1 Relative value perception in an insect: positive and negative incentive
2 contrasts in ants

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Abstract

15 Humans tend to value things not on their absolute values, but relative to reference points such as

16 former experience or expectations. People rate the quality of a new salary relative to their previous

17 salary and the salaries of their peers, instead of appreciating its absolute value. Here, we demonstrate

18 a similar effect in an insect: ants, which had previously experienced a low quality food source, showed

19 higher acceptance of medium quality food (e.g. 0.1M then 0.5M; positive contrast) than if they had

20 received the medium food all along (e.g. 0.5M then 0.5M; control), and vice versa for high expectations.

21 Further experiments demonstrate that these contrast effects arise from cognitive rather than mere

22 sensory or pre-cognitive perceptual causes. Pheromone deposition also correlates with perceived

23 reward value, and ants showed successive contrasts in their pheromone deposition. Relative value

24 perception can therefore be expected to have strong effects not only on individual behaviour, but also

25 on collective decision-making. Contrast effects were also social: the quality of food received from other

26 ants affected the perceived value of food found later. Value judgement is a key element in decision

27 making, and thus relative value perception will strongly influence how animals interact with their

28 environment.

Key Words

30 Incentive contrasts; successive contrasts; relative value perception; foraging; recruitment; private

31 information

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Introduction

33

34 We all compare options when making both large and small decisions, ranging from career choice to

35 the choice of an evening's entertainment. Understanding how options are compared has thus been

36 central to the study of behaviour and economics. Theories explaining the mechanisms by which

37 options are compared and decisions are made have a long tradition (Vlaev et al. 2011), with Expected

38 Utility Theory (EUT) being the most widely used theory in economic models (Mankiw 2011; von

39 Neumann and Morgenstern 1944). EUT suggests that decisions are made by evaluating and comparing

40 the expected pay-off from each option. A rational decision maker then chooses the option resulting in

41 the best end state (i.e. the option providing the greatest utility) (von Neumann and Morgenstern 1944).

42 However, over the past decades economic research on how humans make decisions has started to

43 shift away from a view of (absolute) utility maximization towards more nuanced notions of relative

44 utility, such as reference-dependent evaluations. Kahneman and Tversky (1979) made a major

45 contribution to this shift by introducing Prospect Theory, suggesting that decision making is not based

46 on absolute outcomes, but rather on relative perceptions of gain and losses. In contrast to EUT, the

47 utility attributed to options being evaluated is determined relative to a reference point, such as the

48 status quo or former experience (Kahneman and Tversky 1979; Parducci 1984; Tversky and Kahneman

49 1992; Ungemach, Stewart, and Reimers 2011; Vlaev et al. 2011). Various examples of relative value

50 perception have been described. For example, satisfaction gained from income is perceived not

51 absolutely, but relative to the income of others in the social reference group – such as one's colleagues

52 (Boyce, Brown, and Moore 2010). Overall, Prospect Theory has enriched our understanding of human

53 decision making by conceptualizing it as more nuanced than previously assumed (Tversky and

54 Kahneman 1974, 1981).

55 A similar relativistic pattern can be found in sensory judgements: Humans rated drinks containing the

56 same sucrose concentration sweeter when they were presented with a range of lower concentrations

57 and less sweet when higher concentrations were presented more frequently (McBride 1982; Riskey,

58 Parducci, and Beauchamp 1979). However, these findings also match well with predictions from

59 psychophysics, in which the link between a given stimulus strength and it's sensation is studied

60 (Zwislocki 2009). A key psychophysical finding is that identical stimuli are perceived as more or less

61 intense depending on the strength of reference stimuli.

62 The concept of malleable value perception is not just relevant to humans. Value judgments in animals

63 are also influenced by factors apparently independent of the absolute value of options. For example,

64 capuchin monkeys refuse otherwise acceptable pay (cucumber) in exchanges with a human

65 experimenter if they had witnessed a conspecific obtain a more attractive reward (grape) for equal

66   effort (Brosnan and de Waal 2003). Rats, starlings, and ants, like humans, place greater value on things

67   they work harder for (Aw, Vasconcelos, and Kacelnik 2011; Czaczkes, Brandstetter, et al. 2018; Lydall,

68   Gilmour, and Dwyer 2010), and fish and locusts demonstrate state-dependent learning, wherein they

69   show a preference for options experienced when they were in a poor condition (Aw et al. 2009;

70   Pompilio, Kacelnik, and Behmer 2006). Roces and Núñez aimed to show that in leaf cutting ants

71   perceived value can be influenced by other ants. Ants recruited to higher quality food sources ran

72   faster, deposited more pheromone, but cut smaller leaf fragments, even if the food source the recruits

73   find is replaced by a standardised food source (Roces 1993; Roces and Núñez 1993). However, in these

74   experiments the absolute value and nature of the reference remains unclear, and indeed pheromone

75   presence may have caused the observed behaviours without influencing the ants' expectations or

76   value perception at all. Critically missing from this body of work is a systematic description of value

77   judgment relative to a reference point.

78   A common way in which value is judged is by either comparing two options to each other or by

79   comparing one option to an option experienced in the past. Thus, the perceived value of an option is

80   likely to depend strongly on the strength of contrast between both options and on whether the new

81   option results in a relative gain or a loss. Such value-distortion by comparison effects have been studied

82   for decades using the successive contrasts paradigm. In such experiments, animals are trained to a

83   quality or quantity of reward which is then suddenly increased (positive incentive contrast) or

84   decreased (negative incentive contrast) (Bentosela et al. 2009; Bitterman 1976; Couvillon and

85   Bitterman 1984; Crespi 1942; Flaherty 1982, 1999; Mustaca, Bentosela, and Papini 2000; Weinstein

86   1970b). The reaction of animals towards the post-shift reward is then compared to the reaction of

87   animals which always received the first reward and therefore did not experience a shift. Many

88   mammals, including apes, monkeys, rats and dogs (Bentosela et al. 2009; Brosnan and de Waal 2003;

89   Crespi 1942; Flaherty 1999; Mustaca, Bentosela, and Papini 2000; Pellegrini and Mustaca 2000;

90   Weinstein 1970a) have been shown to respond to successive negative contrast by disrupting their

91   behaviour compared to control animals which had not experienced a change in reward. The animals

92   display behaviour akin to disappointment – slower running speeds to a reward (Bower 1961),

93   depressed licking behaviour (Flaherty, Becker, and Pohorecky 1985; Vogel, Mikulka, and Spear 1968),

94   or reward rejection (Tinklepaugh 1928).

