Bumblebee social learning can lead to suboptimal foraging choices

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Bumblebees are influenced by socially acquired information when deciding on which flowers to forage. In some circumstances, however, this attraction towards conspecifics may lead to suboptimal foraging performance because the presence of multiple pollinators typically results in a faster rate of nectar depletion in the flower. We tested the capacity of bees to learn to avoid flowers occupied by conspecifics when they offered a lower reward than unoccupied similar flowers. Bumblebees were able to discriminate between poorly and highly rewarding flowers by using the presence of a nonsocial cue (a wooden rectangular white block). When poorly rewarding flowers were indicated by social cues (model bees), however, bees did not discriminate between the two flower types except when an additional cue was provided (flower colour). These findings indicate that bumblebees attach particular meaning to conspecific presence on flowers, even when this could lead to suboptimal foraging performance. The relatively lower flexibility in the use of social than nonsocial cues suggests a biased positive value of conspecifics as indicators of rewarded flowers.

A wide range of animals use information that originates from other individuals to make vital decisions regarding habitat, food, mates or predators (Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Hoppitt & Laland, 2013; Leadbeater & Chittka, 2007b). For example, by attending to the outcome of conspecific behaviour, animals can reduce the costs of trial-and-error sampling associated with personal exploration (Galef & Giraldeau, 2001; Hoppitt & Laland, 2013). However, these social learning strategies are only valuable if enough individuals within the group also provide individually acquired knowledge (Rieucau & Giraldeau, 2011). Social learning inevitably increases intraspecific competition and limits alternative and independent sampling, thus potentially leading to suboptimal choices and, in the worst scenario, to informational cascades as observed in market crashes in economics or false flock alarm flight, for example (Giraldeau, Valone, & Templeton, 2002; Rieucau & Giraldeau, 2011). Consequently, animals should not always rely on social cues when they are available, but attach different values to social and individual information depending on the context. Theoretical analyses have predicted strategies about when animals should copy and from whom (Laland, 2004). In some circumstances determined through personal experience or from evolutionary processes, animals

should ignore social stimuli or even actively avoid them while in others it may pay individuals to selectively attend to conspecific cues.

Bumblebees are influenced by the behaviour of conspecifics when deciding from which flower species to forage (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b; Dawson, Avarguès-Weber, Leadbeater, & Chittka, 2013; Kawaguchi, Ohashi, & Toquenaga, 2006; Kawaguchi, Ohashi, & Toquenaga, 2007; Leadbeater & Chittka, 2005, 2007a, 2009; Mirwan & Kevan, 2013; Plowright, et al., 2013; Smolla, Alem, Chittka, & Shultz, 2016; Worden & Papaj, 2005). Uninformed individuals tend to land on flowers occupied by conspecifics and foragers can decide, by observing conspecifics' behaviour, which flower species might be profitable (Dawson, et al., 2013; Worden & Papaj, 2005). Such behaviour is not indiscriminate: bumblebees tend to rely more on social cues when they do not have personal information available about the surrounding floral resources (Jones, Ryan, & Chittka, 2015; Kawaguchi, et al., 2007; Leadbeater & Florent, 2014) or when flower investigation is costly (Saleh, Ohashi, Thomson, & Chittka, 2006). They also tend to avoid occupied flowers in highly competitive contexts (Baude, Danchin, Mugabo, & Dajoz, 2011; Plowright, et al., 2013) or if social information is less reliable than other flower features (Dunlap, Nielsen, Dornhaus, & Papaj, 2016). Finally, bumblebees have been shown to ignore social cues if they are not informative (Leadbeater & Chittka, 2009) and to flexibly treat them as attractive or repellent cues depending on the associated outcome (Dawson, et al., 2013; Saleh & Chittka, 2006).

