2004). Cognitive psychologists have attempted to explain why effort increases perceived value using effort justification and cognitive dissonance theory, wherein the unpleasant dissonance between high effort and low gains is reduced by artificially inflating perceived gains (Festinger, 1962). Many comparative psychologists and ethologists claim that these effort/value effects are a result of within-trial contrast (WTC) or relative changes in state (state-dependent valuation learning).¹ Here, the magnitude of contrast in the state of an animal (energetic or hedonic, i.e., pleasure level) before and after receiving a reward affects the perception of the magnitude of the reward (Aw et al., 2011; Kacelnik & Marsh, 2002; Pompilio et al., 2006; Zentall, 2010). For example, starlings that had to fly for 16 m to receive food might be hungrier than starlings that had to fly 4 m to get the same food and, thus, might value the food received after 16 m more (Kacelnik & Marsh, 2002). As it is reasonable to expect diminishing returns in hedonic state as energy levels are increased, fixed energy gains received at different levels of energy reserves are expected to result in different hedonic gains (Aw et al., 2011; Pompilio et al., 2006). A clear and concise visual explanation of WTC effects is provided by Pompilio et al. (2006, Figure 1). Other behavioral ecologists have explained such findings in animals by describing the beneficial effects such distorted perception would have, either in terms of increased motivation to forage in lean environments (Johnson & Gallagher, 2011) or as a mechanism for increased information acquisition (Bean et al., 1999; Inglis & Ferguson, 1986; Inglis, Forkman, & Lazarus, 1997). The various effects in which effort distorts value perception are also occasionally explained using separate models. For example, contrafreeloading has been argued to arise due to behavioral momentum, where animals trained to do something simply continue doing so, even when other options become available (Podlesnik & Jimenez-Gomez, 2016).

The different models and explanations of effort/value effects aim to understand different explanatory levels (proximate or ultimate), and many of the arguments are not mutually exclusive. However, explanations such as mental accounting and cognitive dissonance seem to postulate advanced cognitive faculties. Demonstrations of contrafreeloading and of effort altering perceived value cover a range of taxa, including humans (adults and children), apes, monkeys, rats, and fish (see Inglis et al., 1997 for

references). Although most demonstrations of effort distorting value perception rely on physical effort, it has been demonstrated in humans that cognitive effort also affects value perception (Hernandez-Lallement et al., 2014). Rats have also been shown, in some situations, to contrafreeload by solving puzzles when free food is available or to take the longer route to a food source (Jensen et al., 1970; Snygg, 1935).

The reasons for showing effort-related value judgments may not be the same for humans and different taxa, especially invertebrates. Although state-dependent value learning has been demonstrated in an insect (Pompilio et al., 2006), to date, there exists no demonstration of effort distorting value perception in an invertebrate. Such demonstrations would be needed to convincingly argue that such effort/value effects occur over a broad range of taxa and to understand how conserved such behavioral “irrationalities” are.

Another limitation of many studies on effort preference in animals is the reliance on linking effort to a neutral conditional stimulus and then testing preference for the stimulus (Clement et al., 2000; Kacelnik & Marsh, 2002; Pompilio et al., 2006). This does not allow conclusions to be drawn about the effect of effort on the hedonic response to a reward, but rather to the cue associated with the reward (Lydall et al., 2010). On the other hand, such methods do provide more biologically relevant data, as they act in the context of naturally co-occurring effects, such as novelty reduction and (outside social insects) satiation. Only recently have studies in mice used untrained behaviors to demonstrate that effort is likely to be increasing the hedonic value of feeding (Johnson & Gallagher, 2011; Lydall et al., 2010, but see Meindl, 2012).

Here, we address several of these issues by investigating effort preference in foraging ants. Many ants, including our study organism *Lasius niger*, deposit pheromone trails to recruit nestmates to valuable resources (Czaczkes, Grüter, & Ratnieks, 2015). The stronger the pheromone trail, the more ants follow it, and, thus, the more resources the colony will invest in exploiting the food to which the trail leads (Hangartner, 1969; von Thienen, Metzler, Choe, & Witte, 2014; Wilson; The Organization of Mass-Foraging, 1962). When recruiting to sugar solutions, *L. niger* workers deposit more pheromone to higher-quality food (Beckers, Deneubourg, & Goss, 1993), as in many other ants (see Detrain, Deneubourg, & Pasteels, 1999, and references therein). However, pheromone deposition in *L. niger* is not fixed absolutely to the quality of the reward. Rather, it is relative to the expectations of the individual forager. For example, foragers that are trained to a high-quality food source but are presented with a medium-quality food source deposit less pheromone than foragers trained to a low-quality food source that then receive the same medium-quality food source (Wendt & Czaczkes, *in preparation*—for preliminary pilot data, see <https://www.animal-economics.com/value-perception>). Thus, pheromone deposition represents an ant’s individual assessment of the value of a resource. As the ants in a colony do not compete over

¹ Within-trial contrast (WTC) and state-dependent learning (SDL) are often portrayed as competing theories (Aw et al., 2011; Meindl, 2012), with WTC focusing on hedonic state and SDL focusing on energetic levels. However, SDL does not explicitly focus on energetic levels, but rather suggests that energetic levels may affect a hedonic state (Aw et al., 2011). It is becoming clear that SDL and WTC are describing the same thing in different words (T. Zentall, personal communication). For simplicity, I will refer to both these models as WTC here.

food, such recruitment communication is expected to be honest. Thus, it is in each worker's best interest to modulate its pheromone deposition in accordance with the perceived value of the resource. By quantifying pheromone deposition rates to a resource, the perceived value of the resource can be ascertained. We use the pheromone deposition paradigm to test whether individual foragers perceive food that requires more physical effort to collect as more valuable. By linking the effort requirements of the food to odor cues, we confirm the preference for cues related to high-physical-effort food. We then present evidence that ants deposit more pheromone for food sources requiring the memorization of a turn at a bifurcation.

Materials and Method

Study Species and Maintenance

We used eight queenless colony fragments of the black garden ant, *L. niger* (Linnaeus), collected from eight different colonies on the University of Regensburg campus. Colonies were housed in a plastic box (40 × 30 × 20 cm) with a layer of plaster on the bottom. Each box contained a circular plaster nest (14 cm in diameter, 2 cm in height). Colonies contained ~1,000 workers and small amounts of brood and were maintained at ambient temperature (21–25°) and humidity (45–55%) on a 12:12 light:dark cycle. Ants from queenless colonies forage, deposit pheromone, and learn normally. As the ants are foraging for carbohydrates in this experiment, the presence of brood or lack of a queen should have

little influence on the ants' behavior. The ants were fed ad libitum three times per week the Bhatkar diet, a mixture of egg, agar, honey, and vitamins (Bhatkar & Whitcomb, 1970), and supplemented with *Drosophila melanogaster* fruit flies. Colonies were deprived of food for 4 days before each trial to give high and consistent motivation for foraging and pheromone deposition. Water was provided ad libitum.