95   However, unlike negative contrast effects, responses to positive successive contrast have rarely been

96   found, even when searched for (Black 1968; Capaldi and Lynch 1967; Bower 1961; Dunham 1968;

97   Papini et al. 2001). This may be due to three possible factors, which have the opposite effect of positive

98   contrast and may counterbalance it: ceiling effects, neophobia, and generalization decrement

99   (Annicchiarico et al. 2016; Flaherty 1999). Ceiling effects may occur when the performance of animals

100 receiving a large reward is at or near a physical limit. The absence of positive contrast may then not be

101 generated by behavioural principles, but through an artefact of experimental design (Bower 1961;

102 Campbell et al. 1970). Neophobia may manifest itself through the reluctance to eat novel food – even

103 if the food is of higher quality than normal (Flaherty 1999). Generalization decrement may occur when

104 animals are trained under one set of stimuli and then tested under another. The strength of the tested

105 response may decrease with increasing differences between the training and testing stimuli (Kimble

106 1961), which may then result in weaker positive contrast effects following a reward shift. Thus, the

107 reward change itself may lead to a decrease in responding just as would any other change in context,

108 such as a change in the brightness of the runway (Capaldi 1978; Premack and Hillix 1962).

109 Even though positive contrast effects proved to be hard to demonstrate in laboratory experiments,

110 there are good theoretical reasons for expecting both positive and negative contrast effects to evolve

111 (McNamara, Fawcett, and Houston 2013): if conditions become rich in the environment of an animal

112 which was initially exposed to poor conditions, it should work harder than if conditions have been rich

113 all along. This is because conditions are likely to worsen in the future and the animal should therefore

114 use good conditions to the fullest while available. By contrast, if the animal was accustomed to rich

115 conditions which then suddenly worsen, it should work less hard than if conditions have always been

116 poor. In this case, rich conditions are likely to return and the animal would do better by waiting for the

117 good conditions to return before continuing to exploit the environment. Lastly, contrast effects should

118 be strongest in animals adapted to rapidly changing conditions, because it enhances the differential

119 allocation of effort between favourable and unfavourable periods (McNamara, Fawcett, and Houston

120 2013).

121 Contrast effects could potentially arise without differential valuation of options; other mechanisms

122 could also in principle produce these results: contrast effects in sensory tasks could derive from simple

123 psychophysical mechanisms (Fechner 1860; Zwislocki 2009), and thus arise from sensory perceptual

124 mechanisms rather than higher level cognitive processing of value. Sensory judgements are also

125 usually made relative to reference points and through constant comparisons with former stimuli

126 (Helson 1964; Vlaev et al. 2011). The position of the reference point in the range of stimuli may thus

127 bias how the stimulus, and thus the value, of a post-shift reward is perceived (Zwislocki 2009). For

128 example, the sweetness of a sucrose solution may be perceived much stronger when the reference

129 point to which it is compared is low. Sensory satiation may also result in apparent contrast effects: the

130 more sweetness receptors are blocked by a sweet reference solution, the fewer receptors will fire

131 when confronted with a post-shift reward, thus making solutions taste less sweet (Bitterman 1976). A

132 final potential driver of apparent contrast effects is related to the theoretical benefits of such

133 behaviour described above: animals may rationally expect the pre-shift reward to be available in the

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134   future again and therefore rationally show lower acceptance towards the post-shift reward, because

135   they are waiting for the pre-shift reward to reoccur.

136   The finding of contrast effects in the honey bee, until now the only invertebrate for which such

137   behaviour was conclusively shown, led to a fourth explanation for contrast effects (Couvillon and

138   Bitterman 1984; Bitterman 1976; Núñez 1966). Bitterman (1976) found that honey bees which were

139   trained to a 40% sucrose solution show many feeding interruptions when experiencing a downshift to

140   20% sucrose. By contrast, bees which were fed on 20% throughout the whole experiment filled their

141   crops immediately. Bees which were shifted from 20% to 40% showed no interruptions at the post-

142   shift solution either. Apart from explaining these results as negative contrast effects, Bitterman

143   suggested two alternative hypotheses: sensory saturation (see above) and changes in satiation level.

144   Individuals may not only store sucrose solutions in their crop, but may also ingest small amounts of

145   sucrose, leading to an increase of haemolymph-sugar levels. Higher blood-sugar levels negatively affect

146   sweetness perception in humans (Mayer-Gross and Walker 1946; Melanson et al. 1999), and a similar

147   effect could cause a post-shift solution to taste less sweet to animals trained on high sucrose

148   concentrations. However, using an odour training paradigm, Couvillon and Bitterman (1984) found

149   negative contrast effects in honeybees and could rule out the above alternative causes.

150   In this study, we investigate positive and negative contrast effects using the successive contrasts

151   paradigm, and define the first relative value curve in an invertebrate; the ant *Lasius niger*. We then

152   demonstrate that relative value perception arises from non-rational cognitive effects, rather than

153   rational decision-making, physiological effects, or psychophysical phenomena. Finally, we

154   demonstrate that information flowing into the nest can influence value perception in outgoing foragers.