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In the current study we investigated whether attraction towards a conspecific bee can also be modulated by the relative value of the information acquired socially. Flowers that were occupied by conspecifics offered relatively lower reward than the other flowers. Would the bees succeed in learning to suppress their attraction to conspecifics and selectively visit unoccupied flowers? We compared the capacity of bees to modulate their initial preference for occupied flowers both in a social (model bees used as indicators) and in a nonsocial context (flower colours or wooden blocks used as indicators).

METHODS

Three bumblebee, *Bombus terrestris*, colonies, provided by Syngenta Bioline Bees (Weert, the Netherlands), were used. The colonies were housed in wooden nestboxes (28 × 16 cm and 11 cm high) connected to a flight arena (117 × 72 m and 30 cm high) covered by a UV-transparent Plexiglas ceiling. Light conditions mimicked the natural daylight spectrum and the flicker frequency of the light was set beyond bumblebee's flicker fusion frequency (Skorupski & Chittka, 2010). The nestboxes and the flight arenas were connected via a Plexiglas tube with sliding doors allowing a controlled individual access to the arena. Individual bees were identified by paint marks, and were removed from the colony after testing. Bees were fed daily with pollen and with a 30% (volume/volume) sucrose solution provided in perforated plastic tubes placed inside the nestbox when necessary. The nest was kept in dim red light (hard to detect for bees) when food was supplied to minimize the chance of bees forming positive associations between food and the visual appearance of nestmates within the nest. However, the bees could see each other in a nest compartment in which food was never provided. The social cues used during the experiments were artificial model bees (see 'social cue' in 'Treatment groups' section below for details) to exclude any possibility of olfactory-mediated recognition. The bees were not allowed to forage in the arena before the experiment.

Artificial flowers consisted of coloured Perspex squares (25 × 25 mm and 5 mm high) offering 20 µl of sucrose solution from a small hole (diameter 5 mm) in the centre. These were randomly placed in the arena on top of transparent cylinder supports (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b).

The bees were first individually subjected to a pretraining phase, consisting of five foraging bouts in which typically six flower visits were necessary to collect a full crop of 30% sucrose solution. A foraging bout ended when the bee stopped visiting flowers and returned to its nest. In this phase, only green (Green 6205 Perspex from Hamar Acrylic Fabrications Ltd, London, U.K.) flowers were displayed and were all rewarded.

The subsequent training phase also consisted of five foraging bouts, in which bees had to discriminate between flowers containing high rewards (50% sucrose solution) from flowers offering low rewards (10% sucrose solution). A cue informed subjects about which flower was offering a high or low reward, but cues varied between treatment groups (Fig. 1). The flowers were either cream (Cream 128 Perspex) or fuchsia (Red 4415 Perspex) coloured in this phase (Fig. 1). These colours were thus novel for the bee and were easily distinguished from each other (0.3 hexagon units) and from the green flowers (respectively 0.3 and 0.4 hexagon units) used in the previous phase (Chittka, 1992; Dyer & Chittka, 2004). In the hexagon colour space, a level of 70% discriminability corresponds to approximately 0.1 hexagon units. After each foraging bout, the flowers were washed with an ethanol solution to remove scent marks and their positions varied within the arena.

A 3 min nonrewarded learning test followed the training period. In this test, the flowers contained only plain water. Each bee was trained and tested individually.

Treatment Groups

Social cue

Bees (N = 10) from this group were first familiarized with conspecifics being associated with rewarding flowers (30% sucrose solution) during the pretraining phase: model bees were placed on six of 12 green flowers displayed with a random spatial arrangement in the arena. The opportunity to associate conspecifics with reward has been shown necessary for social learning to occur (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b). Model bees were shaped using oven-hardening modelling clay (Fimo Soft, Staedtler) and painted with a colour pattern matching that of *B. terrestris*. We used the following paints: yellow (Rheotech, Acrylics Bright Yellow); black (Winsor & Newton, Griffin fast drying oil painting, ivory black) and white (unpainted modelling clay) to reflect natural *B. terrestris* colour properties, as assessed by bumblebee colour vision (Skorupski, Döring, & Chittka, 2007; Stelzer, Raine, Schmitt, & Chittka, 2010) and quantified in a bee colour space model (Chittka, 1992). In the subsequent training phase, six flowers occupied by model bees offered a low reward (10%), while six unoccupied flowers of the same colour offered a high reward (50%; Fig. 1). Only fuchsia flowers were used for half of the tested bees, while the other half experienced only cream flowers, thus avoiding potential colour influence.