Experiment 1—The Effect of Physical Effort 1: Foraging on Vertical or Horizontal Runways

The aim of this experiment was to examine whether the difference in physical effort required to forage at the end of a horizontal or vertical runway changed the perceived value of a food source. This was achieved by allowing a forager to alternately find food of identical quality but different odor at the end of a horizontal or vertical runway. Perceived value was quantified using the pheromone deposition paradigm and attraction to visual and olfactory cues associated with each effort treatment.

A single forager was allowed to enter a moveable drawbridge attached to a fixed 10-cm-long, 1-cm-wide platform held at 45°. The fixed platform was connected to a 40-cm-long, 1-cm-wide runway held either vertically or horizontally (Figure 1B). Running both up and down vertically is more energy consuming per unit distance for insects than running horizontally (Full & Tullis, 1990; Holt & Askew, 2012; Lipp, Wolf, & Lehmann, 2005), and this effect is exacerbated by carrying a load. A small acetate plate

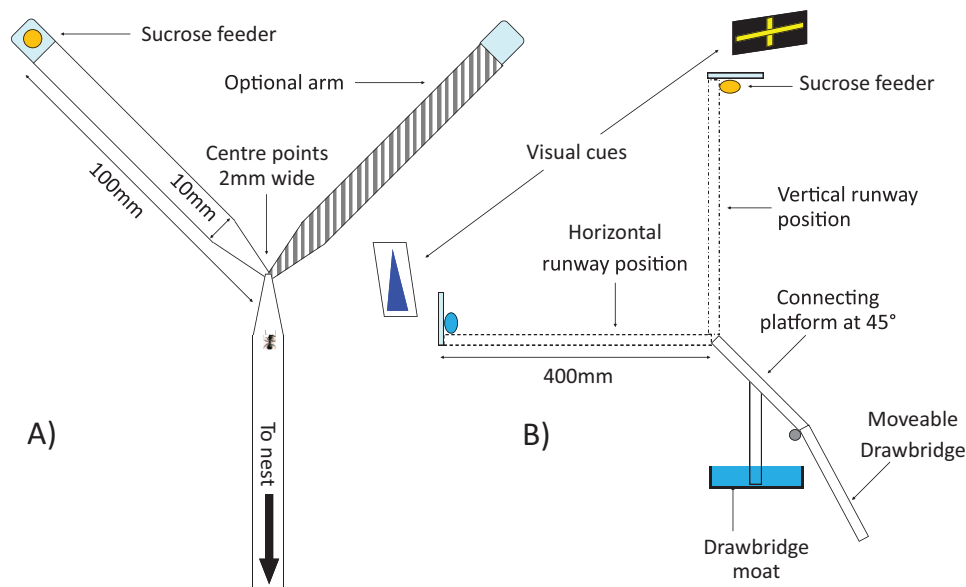


Figure 1. (A) The Y or L, used in Experiment 3. The Y maze design was also used as a choice assay in Experiments 1 and 2. The striped arm (on the right) was either present to form a Y maze or absent to form an L maze. The narrowed junction ensures the ant senses whether a path choice is available. (B) The physical effort runway used in Experiment 1. Runway position could be horizontal (low effort, dashed lines) or vertical (high effort, dot-dashed lines). Feeders offered colored 1 M sucrose. Yellow sucrose was scented with lemon and reached via a lemon-scented runway. Blue sucrose was scented with rosemary and reached via a rosemary-scented runway. The setup used for Experiment 2 was identical to the horizontal runway setup used in Experiment 1, except that in the rough surface treatment, the runway was replaced by an identically sized length of felt and no visual cues or odor cues on the path were provided. See the online article for the color version of this figure.

perpendicular to the runway acted as a feeder, with drops of 1 M sucrose attached to them by adhesion. The droplets of sucrose were scented with 12 μL essential oil (lemon or rosemary) per 250 mL. A supplementary experiment showed no difference in pheromone deposition to sucrose solution scented with these two scents (see S2 in the online supplemental materials). The sucrose was also colored with food coloring (blue or yellow; blue: Brilliant blue FCF, E133, 9.26% pure color, 3.6% aluminum, yellow: Tartrazine, E102, 11.70% pure color, 2.5% aluminum, carrying agent sulfate/chloride; RBV Birkmann GmbH & Co, Halle, Westfalen). Lemon-scented sucrose was always colored yellow, and rosemary-scented sucrose blue. Behind and above the plane of the runway, a prominent colored visual cue was displayed (either black and yellow or blue and white; Figure 1B). The black/yellow visual cue was always associated with the yellow lemon-scented sucrose, and the blue/white visual cue was always associated with the blue rosemary-scented sucrose. Finally, the paper overlays covering the runway were also scented, by storing them for 24 hr in a sealed box in which a large ($\sim 10 \mu\text{L}$) drop of essential oils was left uncovered on a petri dish. The scent of the runway corresponded to the scent of the sucrose associated with the vertical or horizontal treatment. We provided multiple cues in two modalities to increase the speed of acquisition and strength of association between the cues and the effort treatment (Calvert, Spence, & Stein, 2004). The cue combination associated with each effort treatment was varied systematically, so that yellow/lemon was associated with the vertical runway in half the trials and with the horizontal runway in the other half. The sugar drop allowed ad libitum feeding, as pheromone deposition behavior is only released if the forager manages to sufficiently fill its crop (Maillieux, Deneubourg, & Detrain, 2000). *Lasius niger* are sensitive to sucrose, with 1 M sucrose allowing very high energy intakes and, thus, representing a very-high-quality food source (Detrain & Prieur, 2014). When the ant located the drop and began to drink it, the ant was marked with a dot of acrylic paint on the abdomen (see Video S1 in the online supplemental materials). When satiated, the ant returned to the nest and all pheromone deposition behaviors performed on the runway were counted. Pheromone deposition in *L. niger* is a highly stereotyped behavior (Beckers, Deneubourg, & Goss, 1992) and easily quantified by eye. The ant was allowed to return to the nest to unload its sucrose load (see Video S2 in the online supplemental materials or a 7-s video on <https://www.youtube.com/watch?v=lxgw74SizFY>).

In half the trials, the vertical runway was presented first, and in the other half, the horizontal runway was first, according to a pseudorandom schedule. While the ant was in the nest, the runway was replaced with the other effort treatment, and the ant then was allowed to return. This proceeded until the ant had made three visits on a horizontal runway and three on a vertical runway. Pheromone deposition was recorded for all visits for both the outward and the return journey, except for the first outward journey before the ant encountered food, as *L. niger* workers rarely or never deposit pheromone before feeding (personal observation). Travel time in 11 of the 48 ants was recorded on Visits 3–6 for both the outward and the return journey. Travel time was not recorded on Visits 1 and 2, as in these visits, the ant either was not aware that food was present (Visit 1) or had no experience with the current runway setup (Visit 2).

After performing six training visits, the drawbridge was disengaged from the runways, while the ant was in the nest, and connected to a horizontal Y maze, as used in Experiment 3 (see Figure 1A for scales). One arm of the runway was scented with the high-effort odor cue and presented the high-effort visual cue at the end. The other arm presented the low-effort cues. The ant was allowed onto the Y maze, and the arm chosen by the ant, as defined by crossing a line 2 cm from the junction, was noted.