Methods and Results

Study animals

157   Eight stock colonies of the black garden ant *Lasius niger* were collected on the University of Regensburg

158   campus. The colonies were kept in 30x30x10cm foraging boxes with a layer of plaster covering the

159   bottom. Each box contained a circular plaster nest box (14 cm diameter, 2 cm height). The colonies

160   were queenless with around 1000-2000 workers and small amounts of brood. Queenless colonies still

161   forage and lay pheromone trails, and are frequently used in foraging experiments (Devigne and Detrain

162   2002; Dussutour et al. 2004). The colonies were fed with *ad libitum* 0.5M sucrose solution and received

163   *Drosophila* fruit flies once a week. Water was available *ad libitum.*

164   One sub-colony of 500 individuals was formed from each stock colony, and these eight fixed-size sub-

165   colonies were used for our experiments. Sub-colonies were maintained identically to the stock colonies,

166   but did not receive any *Drosophila* fruit flies to prevent brood production, and were starved four days

167   prior to the experiments in order to achieve a uniform and high motivation for foraging (Mailleux,

168   Detrain, and Deneubourg 2006; Josens and Roces 2000). During starvation, water was available *ad*

169   *libitum*. Any ants which died or were removed from the sub-colonies were replaced with ants from the

170   original stock colonies.

General setup

172   The general setup used for all of our three experiments was identical and consisted of a 20 x 1 cm long

173   paper-covered runway which was connected to the sub-colony's nest box via a 40 cm long drawbridge

174   (figure 1A). A 5mm diameter drop of sucrose solution (Sigma-Aldrich) was placed on an acetate feeder

175   at the end of the runway (60cm from the nest). The molarity of the sucrose droplet depended on the

176   experiment, treatment and on the ants' number of visit to the food source.

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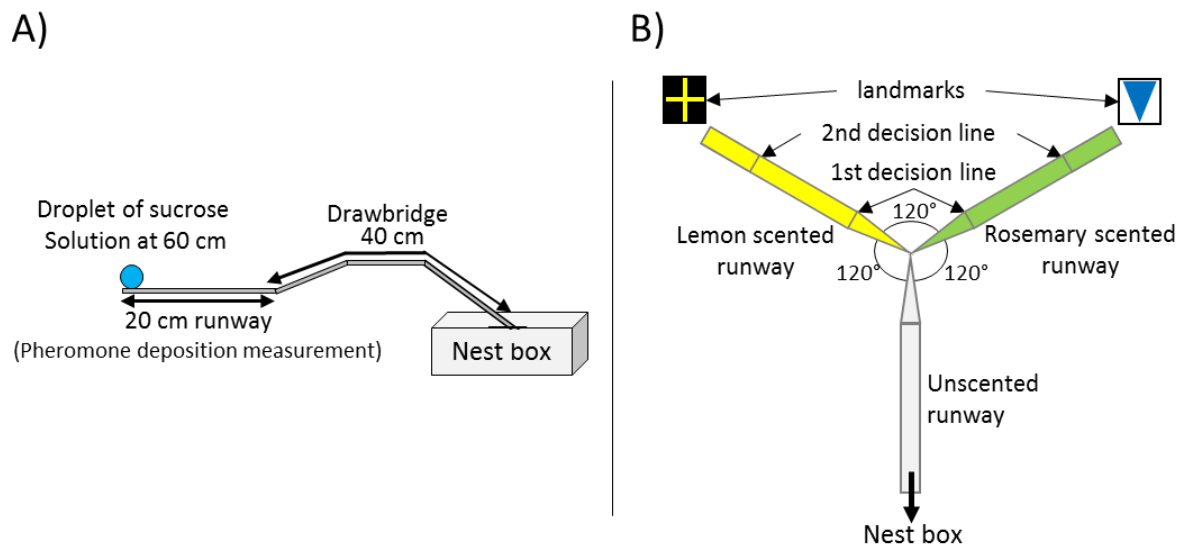
Fig. 1: **A)** General setup used for all presented experiments. The 20 cm long runway is connected to the nest box via a 40 cm long drawbridge. The droplet of sucrose solution is placed at the end of the runway (60 cm distance to the nest). **B)** Y-maze used on the 10th visit of experiment 2. All arms were 10 cm long. The arm connected to the nest box was covered with unscented paper overlays while the other two arms were covered with lemon and rosemary scented paper overlays (one scent on each side). Visual cues (landmarks) were placed directly behind the two scented arms. The first decision line was located 2.5cm from the Y-maze centre and marked the initial decision of an ant while the second decision line was located 7.5cm from the centre and marked the final decision.

186   To begin an experiment, the sub-colony was connected to the runway via the drawbridge. 2-4 ants

187   were allowed onto the runway, and the first ant to reach the feeder was marked with a dot of acrylic

188   paint on its gaster. The marked ant was allowed to drink to repletion at the food source, while all other

189   ants were returned to the nest. As the ant drank at the droplet it was given one of three food

190   acceptance scores. Full acceptance (1) was scored when the ant remained in contact with the drop

191   from the moment of contact and did not interrupt drinking within 3 seconds of initial contact. Partial

192   acceptance (0.5) was scored if feeding was interrupted within 3 seconds after the first contact with the

193   food source, but the ant still filled its crop within 10 minutes (as can be seen by the distention of the

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194   abdominal tergites). Lastly, rejection (0) was scored if the ant refused to feed at the sucrose solution

195   and either returned to the nest immediately or failed to fill its crop within 10 minutes.

196   When the ant had filled its crop or decided not to feed at the sucrose droplet, it was allowed to return

197   to the nest. Inside the nest, the ant unloaded its crop to its nestmates and was then allowed back onto

198   the runway for another visit. The drawbridge was now used to selectively allow only the marked ant

199   onto the runway.

200   In addition to measuring food acceptance, we also measured pheromone deposition. Individual

201   pheromone deposition behaviour correlates with the (perceived) quality of a food source (Beckers,

202   Deneubourg, and Goss 1993; Hangartner 1970; Czaczkes, Grüter, and Ratnieks 2015). Individual ants

203   can adapt the strength of a pheromone trail by either depositing pheromone or not, or varying the

204   intensity of a pheromone trail through number of pheromone depositions (Hangartner 1970; Beckers,

205   Deneubourg, and Goss 1993). Pheromone deposition behaviour in *L. niger* is highly stereotypic. To

206   deposit pheromone, an ant briefly interrupts running to bend its gaster and press the tip of the gaster

207   onto the ground (Beckers, Deneubourg, and Goss 1992). This allows the strength of a pheromone trail

208   to be quantified by counting the number of pheromone depositions over the 20 cm runway leading to

209   the feeder. Pheromone depositions were measured each time the ant moved from the food source

210   back to the nest (inward trip), and each time the ant moved from the nest towards the food source

211   (outward trip). Because *L. niger* foragers almost never lay pheromone when they are not aware of a

212   food source (Beckers, Deneubourg, and Goss 1992), we did not measure pheromone depositions for

213   the very first outward trip (visit 1). The presence of trail pheromone on a path depresses further

214   pheromone deposition (Czaczkes et al. 2013). Thus, each time an ant had passed the 20 cm runway,

215   the paper overlay covering the runway was replaced by a fresh one every time the ant left the runway

216   to feed at the feeder or returned to the nest.

