Title: Label-based expectations affect incentive contrast effects in bumblebees

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Abstract

While classic models of animal decision-making assume that individuals assess the absolute value of options, decades of research has shown that rewards are often evaluated relative to recent experience, creating incentive contrast effects. Contrast effects are often assumed to be purely sensory, yet consumer and experimental psychology tell us that label-based expectations can affect value perception in humans and rodents. However, this has rarely been tested in non-model systems. Bumblebees forage on a variety of flowers that vary in their signals and rewards and show contrast when rewards are lowered. We manipulated bees' expectations of a stimulus' quality, before downshifting the reward to induce incentive contrast. We found that contrast effects were not solely driven by experience with a better reward, but also influenced by experience with associated stimuli. While bees' initial response did not differ between treatments, individuals were faster to accept the lower-quality reward when it was paired with a novel stimulus. We explored the boundaries of these label-based expectations by testing bees along a stimulus gradient and found that expectations generalized to similar stimuli. Such reference-dependent evaluations may play an important role in bees' foraging choices, with the potential to impact floral evolution and plant community dynamics.

Introduction

Classic foraging theory assumes that animals know or can easily assess the absolute value of different options [1,2]. However, a wealth of studies in humans and other animals have demonstrated that rewards are often not perceived in absolute terms. Rather, choices are compared to other options available or to reference points [e.g., 3–5]. This idea forms the basis of Prospect Theory in behavioural economics which suggests that decision-making is based on perception of gains and losses relative to a reference point [6,7]. Reference-based evaluation has the potential to create incentive contrast effects, where a discrepancy between reward expectations and perceived value can lead to an exaggerated response of aversion or preference. A consequence of this is that identical options can be perceived differently depending on an individual's recent experience. Incentive contrast effects are taxonomically broad, having been demonstrated across animals such as mice [8], dogs [9], starlings [10], and goldfish [11].

Humans' expectations of reward quality are often based on experience with associated stimuli (e.g. product labels), which can serve as strong reference points in value perception [12–14]. These label-based expectations can influence decisions in several ways. Product labels similar to those of previously encountered products can lead consumers to accept rewards that would otherwise be less preferred or even rejected, a process known as 'assimilation' [15]. Conversely, labels can also have the opposite effect: if an individual expects a higher quality reward based on a familiar label and then encounters a lower quality one, this can lead to increased aversion [16]. For instance, people given cheap wine from a fancy bottle might enjoy

the wine more than if it were poured from its original bottle or they may show stronger aversion than those who are given the cheap wine in its original bottle [17].

Reference-based evaluation may be particularly relevant to guiding foraging decisions for animals with broad diets, allowing individuals to link sensory properties of foods to their nutritional quality [18–20]. For example, honeybees *Apis* and bumblebees *Bombus* are generalist foragers that associate floral traits such as scents, colours, or patterns (i.e. akin to 'labels') with properties of their rewards [21–24], such as the concentration of nectar [25,26]. Bees evaluate nectar (sucrose solution) in reference to their prior experience and exhibit negative incentive contrast to a solution they previously accepted after experiencing higher quality (i.e. concentration) sucrose [25,27–31]. Incentive contrast in bees can be explained at a sensory level (i.e. gustatory sensitivity), where ingestion of higher concentration sucrose reduces the apparent sweetness of lower concentration sucrose [25,28]. However, the direction and magnitude of contrast effects could also be influenced by prior experience with associated stimuli ('labels') (e.g. see [27,32,33]).

In the present study we tested how bees' label-based expectations of a floral signal (colour) influenced perception and acceptance of a lower-quality reward. In our first experiment, bees were trained to associate a colour with a high-quality sucrose reward. We then offered individuals a downshifted reward paired with either the previously-trained colour or a novel colour and measured their probability of acceptance over successive visits. We both addressed bees' first encounter with the downshifted reward, as well as how long it took them to accept the new reward after gaining experience with it. If bees' response to a reduction in quality is purely sensory (i.e. governed by reward value alone), then we expected individuals to respond similarly to the lower-quality reward, irrespective of flower colour. Conversely, if bees form specific expectations about reward quality based on associated stimuli ('labels'), then we expected their responses to the downshifted reward to be dependent on whether it was paired with the familiar or novel stimulus. We found that bees took longer to accept a downshifted reward on a familiar stimulus, indicating a possible cost to flowers that appear similar but offer lower rewards. In a second experiment we explored how similar floral stimuli needed to be to bear this cost of higher expectations.

Methods

a) Experiment 1: Is incentive contrast affected by label-based expectations?