As binomial data from Y mazes can be statistically weak due to low information density, we also attempted to test preference using a second assay. After testing in the Y maze, the ant was allowed to walk onto a piece of paper and placed in a static four-field olfactometer (17 cm in diameter, 1 cm in depth; see Ruther & Steidle, 2000, for details). A 3-mm filter paper disk soaked in each essential oil was presented below opposite fields in the olfactometer, separated by two control fields. The associated visual cues were presented behind and above the back wall of the appropriate olfactometer field and were visible from within the olfactometer. A clear plastic lid was put in place and the movement of the ant video recorded for 210 s. The proportion of time spent by the ant in each field was manually recorded using CowLog 3.0.2, Helsinki (Pastell, 2016). After testing, the ant was discarded to avoid pseudoreplication.

Experiment 2—The Effect of Physical Effort 2: Foraging Over Rough or Smooth Runways

The results of Experiment 1 were promising, but there were some methodological issues with that experiment. First, ants have an innate preference for climbing uphill (see S2 in the online supplemental materials for an experimental demonstration). Second, as cues (odor and visual) were available to the ants while on the runway, and as ants traveled slower on the vertical runways, they were exposed to the high-effort cues for longer. This may have caused a preference for the high-effort cues. Third, and related to this, for technical reasons, it was not possible to replace the runway overlays between ant visits. Thus, trail pheromone built up on the runways. As our results show, ants deposited more pheromone on the vertical runways and, thus, may have associated trail pheromone (perhaps an unconditional positive stimulus) more strongly with the vertical runways. Finally, travel time data were not taken for some of the ants, making calculation of a pheromone deposition rate impossible for some of the data. As ants walk slower on vertical surfaces, a rate of pheromone deposition per second is the appropriate measure to take here.

To overcome these limitations, we ran Experiment 2. This experiment was broadly similar to Experiment 1. However, rather than using vertical and horizontal runways to affect effort, we presented ants with smooth runways covered in standard printer paper (low effort) and rough runways covered in polyester felt (density 350 g/m^2 ; high effort). Ants find it more difficult to walk on rough felt, as can be seen by them walking more slowly and deliberately (Oettler et al., 2013), but *L. niger* workers do not have an innate preference for rough or smooth substrates, and indeed do not seem to be able to use substrate coarseness as an associative cue (Bernadou & Fourcassié, 2008). This makes surface roughness ideal for our current purposes. Runways were unscented and replaced every time an ant walked over them, thus preventing pheromone build-up. However, a 1-cm-wide strip of odor-

impregnated paper was placed on the apex of the bridge before the runway. The odor of this piece of paper was the same as the one the ant would go on to find at the end of the runway. The aim of this piece of paper was not to teach the ants an odor/runway; rather, it was to get ants used to walking on scented surfaces. We offered no visual cues. Thus, the only cue the ants could associate with the runway roughness and effort was the taste of the reward at the end. Ants were allowed to make 10 repeat visits to the food source, five over a rough runway and five over a smooth runway. Travel times on Visits 6–10 were measured. Ants were then tested on a Y maze odor preference test, as in Experiment 1. To increase sample sizes, each ant was tested four times on the Y maze—after it reached the end of the Y maze, it was allowed to walk onto a piece of paper, and replaced in the nest. The sides of the Y maze presenting each odor were changed and the ant allowed onto the maze again. After making four choices, the ant was discarded.

Experiment 3—The Effect of Turn Learning on Pheromone Deposition

As cognitive effort has also been shown in some taxa to distort value perception, in this experiment, we attempted to ascertain whether having to learn a turn to successfully forage at a feeder affects an ants' pheromone deposition behavior. Ants found food either at the end of a Y maze (presumably requiring more cognitive effort) or at the end of an L maze (identical to the Y maze, but without any directional choice or learning required, presumably resulting in less cognitive effort). Pheromone deposition behaviour was tracked on both the outward and return journeys.

An individual forager was given access via a drawbridge to a maze setup as depicted in Figure 1A, consisting of two or three identical disposable paper segments 10 cm in length and 1 cm in width, narrowing to 2 mm at their tips. The segments were aligned at 120° from each other, so as to form either a Y maze if all three segments were used or a wide L maze if only two segments were used. The narrowing at the junction point ensured that workers could sense whether the junction was a bifurcation (Y maze) or a turn (L maze). Here we assume that having to learn a direction choice in a Y maze is more cognitively demanding than merely having to learn to follow a path to its end. *Lasius niger* learn to take the correct turn at a bifurcation quickly, but not immediately (Czaczkes & Heinze, 2015; Grüter, Czaczkes, & Ratnieks, 2011), implying that some cognitive effort is involved. A drop of sucrose was placed at the end of one arm of the Y maze or the end of the L maze. When satiated, the ant returned to the nest and all pheromone depositions performed on the feeder-laden arm of the maze and the stem were counted. While the ant was in the nest, the paper maze segments were replaced with fresh segments to remove any pheromone and home range markings that might have been deposited, as these can affect pheromone deposition (Czaczkes, Grüter, Ellis, Wood, & Ratnieks, 2013; Czaczkes, Grüter, Jones, & Ratnieks, 2011). The marked ant was then allowed to make another full return visit, with her pheromone deposition on the stem and arm of the maze counted on both her outward and return journey. While drinking at the feeder during the second visit, the paper segments were replaced again. After exiting the maze for the second time, the ant was permanently removed from the colony. In total, 124 ants were tested on the Y maze and 123 on the L maze. The location of the arm (L maze) and the feeder (Y maze) was

varied systematically. A video of the ant returning from feeding at the end of a Y maze is provided in Video S1 in the online supplemental materials.

Statistical Analysis

Statistical analyses were carried out in R 3.1.0 (R Core Team, 2012) using generalized linear mixed models in the LME4 package (Bates et al., 2014). Following Forstmeier and Schielzeth (2011), we included in the tested models only factors and interactions for which we had a priori reasons for including. As multiple data points for pheromone deposition were collected from each individual and multiple ants were tested per colony, ant and colony identity were added as random effects, with ant identity nested inside colony identity. Binomial data (pheromone deposited or not) were modeled using a binomial distribution and logit link function. Count data (number of pheromone depositions for ants that deposited pheromone at least once) were modeled using a Poisson distribution using a log link function. The model formulae used are presented next.

Experiment 1. To test for an effect of runway type (vertical or horizontal) on pheromone deposition, the following model formula was used:

$$\begin{aligned} &\text{Number of pheromone depositions} \\ &= \text{Runway type (vertical or horizontal)} \\ &\quad + \text{Visit number (1 - 6) + Direction (outgoing or returning)} \\ &\quad + \text{Random effects: ant nested within colony} \end{aligned}$$

To test whether ants were more likely to choose the low- or high-effort associated cues on the Y maze experiment, we analyzed ant decision data using an exact binomial test. To test whether ants spent more time in the olfactometer fields offering low- or high-effort associated cues, we analyzed the logit-transformed (Shi, Sand Hu, & Xiao, 2013; Warton & Hui, 2011) proportion of time ants spent in each field using the following formula, with a Gaussian error structure:

$$\begin{aligned} \text{Proportion of time in field} &= \text{Field ID (high-effort cues,} \\ &\quad \text{low-effort cues, control)} \\ &\quad + \text{Random effect: colony} \end{aligned}$$

Experiment 2. The analysis of pheromone deposition in Experiment 2 was in essence identical to that of Experiment 1. However, due to some heteroskedasticity, the rate of pheromone deposition was square root transformed before testing, and, due to zero inflation, we used a zero-inflated model, using the glmmADMB package (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2016).