217   All experimental runs were recorded with a Panasonic DMC-FZ1000 camera to allow for later video

218   analysis.

219   After each experimental run the ant was permanently removed.

220   Details of our statistical analysis methods and samples sizes are provided in online supplement S1.

Experiment 1 – Defining a relative value perception curve

222   The aim of this of experiment was to test whether *Lasius niger* foragers value a given absolute sucrose

223   solution concentration relative to a reference point or based on its absolute value. We used a range of

224   12 molarities as reference points in order to describe a value curve. To exclude effects of the

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225   researcher's expectations on the data, the data for this experiment were collected blind to treatment

226   (Holman et al. 2015).

Experiment 1 - Methods

228   In the first two visits to the apparatus - termed the training visits - the ants' reference point was set by

229   allowing it to feed from a feeder at the end of the runway. The quality of the sucrose solution was

230   varied between ants, with each ant receiving the same quality twice successively. 12 different

231   molarities were used: 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1, 1.5 or 2M. *Lasius niger* workers learn

232   the quality of a feeder within 2 visits (Wendt and Czaczkes 2017). On the third visit (test visit), the food

233   source was replaced by a 0.5M sucrose solution droplet for all ants. Thus, ants trained to qualities

234   <0.5M experienced a positive successive contrast, ants trained to >0.5M experienced negative

235   successive contrast, and the ants trained to 0.5M constituted the control (no contrast). Food

236   acceptance and pheromone depositions were noted for each visit, as described above.

Experiment 1 - Results

238   Ants seemed to value sucrose solution droplets relative to a reference point (figure 2, table S1). While

239   in the training visits acceptance scores increased significantly with increasing molarity of the reference

240   quality (CLMM: 1st visit: estimate= 1.18, z=6.99, p>0.001; 2nd visit: estimate= 1.56, z=9.28, p<0.001, fig.

241   2), in the test (contrast) visit acceptance scores decreased significantly with increasing molarity of the

242   reference quality (CLMM: estimate=-2.59, z= -13.75, p<0.001, fig. 2). Ants which were trained to very

243   low molarities (0.1M: p<0.001) showed significantly higher acceptance of 0.5M sucrose than control

244   ants, while ants trained to high molarities (1.5M: p<0.001, 2M: p<0.001) showed lower acceptance of

245   0.5M than the control group (see supplement Table S2.1 for all pairwise comparisons).

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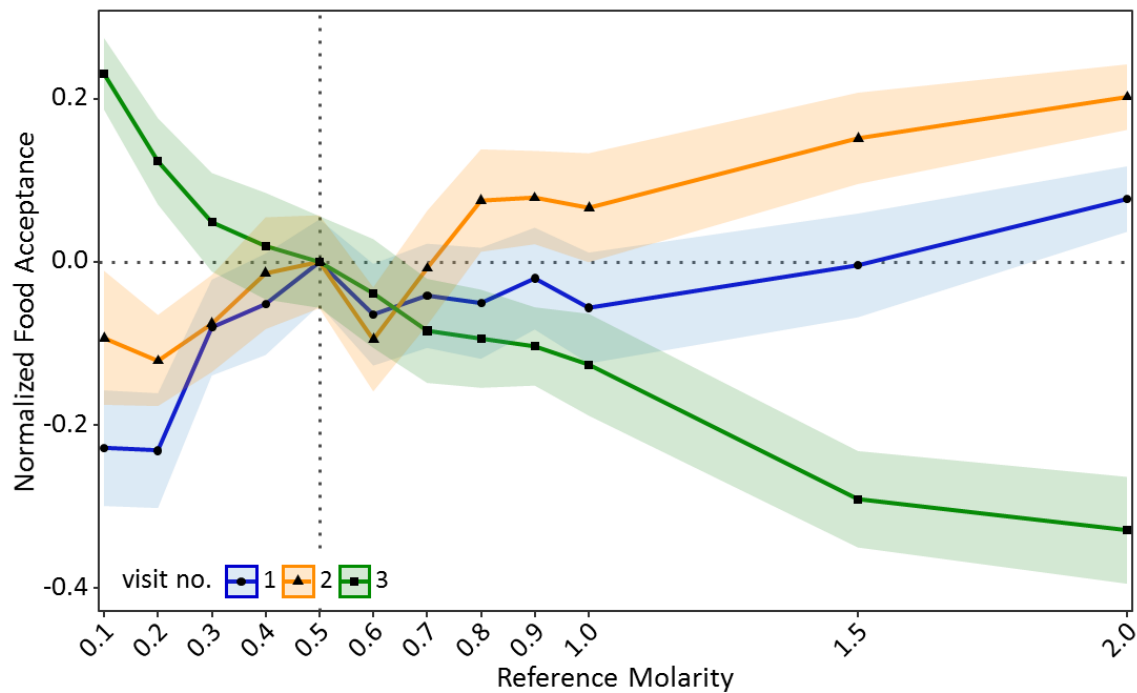
Fig. 2: Food acceptance shown in experiment 1 for the two training visits (visit 1 & 2) in which ants received one of 12 molarities and the test visit (3) in which all ants received 0.5M. Shown are the mean food acceptance (points) and the 95% confidence intervals (coloured ribbons) for each reference molarity and visit. Data was normalized to show the mean food acceptance of the control group (received 0.5M on each visit) at 0 for all three visits. For a non-normalized graph of the data see supplement Figure S2.1.