Flower colour cue

Bees (N = 10) from this treatment group were presented with 12 rewarding (30% sucrose solution) green flowers without any associated cue in the pretraining phase and had to discriminate cream from fuchsia flowers in the training phase. One flower colour (fuchsia or cream depending on bees in a counterbalanced design) was associated with the low (10%) flower reward while the other provided a high (50%) reward (Fig. 1). As these colours can be easily discriminated by the bees, results from this group provide a baseline level of bees' performance in a discrimination task based on reward level comparison.

Nonsocial cue

Bees (N = 10) from this group experienced nonsocial cues placed on half of the 12 green flowers in the pretraining phase to allow positive association between the cue and rewarding flowers. Both occupied and unoccupied flowers were equally rewarding (30% sucrose) in this pretraining phase. The nonsocial cues consisted of cuboid, white wooden blocks (Winsor & Newton, Griffin fast drying oil painting, titanium white) of a size similar to the bees (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b). The bees then had to discriminate flowers by the presence of this nonsocial cue on top of them ('occupied' versus 'unoccupied' flowers) in the training phase (Fig. 1). Occupied flowers offered a low reward (10% sucrose) while unoccupied flowers were highly rewarded (50% sucrose). There were six flowers in each category that were randomly placed in the arena. Their positions varied between foraging bouts. All flowers were of the same colour (fuchsia or cream depending on bees in a counterbalanced design).

Social and flower colour cues

Bees from this group (N = 10) were pretrained with model bees. In the training phase, the bees faced six cream and six fuchsia flowers. One type of flower (fuchsia or cream depending on bees in a counterbalanced design) was associated both with model bees and a low reward (10%) while the other type offered a high reward (50%; Fig. 1).

Data collection was run in parallel with two different colonies used sequentially for the following treatments: the flower colours, nonsocial objects or model bees as indicator of the less profitable
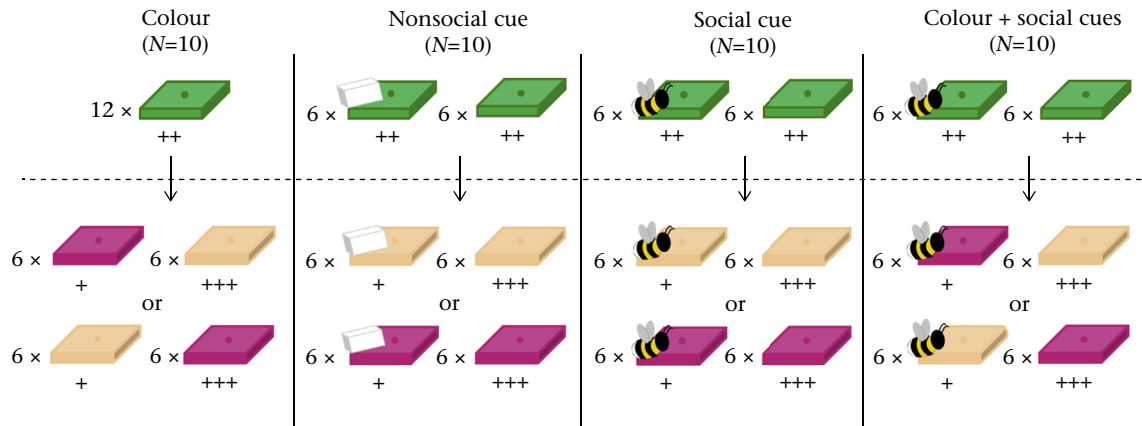
Figure 1. Presentation of the different experimental treatments. Treatment groups differed by the nature of the cue used to discriminate poorly and highly rewarding flowers. In a pretraining phase, the bees were trained for five foraging bouts to collect a mid-level sucrose reward (++; 30% sucrose solution) on 12 green artificial flowers. Bees from the corresponding treatment groups were familiarized with the presence of social or nonsocial cues associated with half of the flowers in this phase. In the subsequent training phase, bees were presented with six artificial flowers of the high-reward category (+++; 50% sucrose solution) and six flowers of the low-reward category (+; 10% sucrose solution) randomly placed into the foraging arena. The training lasted five foraging bouts and was followed by a nonrewarded test (during which the flowers of both categories were filled with water).