As we tested each ant four times in the odor preference test on the Y maze, we could not use a simple binomial exact test. We also noted a side bias. We therefore we used a generalized linear mixed model using a binomial distribution family.

In this model, the intercept estimate acts as our test of whether the number of correct decisions is different from 0.5.

$$\begin{aligned} \text{Decision (correct/incorrect)} &= \text{Correct side (left or right)} \\ &\quad + \text{random effects} \\ &\quad (\text{ant nested within colony}). \end{aligned}$$

Experiment 3. To test for an effect of maze type on pheromone deposition, the following model formula was used:

Number of pheromone depositions = Maze type (Y or L maze)
 + Visit number (1 or 2) + Direction (outgoing or returning)
 + Maze part (arm or stem)
 + Random effects: ant nested within colony

We then performed post hoc pairwise comparisons between Y and L maze data for all possible combinations of the other fixed factors. Czaczkes et al. (2013) found that ants, which had made an error while outgoing that they later corrected, deposited more pheromone when returning. We, therefore, also tested for this effect on the second visit in Experiment 1. Furthermore, as Czaczkes et al. (2013) found that ants that were about to make an error decreased their pheromone deposition, we also tested explicitly for this effect. The model formula used was as follows:

Number of pheromone depositions
 = Decision on Y maze (correct/incorrect)
 + (random effect: colony)

The model was run twice, once for outgoing ants and once for returning ants. Following Simmons, Nelson, and Simonsohn (2012), we report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study—see S3 in the online supplemental materials for details.

The raw data for all experiments can be found in S1 in the online supplemental materials.

Results

Experiment 1—The Effect of Physical Effort 1: Foraging on Vertical or Horizontal Runways

Ants deposited more pheromone when running on high-effort vertical than low-effort horizontal runways ($Z = 18.25, p < .001$; Figure 2A). More pheromone was also deposited in later visits ($Z = 21.52, p < .001$) and when returning to the nest ($Z = 3.87, p < .001$). Ants also walked more slowly on vertical runways both when going outward (high effort $M = 25.3$ s, $SD = 5.7$, low effort $M = 22.9$, $SD = 7.2$) and when returning (high effort $M = 21.3$,

$SD = 4.2$, low effort $M = 18.7$, $SD = 4.1$; $Z = 2.30, p = .027$). Ants walked more slowly in later visits ($Z = -3.10, p = .0037$) and when returning to the nest ($Z = -3.85, p < .001$).

We measured walking speeds for 11 of the ants tested and pheromone deposition rates per second were calculated for the same. Ants had lower pheromone deposition rates on the low-effort horizontal runways than on the high-effort vertical runways ($Z = -3.66, p = .0051$; see Figure S3 in S2 in the online supplemental materials). This effect was stronger for ants outgoing toward the food than returning to the nest, as shown by a significant interaction ($Z = 1.98, p = .048$). Ants had lower pheromone deposition rates on their return journey to the nest ($Z = -3.28, p = .0014$).

When offered a choice between cues associated with high or low effort on a Y maze, significantly more (42/59 = 71%) ants went toward the high-effort cues (binomial test: $p = .0015$, 95% confidence interval [0.58, 0.82]). In a supplementary experiment, a slight but significant preference for vertical paths by naïve scouting ants was found (60.7%—456 out of 751 ants chose a vertical over a horizontal path, binomial test: $p < .001$; see S2 in the online supplemental materials). In the four-field olfactometer assay, there was no difference between the proportion of time ants spent in the fields with high-effort cues, low-effort cues, or no cues ($Z = 0.38, p = .93$).

Experiment 2—The Effect of Physical Effort 2: Foraging Over Rough or Smooth Runways

Ants deposited pheromone at higher rates when running on high-effort rough runways than low-effort smooth runways ($Z = 4.14, p < .001$; Figure 2B). Pheromone was deposited at a lower rate when returning to the nest than when heading toward the food source ($Z = -11.66, p < .001$). Pheromone deposition rates were not affected by the visit number ($Z = -0.56, p = .58$).

When offered a choice between cues associated with high or low effort on a Y maze, significantly more (67/107 = 63%) choices were made for the high-effort cues ($Z = 3.66, p = .00026$). We also noted a significant left bias in our results ($Z = 3.25, p = .0011$). Side biases are relatively common in ant behavior (Hunt et al., 2014).

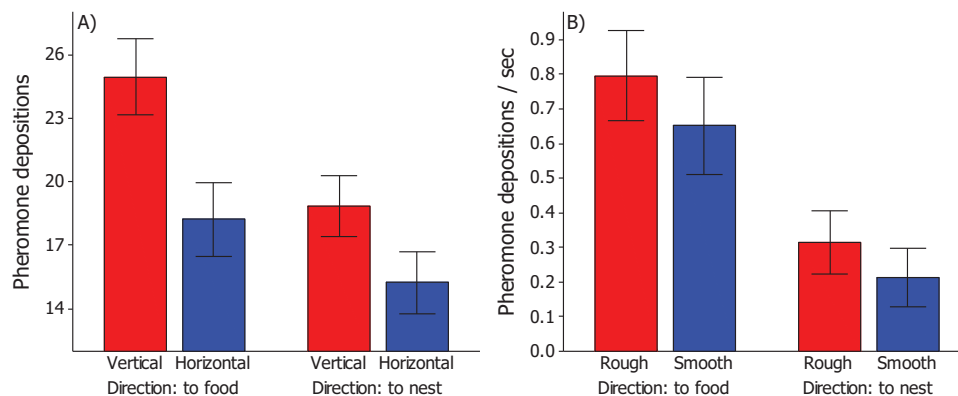


Figure 2. (A) Pheromone deposition on the high-effort vertical runway and low-effort horizontal runway. (B) Pheromone deposition rates on the high-effort rough runway and low-effort smooth runway. Error bars are 95% confidence intervals for the mean. See the online article for the color version of this figure.

Experiment 3—The Effect of Turn Learning on Pheromone Deposition

Overall, ants deposited more pheromone on the Y maze than the L maze ($Z = 4.17, p < .001$; Figure 3). As previously reported (Czaczkes et al., 2013; Czaczkes & Heinze, 2015), ants also deposited more pheromone when returning to the nest than when returning to the food source ($Z = 28.91, p < .001$) and on the second visit ($Z = 16.12, p < .001$). There was no significant difference in the amount of pheromone deposited between the arm and the stem of the mazes ($Z = 1.70, p = .11$). Note that pheromone deposition is much lower in this experiment, largely due to the much shorter distances that pheromone deposition was measured on.

Ants that made a mistake on the Y maze on their return to the feeder (Visit 2) did not deposit more pheromone on the subsequent return to the nest ($Z = 0.79, p = .43$). While the outgoing ants that were going to make a mistake did deposit less pheromone on the stem of the maze (i.e., before making a decision), this difference was not significant ($Z = -1.04, p = .30$).