A similar pattern was found for pheromone deposition behaviour on the way back to the nest (figure 3). In the training visits, number of pheromone depositions increased significantly with increasing molarity of the reference solution (GLMM: estimate= 0.86, z= 13.86, p<0.001). Additionally, ants performed significantly more pheromone depositions on the second return to the nest compared to the first return visit (GLMM: estimate= 0.31, z= 4.64, p<0.001). By contrast, on the test visit pheromone depositions decreased significantly with increasing molarity of the reference solution (GLMM: estimate= -0.82, z= -9.75, p<0.001, fig. 3). Ants which deposited more pheromone during the training visits generally deposited more pheromone on the test visit compared to ants which deposited less pheromone during the training visits (GLMM: estimate= 0.16, z= 15.99, p<0.001). Ants which were trained to very low molarities (0.2M: p<0.01) deposited significantly more pheromone depositions in the test visit than control ants, while ants trained to high molarities (1M: p<0.001, 1.5M: p<0.001, 2M: p<0.001) deposited less pheromone depositions than the control group (see supplement Table S2.2 for pairwise comparisons).

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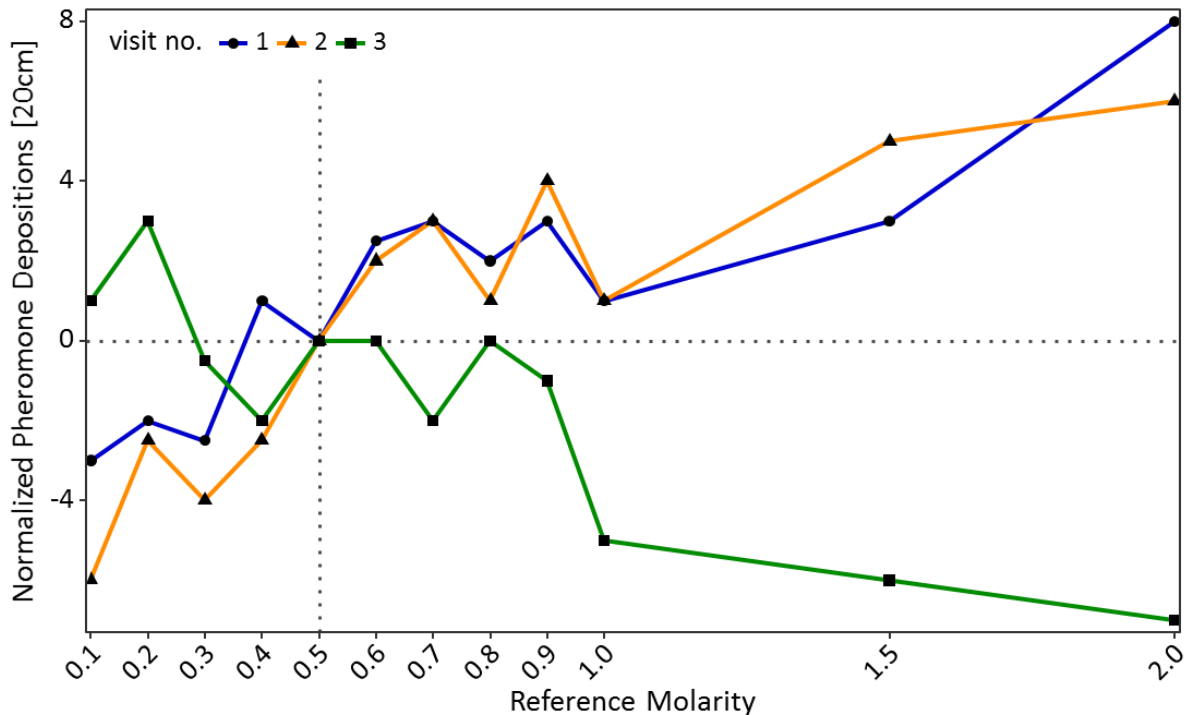
266

267 Fig. 3: Pheromone depositions on the way back to the nest shown in experiment 1 for the two training visits (visit
268 1 & 2) in which ants received one of 12 molarities and the test visit (3) in which all ants received 0.5M. Shown is
269 the median number of pheromone depositions (points) measured on a 20 cm track right behind the food source
270 for each reference molarity and visit. Data was normalized to show the median number of pheromone
271 depositions of the control group (received 0.5M on each visit) at 0 for all three visits. For a non-normalized graph
272 of the data with error ribbons see supplement Figure S2.2.

273

Experiment 2 – ruling out alternative explanations using scent training

275 The results of experiment 1 are consistent with relative value perception stemming from the

276 psychological effects of successive contrasts. However, alternative hypotheses could also explain these

277 results. Four possible alternatives must be excluded: sensory saturation, ingested sucrose changing

278 haemolymph-sugar levels, psychophysical sensory contrast effects and the fact that ants may expect

279 pre-shift solutions to return in later visits (see introduction). To rule out the above four alternative

280 explanations, we carried out experiment 2.

Experiment 2 - Methods

282 To rule out the alternative non-psychological explanations for the contrast effects we described above,

283 we needed to change the expectation of the ants while exposing all ants to identical training regimes.

284 This would provide a reference point for testing relative value perception while keeping sensory

285 saturation, haemolymph-sugar levels, and psychophysical effects the same until the switch occurred.

286 To this end, we trained ants over 8 visits to associate a high sucrose molarity (1.5M) with one scent,

287 and a low molarity (0.25M) with a different scent. Then, in the 9th testing phase, we used scents to

288 trigger an expectation of either high or low molarity, which was then contrasted with a medium (0.5M)

10

289   unscented solution. Finally, preference for the high-quality associated odour was tested for using a Y-

290   maze.