flowers. The last condition, in which both the flower colour and the presence of a model bee could be used as indicator, was tested afterwards with a third colony.

Statistical Analysis

The experiments were video-recorded and the bees' choices for the flowers assessed with the videos to allow accurate recording. A bee's choice was scored if the bee landed on the flower even if it did not sample the sucrose solution.

The performance (i.e. proportion of landings on highly rewarding flowers) of bees during a foraging bout in the training phase as well as during the nonrewarded tests was compared to a theoretical chance level of 50% with nonparametric Wilcoxon tests.

Evidence for learning was examined by testing whether performance changed during the training phase. Separate generalized linear mixed models (GLMMs) were fitted for each of the treatment groups (R software, version 3.3.2, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org; lme4 package, Bates, Mächler, Bolker, & Walker, 2014). The proportion of landings on highly rewarding flowers was the dependent variable for these tests; thus, a binomial error structure was used. There was a repeated measures design, with individual subject serving as a random effect. Initially, colony, rewarded colour (fuchsia or cream) and foraging bout number were used as fixed effects (colony was treated as a fixed effect because only three colonies were used in the experiment). However, neither colony nor rewarded colour improved model fit (ΔAIC < 2, Burnham & Anderson, 2004) and were consequently dropped from the final model (which thus had only foraging bout number as a fixed effect). Significance of the fixed effect was tested using likelihood ratio tests (LRTs).

The performance of bees in the nonrewarded test performed after training was compared between treatment groups using nonparametric Mann−Whitney U tests.

While variation between groups in the second and third sets of analyses would indirectly imply variation in the rate of learning between groups, this was tested directly in the fourth set of analyses. GLMMs with a binomial family were used, with the proportion of landings on highly rewarding flowers as the dependent variable. Individual subjects served as a random effect. Foraging bout number, the treatment group and the interaction between these variables were included as independent variables. Significance of the fixed effects was tested using LRTs.

Ethical Note

All bees were kept in their natal colony environment in naturally dark conditions. Pollen and sucrose solution were provided with minimum disturbance of the bees and under dark conditions (red light, poorly visible to the bees). The colonies were never short of food. During the experiments, forager bees were only trained and tested if they voluntarily engaged in foraging behaviour. The bees were tagged with a dot of paint on the thorax while feeding. All necessary bee handling procedures and transfers were carefully done using plastic pots rather than forceps to reduce stress of handling. After completing the experiments, the tested bees were removed from the colony and euthanized by placing them in a freezer to avoid any possibility of testing the same bee twice if the paint mark came off. Bees' natural response to low temperatures is to enter a hibernation-like state, so that they are asleep before dying; this is therefore a humane way of killing insects.

RESULTS

Social Cue

When conspecific models were used as a reliable indicator of poorly rewarding flowers, bees initially showed no preference for either occupied or unoccupied flowers ($N = 10$, first foraging bout: mean ± SEM = 46.7 ± 3.7%). This is in line with other studies (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b) in which bees showed attraction to the flower type indicated by conspecifics (stimulus enhancement), but not necessarily to the individual flowers occupied by other bees (local enhancement). Moreover, bees persisted in visiting flowers occupied by conspecific models during the five foraging bouts as their preference did not differ significantly from 50% (chance level) in any of the training bouts ($N = 10$, first foraging bout: mean ± SEM = 46.7 ± 3.7% of landings on the high-reward unoccupied flowers; $Z = 1.62$, $P = 0.11$; last foraging bout: mean ± SEM = 55.8 ± 3.9% of landings on the unoccupied flowers; $Z = 0.41$, $P = 0.68$; Fig. 2a). There was no significant effect of the foraging bout number on performance showing that the bees did not change their performance in the discrimination task