Discussion

Our results demonstrate that effort increases the perceived value of a food source in an insect. Using a pheromone deposition paradigm allowed us to explore value perception without prior training. By also using a more traditional association-based method, we provide separate evidence for the value distortion by effort effect, while also supporting our claim that pheromone deposition is a good assay for quantifying value perception and preference.

In Experiments 1 and 2, higher effort caused costs both in terms of time and energy. Ants and other insects tend to maintain metabolic rates stable while traveling on slopes or vertically but reduce walking speed (Full & Tullis, 1990; Holt & Askew, 2012; Lipp et al., 2005). This results in higher metabolic costs per unit distance. The metabolic costs of running on rougher surfaces, and whether ants compensate in terms of speed, are not known. It is not clear whether it was the delay or the increased metabolic costs that caused the value perception distortions we report. Metabolic effort and differences in energetic state have been consistently shown to result in value perception distortion, but results from experiments on delay have been mixed, with some studies finding strong effects, some finding no effects, and some finding effects additive with energetic costs (Arantes & Grace, 2008; Aw et al., 2011; DiGian, Friedrich, & Zentall, 2004; Meindl, 2012; Vasconcelos, Urciuoli, & Lionello-DeNolf, 2007). However, the energetic cost of walking in at least one ant measured is insignificant compared with the energetic content of retrieved food (Gissel Nielsen, 2001). Different taxa respond to delay and effort costs differently (Stevens, Rosati, Ross, & Hauser, 2005), which may explain the inconsistent results between studies. The lack of effect in the olfactometer assay in Experiment 1 was likely due to the disturbance caused by placing the ants in the apparatus, and the fact that the assay allows less natural behavior than the undisturbed goal-directed walking in the Y maze and on the runways. When in the olfactometer, the ants seemed to be attempting to escape, rather than searching for food.

The results of Experiment 1 are suggestive of effort distorting value perception but, due to some design flaws (see Method), do not

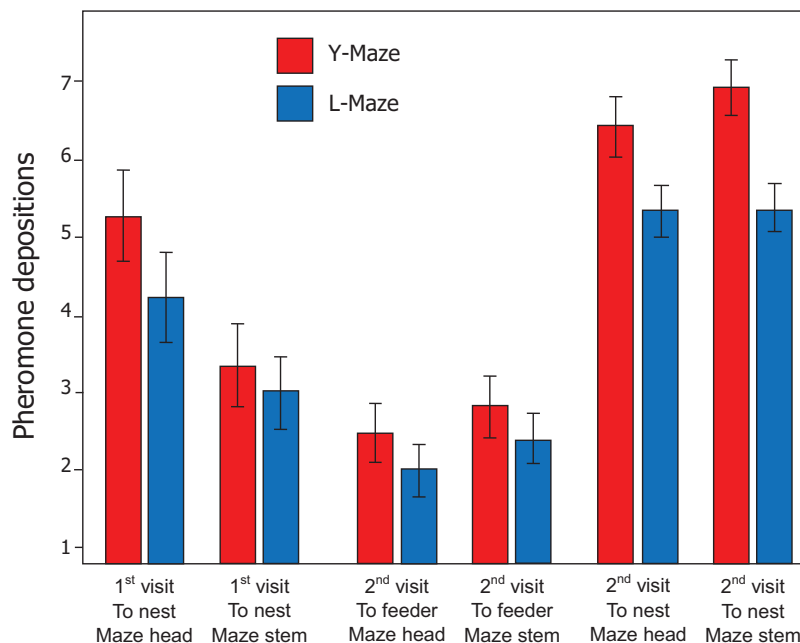


Figure 3. Pheromone deposition on the Y or L mazes. Ants deposit more pheromone on Y than L mazes. Pairwise comparisons of Y and L mazes—1st visit to nest/larm: $Z = 3.78, p < .001$; 1st visit to nest/lstem: $Z = 1.50, p = .13$; 2nd visit to feeder/larm: $Z = 2.51, p = .012$; 2nd visit to feeder/lstem: $Z = 1.94, p = .052$; 2nd visit to nest/larm: $Z = 4.95, p < .001$; 2nd visit to nest/lstem: $Z = 6.91, p < .001$. Error bars are 95% confidence intervals for the mean. See the online article for the color version of this figure.

constitute strong evidence on their own. Experiment 2 was designed to overcome these weaknesses, and succeeded. The results of Experiment 2 do constitute strong evidence of effort distorting value perception. In light of those results, we can be confident that much of the effect seen in Experiment 1 was also driven by effort, not other causes.

The results of Experiment 3 are more ambiguous and can be explained in terms of ecologically sensible behavior: It has been previously reported that ants deposit more pheromone on hard-to-learn routes, which presumably require increased cognitive effort (Czaczkes et al., 2013; Czaczkes, Weichselgartner, Bernadou, & Heinze, 2016). They may do this to help their sisters on difficult routes. Moreover, the exact nature of the costs (if any) caused by the cognitive effort treatment in our experiment is not clear. Although learning is likely to be metabolically costly (Burns, Foucaud, & Mery, 2011; Jaumann, Scudelari, & Naug, 2013), it is not clear how energetically costly learning one turn on a Y maze is. The costs of learning in this case, if any, may well be affective in nature. Thus, although we present the results of Experiments 3 as worthy of consideration in terms of value perception distortion, we refrain from making any strong claims based on those data. We hope that future studies can further explore value perception distortion due to cognitive effort in invertebrates.

The effects of physical effort and the putative effects of cognitive effort we report can be understood in terms of the WTC models (Kacelnik & Marsh, 2002; Pompilio et al., 2006; Zentall, 2010, 2013). For this to work, however, some form of hedonic state—a generalized integrator of both physical and mental states—must be postulated. Changes in this integrator can then be tracked to note contrast magnitude. Even when putting aside the results of Experiment 3, we feel that this is a reasonable assumption. Indeed, similar calls for a unified “common currency” for driving behavior have been convincingly made (Cabanac, 1992; McFarland & Sibly, 1975). Such a metric would integrate many different inputs, both internal and external, such as hunger, fear, sexual arousal, social status, and so forth. Such an integrator may well be physiological in nature (Fairclough & Houston, 2004). A unified integrator also resolves the apparent conflict between SDL and WTC effects. State-dependent models of the effort/value distortion effect also have the benefits of elegantly explaining several related findings. They well explain why other aversive stimuli, such as delay to reward or even a lack of reward, can have similar and additive distortive effects on value perception (DiGian et al., 2004; Lydall et al., 2010). In addition, a state-dependent model based on an integrated hedonic metric of state can reconcile the positive effects of effort on value perception with the empirical and intuitive fact that effort is, generally speaking, aversive. One remaining puzzle in our study is whether climbing vertically results in a negative hedonic impact for ants, given that ants have a weak preference for climbing vertical runways (see S2 in the online supplemental materials). This may indicate a distinction between *liking* and *wanting* as in humans (Robinson & Berridge, 1993): Ants may want to climb uphill, but may not like it.