291   For a detailed description of the methods used, see online supplement S3.1.

Experiment 2 - Results

293   During training, ants behaved as expected, showing higher acceptance and pheromone deposition for

294   1.5M than 0.25M on all but the very first visit to 0.25M (Food acceptance: CLMM: estimate = -1.13, z=

295   3.38, p<0.001; pheromone depositions outward journey: GLMM: estimate= 1.79, z= 17.10, p<0.001;

296   pheromone depositions inward journey: GLMM: estimate= -1.20, z= -10.10, p<0.001, figures 4A, C &

297   E). Furthermore, food acceptance and pheromone depositions both on the outward and inward

298   journeys decreased with increasing experience with the 0.25M feeder and increased with increasing

299   experience with the 1.5M feeder (Food acceptance: CLMM: estimate = -1.13, z= 3.38, p<0.001;

300   pheromone depositions outward journey: GLMM: estimate= -0.31, z= -17.07, p<0.001; pheromone

301   depositions inward journey: GLMM: estimate = -0.21, z= -7.02, p<0.001).

302   On the outward journey of the 9th (test) visit, ants walking towards the feeder while exposed to 1.5M

303   sucrose-associated cues deposited more pheromone (median=15, fig. 4D) compared to ants exposed

304   to 0.25M-associated cues (median=2, GLMM: estimate= -1.32, z= -13.51, p<0.001). Moreover, in the

305   learning probe, 87% of ants chose the 1.5M associated arm. This demonstrates that ants formed a

306   robust expectation of food molarity based on the cues learned during training.

307   Ants exposed to 1.5M-associated cues during the 9th visit showed significantly lower food acceptance

308   towards the unscented 0.5M feeder than ants exposed to 0.25M-associated cues (CLMM: estimate=

309   1.07, z= 2.15, p= 0.03, figure 4B, table S1). Although ants exposed to high molarity associated cues on

310   their outwards journey showed a significantly higher number of pheromone depositions on their

311   return journey than ants confronted with low molarity scent (GLMM: estimate= -1.36, z= -5.50,

312   p<0.001, figure 4E & F), the number of pheromone depositions decreased drastically for both

313   treatments compared to training visits (median 1.5M = 0, median 0.25M = 0, figure 4E & F, table S1).
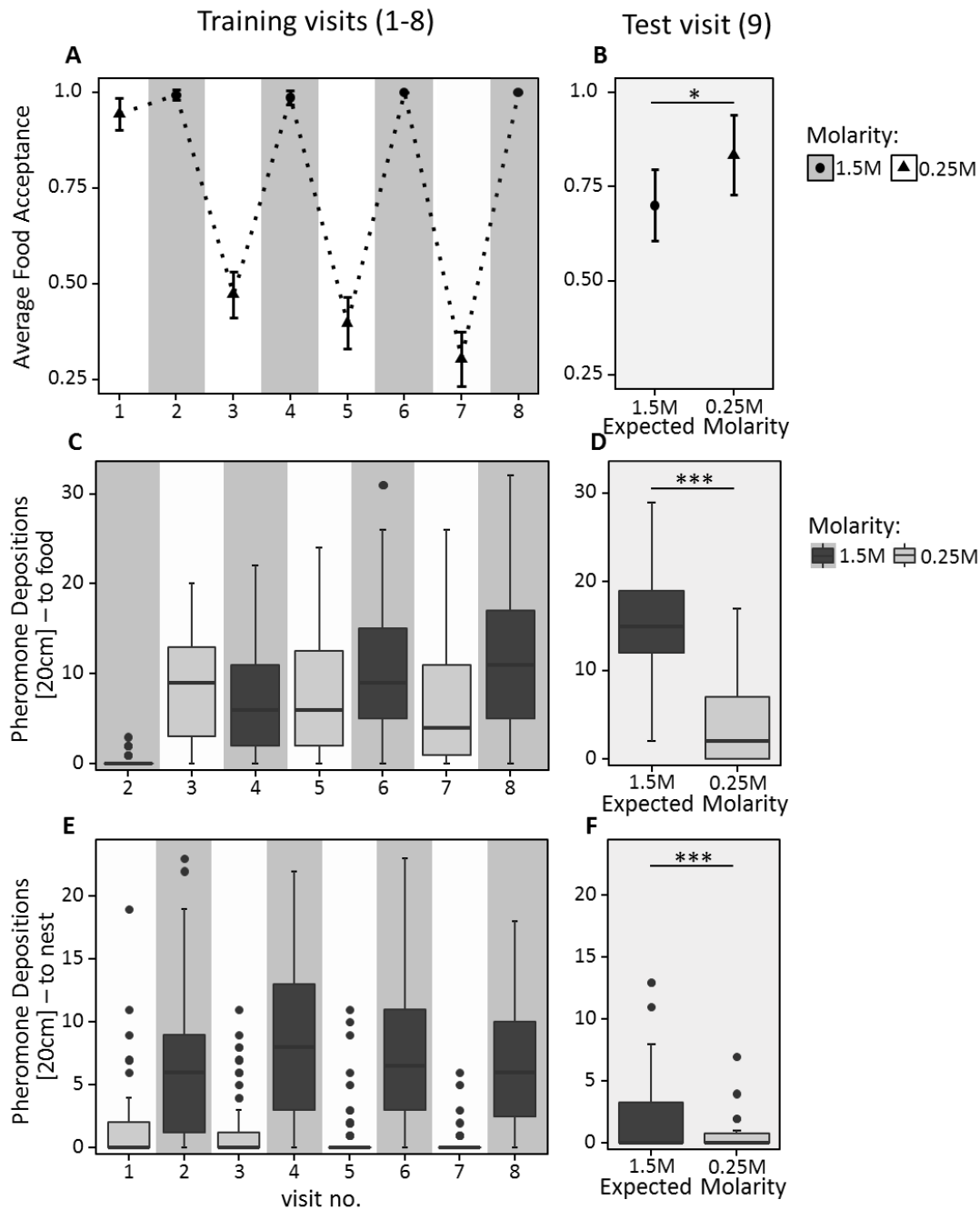
Fig. 4: A) & B) Food acceptance C) & D) Number of pheromone depositions on the way to the food source and E) & F) Number of pheromone depositions on the way back to the nest shown in experiment 2 for A), C) & E) the eight training visits (visits 1-8) in which ants received 0.25M coupled with one scent and 1.5M coupled with another scent in an alternating order, always starting with 0.25M. and B), D) & F) the test visit (visit 9) in which ants always received unscented 0.5M sucrose solution, but the runway leading towards the food source was impregnated with one of the learned scents, triggering an expectation towards receiving either high or low molarities at the end of the runway. A) & B) Shown are the mean food acceptance (points) and the 95% confidence intervals (error bars) for each visit; C) - F) Shown are the median number of pheromone depositions on a 20 cm track right in front of the food source and the 75%/25% quantiles for each visit.