during training (LRT: $\chi_1^2 = 0.64$, $P = 0.42$). This difficulty in learning to avoid occupied flowers was confirmed by their behaviour in the nonrewarding test, where bees' choices did not differ significantly from chance (mean $\pm$ SEM $= 56.2 \pm 3.7\%$ of landings on the unoccupied flowers that were associated with high reward in the training phase; $Z = 1.62$, $P = 0.11$; Fig. 2b).

Flower Colour Cue

To verify that the difficulty in learning to selectively visit unoccupied flowers in the social treatment was not due to a lack of motivation to discriminate between two rewarded flower types, we trained a novel group of bees again with highly profitable artificial flowers (50% sucrose solution reward) versus less rewarding flowers (10% sucrose) but this time the two flower types differed in colour, an obvious visual cue for the bees. Bees from this group quickly succeeded in preferentially visiting the highly rewarding flowers. Bees significantly improved their performance across the five foraging bouts ($\chi_1^2 = 4.90$, $P = 0.03$; Fig. 2a). In their first foraging bout, there was no evidence for a preference for either flower ($N = 10$; mean $\pm$ SEM $= 49.7 \pm 11.5\%$ of landings were on correct highly rewarding flowers; $Z = 0.81$, $P = 0.42$; Fig. 2a), but in the last foraging bout, they significantly preferred the highly rewarding flowers ($N = 10$; mean $\pm$ SEM $= 74.4.0 \pm 10.9\%$; $Z = 2.44$, $P = 0.01$; Fig. 2a). In the subsequent nonrewarding test, the bees again preferred the flower colour that had been associated with high rewards during the training phase (mean $\pm$ SEM $= 79.1 \pm 7.3\%$; $Z = 2.92$, $P = 0.003$; Fig. 2b).

NonSocial Artificial Cue

The bees' performance in the colour group confirms that the failure of the bees to use social cues as unique indicators of less rewarding flowers was not due to a lack of motivation for a learning task based on different reward levels. Results from the social cue group were also compared with the behaviour of bees that had to rely on the presence of cues of similar perceptual saliency except bearing no ecological meaning. Bees that were thus familiarized with wooden blocks attached to flowers in the pretraining phase were initially attracted to the flowers associated with the blocks in the subsequent training phase (first foraging bout: $N = 10$,

mean $\pm$ SEM $= 37.3 \pm 3.3\%$ of landings were on highly rewarding unoccupied flowers; $Z = 3.11$, $P = 0.002$; Fig. 2a). Their initial preference in the training phase was thus already different from those bees in the social cue group. In line with previous observations (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b), bees in the nonsocial cue group generalized the cue presented to them in the pretraining phase (wooden block) to the new flowers where the wooden block was the only familiar element, and initially preferred these flowers. Bees in the social group conversely found all flowers of the type that were perceived to be visited by a conspecific attractive, without preferring the individual occupied flowers. In addition, there was another pronounced difference in that bees from the nonsocial cue group subsequently succeeded in reversing their preference, progressively increasing the proportion of their choices for the alternative unoccupied flowers (last foraging bout: mean $\pm$ SEM $= 73.6 \pm 4.5\%$ of choices made on unoccupied flowers; $Z = 3.73$, $P < 0.001$); there was thus a significant improvement in performance across the five foraging bouts ($\chi_1^2 = 19.96$, $P < 0.001$; Fig. 2a). The learned aversion towards the nonsocial cues was confirmed by the bees' behaviour in the nonrewarding test (mean $\pm$ SEM $= 78.9 \pm 3.1\%$ of landings on the flowers without a wooden block attached; $Z = 4.04$, $P < 0.001$; Fig. 2b). It thus appeared that bees showed a greater capacity to learn with wooden block cues than to learn with social cues. In line with this conclusion, there was a significant interaction during the training phase between group (social versus nonsocial) and foraging bout ($\chi_1^2 = 7.61$, $P = 0.006$), and a significant difference in the performance of the two groups in the nonrewarded test ($Z = 3.41$, $P < 0.001$).