Affective state, the currency of our proposed unified integrator, strongly affects cognitive biases. Mammals, birds, and even honeybees that are in a negative affective state (e.g., agitated or with poor welfare) show *pessimism*, in that they interpret mixed stimuli as predominantly negative (Bateson, Desire, Gartside, & Wright, 2011; Harding, Paul, & Mendl, 2004; Matheson, Asher, & Bateson, 2008).

Such affective states have been argued to act as integrators of experience from the environment, functioning as proxy Bayesian priors. However, this understanding of how (affective) state affects perception is at odds with the finding that effort increases perceived value. Hard work should reduce affective state, thus reducing the perceived value of the reward. Similarly, in studies of incentive contrasts, prior high reward reduced the perceived value of moderate rewards, and vice versa for prior low rewards (Couvillon & Bitterman, 1984; Flaherty, 1996). Clearly, we are still far from a unified understanding of reward perception in either vertebrates or invertebrates.

Here we provide the first demonstration that effort can distort value perception in an invertebrate. Our results also help to explain the finding that, at a collective level, ants will preferentially exploit a food source found after an ascent rather than an otherwise identical one reached via a descending path (Bles, Lozet, de Biseau, Campo, & Deneubourg, 2017). Many invertebrates, especially social insects, have been shown to possess remarkable cognitive abilities, such as learning of abstract concepts and making abstract associations (Avarguès-Weber, Dyer, Combe, & Giurfa, 2012; Avarguès-Weber & Giurfa, 2013; Czaczkes, Schlosser, Heinze, & Witte, 2014; Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001; Menzel, 2012). That invertebrates also show directly analogous cognitive patterns to those found in vertebrates (including humans) suggests that invertebrates represent a good, and tractable, model for studying cognitive phenomena (Menzel, 2012). Some ants in particular, due to their easily observed pheromone deposition behavior, may be an overlooked model for studying value perception and economic decision-making.

References

- Arantes, J., & Grace, R. C. (2008). Failure to obtain value enhancement by within-trial contrast in simultaneous and successive discriminations. *Learning and Behavior*, *36*, 1–11. <http://dx.doi.org/10.3758/LB.36.1.1>
- Arkes, H. R., & Blumer, C. (1985). The psychology of sunk cost. *Organizational Behavior and Human Decision Processes*, *35*, 124–140. [http://dx.doi.org/10.1016/0749-5978\(85\)90049-4](http://dx.doi.org/10.1016/0749-5978(85)90049-4)
- Avarguès-Weber, A., Dyer, A. G., Combe, M., & Giurfa, M. (2012). Simultaneous mastering of two abstract concepts by the miniature brain of bees. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 7481–7486. <http://dx.doi.org/10.1073/pnas.1202576109>
- Avarguès-Weber, A., & Giurfa, M. (2013). Conceptual learning by miniature brains. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131907. <http://dx.doi.org/10.1098/rspb.2013.1907>
- Aw, J. M., Vasconcelos, M., & Kacelnik, A. (2011). How costs affect preferences: Experiments on state dependence, hedonic state and within-trial contrast in starlings. *Animal Behaviour*, *81*, 1117–1128. <http://dx.doi.org/10.1016/j.anbehav.2011.02.015>
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., & Singmann, H. (2014). *lme4: Linear mixed-effects models using Eigen and S4 (Version 1.1–5)*. Retrieved from <http://cran.r-project.org/web/packages/lme4/index.html>
- Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A. (2011). Agitated honeybees exhibit pessimistic cognitive biases. *Current Biology*, *21*, 1070–1073. <http://dx.doi.org/10.1016/j.cub.2011.05.017>
- Bean, D., Mason, G. J., & Bateson, M. (1999). Contrafreeloading in starlings: Testing the information hypothesis. *Behaviour*, *136*, 1267–1282. <http://dx.doi.org/10.1163/156853999500712>
- Beckers, R., Deneubourg, J., & Goss, S. (1992). Trail laying behaviour during food recruitment in the ant *Lasius niger* (L.). *Insectes Sociaux*, *39*, 59–72. <http://dx.doi.org/10.1007/BF01240531>