Experiment 3 – expectation setting via trophallaxis: the nest as an information hub

Ants receive information about available food sources, such as food odour and palatability, through food exchanges (trophallaxis) inside the nest (Provecho and Josens 2009; Josens et al. 2016). An ant beginning a food scouting bout may not have direct information about the quality of the food sources available in the environment, but nonetheless must make a value judgement on their first visit to a food source. The aim of this experiment was to ascertain whether information about sucrose concentrations gained through trophallaxis in the nest affected the perceived value of food sources found outside the nest.

## Experiment 3 - Methods

An ant (forager) was allowed to feed at an unscented sucrose solution droplet of either 0.16, 0.5 or 1.5M at the end of a 60cm long runway. Once the ant had fed and returned to the nest, we observed the number of contacts with other nestmates which occurred until trophallaxis was initiated. When trophallaxis began, we noted the time spent in trophallaxis with the first trophallactic partner. When trophallaxis stopped, the receiving trophallactic partner (receiver) was gently moved from the nest and placed onto the start of a 20cm long runway, offering unscented 0.5M sucrose solution at the end. As the receiver fed, we noted its food acceptance.

Experiment 3 - Results

The time spent in trophallaxis with the receiver increased significantly with increasing molarity (GLMM: estimate= 0.13, z= 4.79, p<0.001).

Acceptance scores of receivers towards 0.5M decreased with increasing molarity of the sucrose solution received through trophallaxis. The interaction of reference molarity and trophallaxis time significantly predicted acceptance (CLMM: estimate=-0.06, z= -2.34, p= 0.02, fig. 5). Ants which received 0.16M inside the nest showed significantly higher acceptance of 0.5M sucrose than ants which received 1.5M (p<0.01, see supplement Table S4.1 for pairwise comparisons).
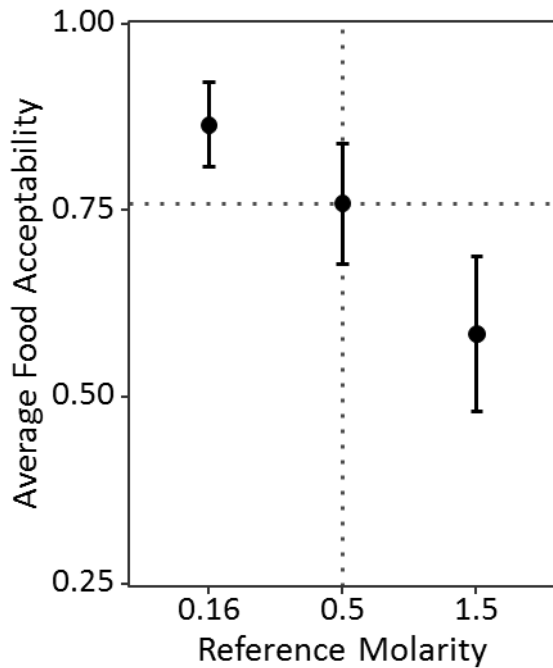
351

352 Fig. 5: Food acceptance shown in experiment 3 for the receivers which received either 0.16, 0.5 or 1.5M through
353 trophallaxis in the nest and then found 0.5M at the end of the runway. Shown are the mean food acceptance
354 (points) and the 95% confidence intervals (error bars) for each reference molarity.

Discussion

356 Kahneman and Tversky's (1979) introduction of Prospect Theory contributed to a major shift in

357 economic research by suggesting that humans do not perceive value in absolute terms, but relative to

358 reference points. Here, we demonstrate parallel findings in an insect, providing for the first time to our

359 knowledge a detailed description of relative value perception in an invertebrate. Positive contrast

360 effects were shown by ants which were trained to low molarities (figures 2 & 3). These ants showed

361 higher acceptance scores and deposited more pheromone after being shifted to medium quality than

362 unshifted ants which received medium quality food throughout the whole experiment. Conversely,

363 ants trained to high molarities showed lower acceptance after being shifted to medium quality

364 compared to the unshifted control, showing negative contrast effects.

365 Another prediction of Prospect Theory, that gains are underemphasized and losses are

366 overemphasized (Tversky and Kahneman 1992), is not supported by the data of our main experiment.

367 Indeed, gains seem to be overvalued while losses are undervalued. This may be due to the

368 psychophysics of our study system: a basic tenant of psychophysics is that the Just Noticeable

369 Difference (JNDs) between two stimuli is a function of the relative difference between the stimuli

370 (Fechner 1860; Stevens 1957; Zwislocki 2009). Thus, ants shifted from 0.1M to medium (0.5M) quality

371 experience a 5-fold increase in molarity, while those down-shifted from 0.9M to 0.5M experience less

372 than a two-fold decrease, although the absolute change was of the same magnitude. This would

373   predict larger shift-changes, in terms of absolute molarity change, for gains than for losses. Indeed, the

374   fact that this is also not seen may imply that losses are indeed – relatively speaking – looming larger

375   than gains for the ants. Finally, it must be kept in mind that acceptance scores are unlikely to be linear,

376   and that pheromone deposition behaviour shows large variation (Beckers, Deneubourg, and Goss

377   1992), making it difficult to use either of these factors to test for over- and undervaluation of gains and

378   losses.

379   While the results of experiment 1 can be explained using alternative, non-psychological mechanisms

380   (sensory saturation and changes in satiation) or rational behaviour based on future expectations, the

381   results of experiment 2 cannot. Ants which were expecting high molarities after scent training showed

382   lower acceptance scores when confronted with unscented medium quality food than ants which

383   expected to find low quality food (figure 4B). This is in spite of all ants undergoing identical training

384   experiences. The only difference between the groups was the odour of the runway on the 9th (test)

385   visit. It is thus unlikely that sensory saturation, increased haemolymph-sugar levels, simple

386   psychophysical effects or expecting pre-shift solutions to return can fully explain the behaviour of the

387   ants in our experiments.