We used worker bumblebees *Bombus impatiens* from commercially-reared colonies (n=3) (Koppert, USA). We used 20 bees per treatment (10 for each colour combination), with treatments equally represented across colonies (Table S2). Individuals were trained to a colour (blue or yellow) paired with a high-quality reward (8µl of 50% w/w sucrose) over three consecutive trials spaced 5 minutes apart. Within each trial, individuals visited ~10 rewarding flowers and consumed all rewards; the number of flowers visited did not differ across treatments (for additional information see Supplementary Material). Following these three training trials, bees were presented with a lower quality reward in a 'test' trial (8µl of 30% w/w sucrose) paired with either the familiar or a novel colour (Figure 1a). Our experimental nectar concentrations were designed to match natural variation found in bumblebee-visited flowers [34]. In the test trial we recorded bees' responses to downshifted rewards over their first 20 visits to flowers. We chose 20 successive visits based on our expectation that bees would increasingly accept the

downshifted reward over this timescale. Acceptance was measured as bees consuming the solution, while rejection was characterized by bees probing the solution and exiting the flower without imbibing (video S1).

b) Experiment 2: Do responses generalize to similar stimuli?

To determine how similar stimuli needed to be to bear the cost of higher expectations, we tested bees using a range of colour stimuli. Individuals (n= 85 from 5 colonies; Table S1) were trained to a blue stimulus paired with a high-quality reward across three training trials (Figure 1b). We then presented individuals with one of five possible colours. Four of these stimuli ranged from blue to green and were increasingly different from the originally-trained colour whilst still being discriminable to foragers [35] (chromatic contrasts calculated in the bee colour space model [36,37]; Table S1). The fifth colour was yellow, serving as a 'novel' stimulus as in Experiment 1. We used a slightly different blue stimulus in Experiment 2 than Experiment 1, while the yellow was the same across both experiments. Again, we measured individuals' acceptance of the downshifted reward over their first 20 visits.

c) Data analysis

Analyses were carried out in R version 4.0.5 [38]. We used generalized linear models (GLMs) and linear mixed-effect models (GLMMs) with the glm() and glmer() functions in the lme4 package [39]. We first addressed whether bees across treatments differed from each other in their initial acceptance of the downshifted reward on their first floral visit using binomial GLMs including 'acceptance' (accept/ reject) as the response variable and 'stimulus type' (familiar/ novel) as the explanatory variable. After finding that treatments did not differ in their initial acceptance, to address the possibility that this was due to a lack of statistical power, we also addressed whether bees' acceptance behavior differed across treatments over their first five visits using binomial GLMMs including the response variable 'acceptance' and the explanatory variables 'stimulus type' (different for each experiment; see Fig. 1) and 'visit number' (continuous variable), and 'bee' and 'colony' as random factors. To determine whether bees' acceptance behavior varied across all 20 visits as they gained experience with the new flower type, we ran binomial GLMMs with the response variable 'acceptance', the explanatory variables 'stimulus type' (different for each experiment; see Figure 1), 'visit number' (continuous variable), and 'bee' as a random factor. We also included 'colony' as a random factor in Experiment 2, but not Experiment 1 due to a singularity issue. Finally, to determine whether the number of visits before acceptance differed across treatments, we carried out a GLM with a quasi-Poisson distribution using 'number of visits until acceptance' as the response variable and 'stimulus type' as the explanatory variable. Data and analyses are available on Dryad [40].

Results

a) Experiment 1

There was no difference between treatments in bees' acceptance on their first visit (z = -0.644, p =0.519; Figure S2), nor in acceptance across the first five visits (treatment: z= -1.035, p=0.301).

However, bees which encountered the novel stimulus accepted the reward faster over the first 20 visits compared with bees that encountered the same stimulus (stimulus × visit number: z = 2.508, p = 0.0122; stimulus: z = -0.211, p = 0.833; Figure 2a). As was expected from previous work on contrast effects, all bees were more likely to accept the downshifted reward over successive visits (visit number: z = 7.448, p <0.001). The colour bees were trained to (blue vs. yellow) did not affect acceptance (Figure S4). There was no difference between treatments in the number of visits before acceptance (t_{38} = 0.790, p = 0.435; Figure S3).

b) Experiment 2

When we tested bees across a range of stimuli that varied in their degree of difference from the trained stimulus, we found that they generalized their responses, showing similar rejection behaviour across the full range of blue/green stimuli (treatment: z = -1.296, p = 0.194; treatment × visit number: z = 1.611, p = 0.12; Figure 2b; Table S3). In line with our results from Experiment 1, we found a strong trend towards bees being more likely to accept the novel yellow colour compared to Blue A across visits (Yellow-Blue A comparison: treatment × visit number: z = 1.815, p = 0.0696; Figure 2b); this effect may not have been as strong as in Experiment 1 because the stimuli were more similar to each other (Table S1). Again, bees were more likely to accept the downshifted reward across visits (z = 6.268, p < 0.001) and treatments did not differ in bees' acceptance on their first visit (z= -1.185, p=0.236; Figure S5), nor in their acceptance across the first five visits (treatment: z = -0.917, p = 0.359). There was also no difference in the number of visits before acceptance (t_{83} = 0.152, p = 0.879; Figure S6).