- Beckers, R., Deneubourg, J. L., & Goss, S. (1993). Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, *6*, 751–759. <http://dx.doi.org/10.1007/BF01201674>
- Bernadou, A., & Fourcassié, V. (2008). Does substrate coarseness matter for foraging ants? An experiment with *Lasius niger* (Hymenoptera; Formicidae). *Journal of Insect Physiology*, *54*, 534–542. <http://dx.doi.org/10.1016/j.jinsphys.2007.12.001>
- Bhatkar, A., & Whitcomb, W. H. (1970). Artificial diet for rearing various species of ants. *The Florida Entomologist*, *53*, 229–232. <http://dx.doi.org/10.2307/3493193>
- Bles, O., Zoet, N., de Biseau, J. C., Campo, A., & Deneubourg, J.-L. (2017). Effect of the land area elevation on the collective choice in ants. *Scientific Reports*, *7*, 8745. <http://dx.doi.org/10.1038/s41598-017-08592-9>
- Bums, J. G., Foucaud, J., & Mery, F. (2011). Costs of memory: Lessons from “mini” brains. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*, 923–929. <http://dx.doi.org/10.1098/rspb.2010.2488>
- Cabanac, M. (1992). Pleasure: The common currency. *Journal of Theoretical Biology*, *155*, 173–200. [http://dx.doi.org/10.1016/S0022-5193\(05\)80594-6](http://dx.doi.org/10.1016/S0022-5193(05)80594-6)
- Calvert, G., Spence, C., & Stein, B. E. (2004). *The handbook of multisensory processes*. Cambridge, MA: MIT Press.
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*, 129–136. [http://dx.doi.org/10.1016/0040-5809\(76\)90040-X](http://dx.doi.org/10.1016/0040-5809(76)90040-X)
- Clement, T. S., Feltus, J. R., Kaiser, D. H., & Zentall, T. R. (2000). “Work ethic” in pigeons: Reward value is directly related to the effort or time required to obtain the reward. *Psychonomic Bulletin and Review*, *7*, 100–106. <http://dx.doi.org/10.3758/BF03210727>
- Couvillon, P. A., & Bitterman, M. E. (1984). The overlearning-extinction effect and successive negative contrast in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, *98*, 100.
- Czaczkes, T. J., Castorena, M., Schürch, R., & Heinze, J. (2017). Pheromone trail following in the ant *Lasius niger*: High accuracy and variability but no effect of task state. *Physiological Entomology*, *42*, 91–97. <http://dx.doi.org/10.1111/phen.12174>
- Czaczkes, T. J., Grüter, C., Ellis, L., Wood, E., & Ratnieks, F. L. (2013). Ant foraging on complex trails: Route learning and the role of trail pheromones in *Lasius niger*. *The Journal of Experimental Biology*, *216*, 188–197. <http://dx.doi.org/10.1242/jeb.076570>
- Czaczkes, T. J., Grüter, C., Jones, S. M., & Ratnieks, F. L. W. (2011). Synergy between social and private information increases foraging efficiency in ants. *Biology Letters*, *7*, 521–524. <http://dx.doi.org/10.1098/rsbl.2011.0067>
- Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. W. (2015). Trail pheromones: An integrative view of their role in social insect colony organization. *Annual Review of Entomology*, *60*, 581–599. <http://dx.doi.org/10.1146/annurev-ento-010814-020627>
- Czaczkes, T. J., & Heinze, J. (2015). Ants adjust their pheromone deposition to a changing environment and their probability of making errors. *Proceedings of the Royal Society B-Biological Sciences*, *282*, 20150679. <http://dx.doi.org/10.1098/rspb.2015.0679>
- Czaczkes, T. J., Schlosser, L., Heinze, J., & Witte, V. (2014). Ants use directionless odour cues to recall odour-associated locations. *Behavioral Ecology and Sociobiology*, *68*, 981–988. <http://dx.doi.org/10.1007/s00265-014-1710-2>
- Czaczkes, T. J., Weichselgartner, T., Bernadou, A., & Heinze, J. (2016). The Effect of trail pheromone and path confinement on learning of complex routes in the ant *Lasius niger*. *PLoS ONE*, *11*, e0149720. <http://dx.doi.org/10.1371/journal.pone.0149720>
- Detrain, C., Deneubourg, J.-L., & Pasteels, J. M. (1999). Decision-making in foraging by social insects. In *Information processing in social insects* (pp. 331–354). Basel, Switzerland: Springer. http://dx.doi.org/10.1007/978-3-0348-8739-7_18
- Detrain, C., & Prieur, J. (2014). Sensitivity and feeding efficiency of the black garden ant *Lasius niger* to sugar resources. *Journal of Insect Physiology*, *64*, 74–80. <http://dx.doi.org/10.1016/j.jinsphys.2014.03.010>
- Digian, K. A., Friedrich, A. M., & Zentall, T. R. (2004). Discriminative stimuli that follow a delay have added value for pigeons. *Psychonomic Bulletin and Review*, *11*, 889–895. <http://dx.doi.org/10.3758/BF03196717>
- Fairclough, S. H., & Houston, K. (2004). A metabolic measure of mental effort. *Biological Psychology*, *66*, 177–190. <http://dx.doi.org/10.1016/j.biopsycho.2003.10.001>
- Festinger, L. (1962). *A theory of cognitive dissonance* (Vol. 2). Stanford, CA: Stanford University Press.
- Flaherty, C. F. (1996). *Incentive relativity. Problems in the behavioural sciences, vol. 13*. New York, NY: Cambridge University Press.
- Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner’s curse. *Behavioral Ecology and Sociobiology*, *65*, 47–55. <http://dx.doi.org/10.1007/s00265-010-1038-5>
- Friedrich, A. M., Clement, T. S., & Zentall, T. R. (2005). Discriminative stimuli that follow the absence of reinforcement are preferred by pigeons over those that follow reinforcement. *Learning and Behavior*, *33*, 337–342. <http://dx.doi.org/10.3758/BF03192862>
- Full, R. J., & Tullis, A. (1990). Energetics of ascent: Insects on inclines. *The Journal of Experimental Biology*, *149*, 307–317.
- Gissel Nielsen, M. (2001). Energetic cost of foraging in the ant *Rhytidoponera aurata* in tropical Australia. *Physiological Entomology*, *26*, 248–253. <http://dx.doi.org/10.1046/j.0307-6962.2001.00242.x>
- Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concepts of “sameness” and “difference” in an insect. *Nature*, *410*, 930–933. <http://dx.doi.org/10.1038/35073582>
- Grüter, C., Czaczkes, T. J., & Ratnieks, F. L. W. (2011). Decision making in ant foragers (*Lasius niger*) facing conflicting private and social information. *Behavioral Ecology and Sociobiology*, *65*, 141–148. <http://dx.doi.org/10.1007/s00265-010-1020-2>
- Hangartner, W. (1969). Orientierung von *Lasius fuliginosus* Latr. An Einer Gabelung der Geruchspur. *Insectes Sociaux*, *16*, 55–60. <http://dx.doi.org/10.1007/BF02224462>
- Harding, E. J., Paul, E. S., & Mendl, M. (2004). Animal behaviour: Cognitive bias and affective state. *Nature*, *427*, 312. <http://dx.doi.org/10.1038/427312a>
- Hernandez-Lallement, J., Kuss, K., Trautner, P., Weber, B., Falk, A., & Fließbach, K. (2014). Effort increases sensitivity to reward and loss magnitude in the human brain. *Social Cognitive and Affective Neuroscience*, *9*, 342–349. <http://dx.doi.org/10.1093/scan/nss147>
- Holt, N. C., & Askew, G. N. (2012). Locomotion on a slope in leaf-cutter ants: Metabolic energy use, behavioural adaptations and the implications for route selection on hilly terrain. *The Journal of Experimental Biology*, *215*, 2545–2550. <http://dx.doi.org/10.1242/jeb.057695>
- Hunt, E. R., O’Shea-Wheller, T., Albery, G. F., Bridger, T. H., Gumm, M., & Franks, N. R. (2014). Ants show a leftward turning bias when exploring unknown nest sites. *Biology Letters*, *10*, 20140945. <http://dx.doi.org/10.1098/rsbl.2014.0945>
- Inglis, I. R., & Ferguson, N. J. K. (1986). Starlings search for food rather than eat freely-available, identical food. *Animal Behaviour*, *34*, 614–617. [http://dx.doi.org/10.1016/S0003-3472\(86\)80136-1](http://dx.doi.org/10.1016/S0003-3472(86)80136-1)
- Inglis, I. R., Forkman, B., & Lazarus, J. (1997). Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour*, *53*, 1171–1191. <http://dx.doi.org/10.1006/anbe.1996.0320>
- Jaumann, S., Scudelari, R., & Naug, D. (2013). Energetic cost of learning and memory can cause cognitive impairment in honeybees. *Biology Letters*, *9*, 20130149. <http://dx.doi.org/10.1098/rsbl.2013.0149>