388   Contrast effects were stronger in experiment 1 than in experiment 2. Possible explanations for this

389   pattern are given in supplementary note 1. The fact that we nonetheless see both positive and negative

390   contrasts suggests that such contrast effects are very pronounced. The reduced pheromone deposition

391   seen in the final return in experiment 2 may be due to the change in environment (scented runways

392   to unscented runways) causing a disruption in recruitment behaviour, perhaps due to generalization

393   decrement (E. D. Capaldi 1978; Kimble 1961) or neophobia (Barnett 1958; Johnson 2000, 2000;

394   Mitchell 1976; Pliner and Loewen 1997).

395   Ants which received information about the quality of a food source through trophallactic interactions

396   inside the nest are able to use this information when evaluating new food sources outside the nest.

397   Ants which received low quality (0.16M) food from a returning forager were more likely to accept

398   medium (0.5M) food when foraging themselves than ants which had received good (1.5M) food via

399   trophallaxis (fig. 5). Apart from ants valuing the medium quality food source based only on the quality

400   they received from the returning forager, there is another possible explanation which may lead to the

401   same pattern of food acceptance as shown in this experiment (fig. 5). Ants which expected to find a

402   high quality food source outside the nest may not have accepted a medium quality food source in

403   order to search for the high quality food source which is supposed to be available outside the nest,

404   leading to low food acceptance scores when the reference point was high (Wendt and Czaczkes 2017).

405 Our results suggest that information about sucrose concentrations gained through trophallactic

406 interactions inside the nest can affect the way a newly discovered food source is valued outside the

407 nest. Trophallaxis is a rich source of information: it has been shown to contain chemical cues, growth

408 proteins, and hormones (LeBoeuf et al. 2016). Transfer of scented food (Provecho and Josens 2009;

409 Josens et al. 2016) and aphid-associated information (Hayashi et al. 2017) through trophallactic

410 contacts inside the nest, as well as information about available food qualities gained directly or through

411 pheromone trails (Beckers, Lachaud, and Fresneau 1994; Czaczkes and Beckwith 2018; Roces and

412 Núñez 1993; Roces 1993; Wendt and Czaczkes 2017) have been shown to shape ant behaviour outside

413 the nest. By taking into account information gained inside the nest, recruited workers will be able to

414 evaluate newly discovered food sources in relation to other food sources available in the environment.

415 They will also be able to make better informed decisions on whether it is worth exploiting a new food

416 source or ignore it. Such a pattern would lead to individual ants being more likely to forego food

417 sources which are of lower quality than the average available food sources and thus allows colonies to

418 only exploit above-average food sources. Ants can also use this information to choose between various

419 information use strategies, such as whether to continue exploiting known food sources or be recruited

420 to follow pheromone trails leading to other food sources (Czaczkes and Beckwith 2018). Ultimately,

421 we see the nest serving as an information hub, in which information about currently available food

422 sources can be collected, synthesised, and fed back to outgoing foragers. Relative value perception can

423 therefore be expected to have strong effects not only on the individual behaviour of animals, but also

424 on the collective behaviour of insect colonies, potentially allowing colonies to ignore usually acceptable

425 options in favour of better ones

426 A broad range of behaviours relevant to behavioural economics have now been described in

427 invertebrates. These include overvaluing rewards in which more effort was invested (Czaczkes et al.

428 2018), self-control (Cheng et al. 2002; Wendt and Czaczkes 2017), and state dependent learning

429 (Pompilio, Kacelnik, and Behmer 2006). Many other parallels to human behaviour and cognition have

430 also been described in insects, such as abstract association learning (Czaczkes et al. 2014; Giurfa,

431 Eichmann, and Menzel 1996; Hateren, Srinivasan, and Wait 1990), concept learning (Giurfa et al. 2001),

432 and reward changes affecting voluntary task switching (Czaczkes et al. 2018). Applying concepts from

433 behavioural economics to the study of animal behaviour is likely to yield many further insights.

434 Moreover, the benefits of an interdisciplinary approach are likely to flow both ways. We suggest that

435 invertebrates make attractive models for a broader understanding of behavioural economics in

436 humans. Using animal models allows researchers to avoid pitfalls associated with studies on humans,

437 such as cultural and educational differences (Carter and Irons 1991; Guiso, Sapienza, and Zingales

438 2006) second-guessing of experimenters, and non-relevant reward sizes (Levitt and List 2007) as well

439 as relaxing ethical concerns.

440 Due to its complexity, building models which can accurately predict human behaviour is a challenge.

441 This is compounded by the fact that data on humans obtained in laboratory experiments

442 overwhelmingly stem from game-like designs that are highly artificial and where the economic

443 incentives that can be provided to experimental subjects are severely limited by the research budget

444 of the experimenter (Kahneman and Tversky 1979; Levitt and List 2007). At the same time, there has

445 been much progress in field studies on humans to clearly measure causal relationships (Harrison and

446 List 2004). However, the usefulness of these new techniques (such as field experiments) is clearly

447 constrained by the range of questions and settings to which they can be meaningfully applied. Hence,

448 while behavioural studies on invertebrates also have their limitations (for example, in that inducing

449 expectations is more of a challenge), they can be easily designed to be ecologically meaningful, and

450 offer rewards which are in line with the real-life budgets under which the animals operate. Therefore,

451 we propose that economic models to predict invertebrate decision making may be a complementary

452 step on the way to predict human behaviour.

453 While there is a well-developed tradition of integrating economics and biology (Aw et al. 2009; Aw,

454 Vasconcelos, and Kacelnik 2011; Cheng et al. 2002; Czaczkes et al. 2018; Evans and Westergaard 2006;

455 Lydall, Gilmour, and Dwyer 2010; Wendt and Czaczkes 2017), we feel a critical mass of evidence is now

456 available to consider comparative behavioural economics as a relevant discipline for both biologists

457 and economists.

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