Discussion

Bees' perception of floral rewards is strongly influenced by prior experience. By comparing bees' acceptance behaviour towards downshifted rewards paired with familiar or novel colour stimuli, we found that incentive contrast effects were not only sensory, but also affected by individuals' prior experience with associated stimuli. Bees' initial rejection behaviour did not differ between treatments, with bees showing high rates of initial rejection in both familiar and novel treatments. Over repeated presentations, however, individuals were faster to accept a lower-quality reward when it was paired with a novel stimulus. Thus, both immediate taste perception and prior expectations based on stimulus value influence incentive contrast. While previous work has shown that bumblebees that encounter a downshifted reward are more likely to switch to a new colour than bees that encounter the same quality reward [29,30], ours is the first to demonstrate that incentive contrast effects are stimulus-dependent. These results indicate that when foraging, bumblebees will likely have different criteria of a flower's acceptability based on their previous experience with similar flower types, rather than based on their experience with floral rewards *per se*.

At a cognitive level, our results can be explained by when bees learn, they form associations between a specific stimulus and reward. If this stimulus is then changed to predict a lower-quality reward, there is a greater discrepancy between expectation and outcome than for a novel stimulus that does not carry this reward expectation. Thus, the behavioural response of rejection is stronger for the learned stimulus than the novel one. Upon repeated visits to the test flowers, bees in the familiar treatment undergo extinction of the previously learned association. While bees in the novel treatment also have expectations of reward value based on their training

experience, the association will be less strong and thus they more readily accept the new flower faster. Extinction of reward expectations based on floral signal has similarly been shown to influence acceptance behavior in honeybees [41]. Our result and proposed cognitive mechanism is supported by classic work on incentive contrast in rats [42,43]. For example, rats only showed incentive contrast in contexts when they expected a higher reward, and not in contexts that predicted a lower reward [43]. However, while this topic has been explored in experimental psychology using model organisms, few studies have directly addressed how label-based expectations influence acceptance behaviour in other animals and in ecologically-relevant scenarios. One exception comes from a study using ants (*Lasius niger*) that found equivalent results to our own [33]. However, in a different study with this species, when the odour of the reward was manipulated, ants formed label-based expectations in the opposite direction ('assimilation'), consuming more of the downshifted reward when it contained the odour that was previously associated with a high-quality reward [32]. This result may be explained by the odour cues being incorporated into the reward rather than the label or associated stimulus, meaning that the odour-containing downshifted reward may have been perceived as more similar to the previous, higher-quality reward instead of altering ants' reward expectation.

What are the implications of our findings for bumblebee foraging behaviour? Floral rewards can be dynamic, with nectar concentration varying within and between species [44–46]. Bumblebees can respond flexibly to this variability, switching between the flowers they visit based on their reward history [47,48]. When a flower type or patch drops in reward value, foragers will switch to visiting alternative food sources. For instance, bumblebees will fly farther and bypass more flowers following a sequences of encounters with unrewarded flowers [49]. Results from the present study suggest that, in addition to this, bees may have different acceptability thresholds of different flowers depending on their previous experience with the same or similar species.

In our second experiment, we found that bees generalized their expectations of quality to similar colours; this finding is in line with our understanding of how bees learn, requiring differential conditioning for fine-colour discrimination such as this [50,51] (as opposed to absolute conditioning used in these experiments). These results may have implications for floral signalling. Co-flowering species with similar floral traits (e.g. colour) can benefit from facilitation, i.e. increased fitness due to increased pollinator sharing (e.g. [52–54]). Our results indicate that there may also be costs to having similar floral traits to other species: without having similarly high rewards, these plants may bear the cost of bees being more sensitive to a lower-quality reward than they would on a novel flower. Likewise, there may be a benefit to being dissimilar: rare flower types that have a novel signal may 'get away' with offering cheaper rewards. Our findings also indicate that bees may be less tolerant of reward variability within than between species. This would both favour novel species within a patch and could exert pressure on a given species to not exceed certain limits of reward variability. Indeed, nectar sugar concentrations are generally less variable within than between species [55]. Bees' discrimination against lower-quality flowers that they expect to have higher rewards may also help explain 'honest' signalling of floral rewards within [56] and across species [57].

Taken as a whole, our results indicate that floral signals can serve as labels that mediate bees' expectations of floral rewards. Of course, real flowers have additional levels of complexity such as multimodal stimuli [58] and multiple rewards [59–62]. Future work might address how bees' relative value perception of flowers is affected by multiple rewards on different axes of reward quality [63]. Additionally, real flowers will have greater variability in reward quality than the

artificial flowers used here, and this variability may differ across floral communities [44,64]. Going forward, future research could explore how this environmental noise influences incentive contrast effects. By determining how decision-making is guided by experience with floral stimuli, we can make more informed predictions both about bees' foraging behaviour and the evolution of signalling traits in flowers.

Figure legend

Figure 1. Experimental design for a) Experiment 1 and b) Experiment 2. In both experiments, we trained bees to a high-quality reward before offering them a downshifted reward paired with either a familiar, similar, or novel stimulus.

Figure 2. (a) Experiment 1: Proportion of bees accepting downshifted rewards paired with a familiar or novel colour stimulus across the first 20 visits in the test trial. Shaded error bars show 95% confidence intervals. **(b)** Experiment 2: Proportion of bees accepting the downshifted reward across visits in the test trial across the five stimuli.

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