- Jensen, G. D., Leung, C. M., & Hess, D. T. (1970). "Freeloading" in the skinner box contrasted with freeloading in the runway. *Psychological Reports*, 27, 67–73. <http://dx.doi.org/10.2466/pr0.1970.27.1.67>
- Johnson, A. W., & Gallagher, M. (2011). Greater effort boosts the affective taste properties of food. *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 1450–1456. <http://dx.doi.org/10.1098/rspb.2010.1581>
- Kacelnik, A., & Marsh, B. (2002). Cost can increase preference in starlings. *Animal Behaviour*, 63, 245–250. <http://dx.doi.org/10.1006/anbe.2001.1900>
- Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, 47, 263–292. <http://dx.doi.org/10.2307/1914185>
- Lipp, A., Wolf, H., & Lehmann, F.-O. (2005). Walking on inclines: Energetics of locomotion in the ant *Camponotus*. *The Journal of Experimental Biology*, 208, 707–719. <http://dx.doi.org/10.1242/jeb.01434>
- Lydall, E. S., Gilmour, G., & Dwyer, D. M. (2010). Rats place greater value on rewards produced by high effort: An animal analogue of the "effort justification" effect. *Journal of Experimental Social Psychology*, 46, 1134–1137. <http://dx.doi.org/10.1016/j.jesp.2010.05.011>
- Magalhães, P., & Geoffrey White, K. (2016). The sunk cost effect across species: A review of persistence in a course of action due to prior investment. *Journal of the Experimental Analysis of Behavior*, 105, 339–361. <http://dx.doi.org/10.1002/jeab.202>
- Mailleux, A.-C., Deneubourg, J.-L., & Detrain, C. (2000). How do ants assess food volume? *Animal Behaviour*, 59, 1061–1069. <http://dx.doi.org/10.1006/anbe.2000.1396>
- Matheson, S. M., Asher, L., & Bateson, M. (2008). Larger, enriched cages are associated with "optimistic" response biases in captive European starlings (*Sturnus vulgaris*). *Applied Animal Behaviour Science*, 109, 374–383. <http://dx.doi.org/10.1016/j.applanim.2007.03.007>
- McFarland, D. J., & Sibly, R. M. (1975). The behavioural final common path. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 270, 265–293. <http://dx.doi.org/10.1098/rstb.1975.0009>
- Meindl, J. N. (2012). Understanding preference shifts: A review of within-trial contrast and state-dependent valuation. *The Behavior Analyst*, 35, 179–195. <http://dx.doi.org/10.1007/BF03392277>
- Menzel, R. (2012). The honeybee as a model for understanding the basis of cognition. *Nature Reviews Neuroscience*, 13, 758–768. <http://dx.doi.org/10.1038/nrn3357>
- Oettler, J., Schmid, V. S., Zankl, N., Rey, O., Dress, A., & Heinze, J. (2013). Fermat's principle of least time predicts refraction of ant trails at substrate borders. *PLoS ONE*, 8, e59739. <http://dx.doi.org/10.1371/journal.pone.0059739>
- Ogura, T. (2011). Contrafreeloading and the value of control over visual stimuli in Japanese macaques (*Macaca fuscata*). *Animal Cognition*, 14, 427–431. <http://dx.doi.org/10.1007/s10071-010-0377-y>
- Pastell, M. (2016). CowLog – Cross-Platform Application for Coding Behaviours from Video. *Journal of Open Research Software*, 4, e15. <http://dx.doi.org/10.5334/jors.113>
- Podlesnik, C. A., & Jimenez-Gomez, C. (2016). Contrafreeloading, reinforcement rate, and behavioral momentum. *Behavioural Processes*, 128, 24–28. <http://dx.doi.org/10.1016/j.beproc.2016.03.022>
- Pomplio, L., Kacelnik, A., & Behmer, S. T. (2006). State-dependent learned valuation drives choice in an invertebrate. *Science*, 311, 1613–1615. <http://dx.doi.org/10.1126/science.1123924>
- R Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>
- Robinson, T. E., & Berridge, K. C. (1993). The neural basis of drug craving: An incentive-sensitization theory of addiction. *Brain Research Reviews*, 18, 247–291. [http://dx.doi.org/10.1016/0165-0173\(93\)90013-P](http://dx.doi.org/10.1016/0165-0173(93)90013-P)
- Ruther, J., & Steidle, J. L. M. (2000). Mites as matchmakers: Semiochemicals from host-associated mites attract both sexes of the parasitoid *Lariophagus distinguendus*. *Journal of Chemical Ecology*, 26, 1205–1217. <http://dx.doi.org/10.1023/A:1005484027559>
- Shi, P. J., Sand Hu, H. S., & Xiao, H. J. (2013). Logistic regression is a better method of analysis than linear regression of arcsine square root transformed proportional diapause data of *Pieris melete* (Lepidoptera: Pieridae). *The Florida Entomologist*, 96, 1183–1185. <http://dx.doi.org/10.1653/024.096.0361>
- Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2012). *A 21 word solution*. SSRN Scholarly Paper No. ID 2160588. Rochester, NY: Social Science Research Network. Retrieved from <https://papers.ssrn.com/abstract=2160588>
- Singh, D., & Query, W. T. (1971). Preference for work over "freeloading" in children. *Psychonomic Science*, 24, 77–79. <http://dx.doi.org/10.3758/BF03337901>
- Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., & Bolker, B. (2016). *glmmADMB: Generalized linear mixed models using AD Model Builder* (R package Version 0.8.3.3). <https://rdrr.io/rforge/glmmADMB/>
- Snygg, D. (1935). Mazes in which rats take the longer path to food. *The Journal of Psychology: Interdisciplinary and Applied*, 1, 153–166. <http://dx.doi.org/10.1080/00223980.1935.9917250>
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory* (1st ed., p. 246). Princeton, NJ: Princeton University Press.
- Stevens, J. R., Rosati, A. G., Ross, K. R., & Hauser, M. D. (2005). Will travel for food: Spatial discounting in two new world monkeys. *Current Biology*, 15, 1855–1860. <http://dx.doi.org/10.1016/j.cub.2005.09.016>
- Tarte, R. D. (1981). Contrafreeloading in humans. *Psychological Reports*, 49, 859–866. <http://dx.doi.org/10.2466/pr0.1981.49.3.859>
- Thaler, R. H. (2004). Mental accounting matters. In *Advances in behavioral economics* (pp. 75–103). New York, NY: Princeton University Press.
- Vasconcelos, M., Urcuioli, P. J., & Lionello-DeNolf, K. M. (2007). Failure to replicate the "work ethic" effect in pigeons. *Journal of the Experimental Analysis of Behavior*, 87, 383–399. <http://dx.doi.org/10.1901/jeab.2007.68-06>
- von Thienen, W., Metzler, D., Choe, D.-H., & Witte, V. (2014). Pheromone communication in ants: A detailed analysis of concentration-dependent decisions in three species. *Behavioral Ecology and Sociobiology*, 68, 1611–1627. <http://dx.doi.org/10.1007/s00265-014-1770-3>
- Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, 92, 3–10. <http://dx.doi.org/10.1890/10-0340.1>
- Wilson, E. O., & The Organization of Mass-Foraging. (1962). Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith) I. The Organization of Mass-Foraging. *Animal Behaviour*, 10, 134–147. [http://dx.doi.org/10.1016/0003-3472\(62\)90141-0](http://dx.doi.org/10.1016/0003-3472(62)90141-0)
- Zentall, T. R. (2010). Justification of effort by humans and pigeons cognitive dissonance or contrast? *Current Directions in Psychological Science*, 19, 296–300. <http://dx.doi.org/10.1177/0963721410383381>
- Zentall, T. R. (2013). Animals prefer reinforcement that follows greater effort: Justification of effort or within-trial contrast? *Comparative Cognition and Behavior Reviews*, 8, 60–77. <http://dx.doi.org/10.3819/ccbr.2013.80004>
- Zentall, T. R. (2015). When animals misbehave: Analogs of human biases and suboptimal choice. *Behavioural Processes*, 112, 3–13. <http://dx.doi.org/10.1016/j.beproc.2014.08.001>
- Zink, C. F., Pagnoni, G., Martin-Skurski, M. E., Chappelow, J. C., & Berns, G. S. (2004). Human striatal responses to monetary reward depend on saliency. *Neuron*, 42, 509–517. [http://dx.doi.org/10.1016/S0896-6273\(04\)00183-7](http://dx.doi.org/10.1016/S0896-6273(04)00183-7)

Received August 17, 2017

Revision received December 14, 2017

Accepted December 14, 2017 ■