Social and Colour Cues

Finally, another group of bees faced a situation in which flower colours could be used as an indicator of reward level in conjunction with the presence of conspecifics. In this case, results were different from the condition where only social cues were provided, as bees were able to learn to avoid occupied flowers when associated with an additional colour cue. The bees were first attracted by the occupied flower type (first foraging bout: $N = 10$, mean $\pm$ SEM $= 36.0 \pm 11.9\%$ of landings were on the highly rewarding alternative flower type; $Z = 2.43$, $P = 0.02$; Fig. 2a) but easily learned to preferentially visit the alternative more rewarded flower colour (last foraging bout:
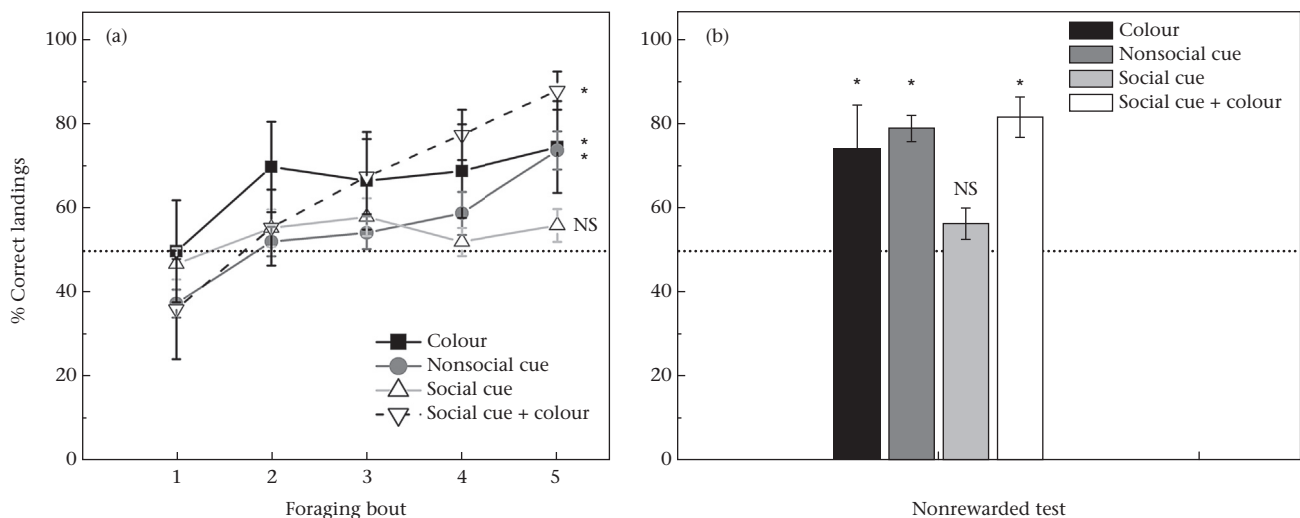

Figure 2. Performance of the different treatment groups. (a) Percentage of landings on flowers of the high-reward category in the five foraging bouts during training. (b) Percentage of landings on flowers of the high-reward category in the nonrewarded test. The dotted lines indicate chance level (50%). The data represent the means $\pm$ SEM ($N = 10$ for each treatment group). *$P < 0.055$ (training: foraging bout effect; nonrewarded test: comparison with a theoretical 50% chance level).

mean ± SEM = 87.8 ± 4.5% of landings on the unoccupied flowers; $Z = 4.07$, $P < 0.001$; Fig. 2a). There was a significant improvement in performance across the five foraging bouts ($\chi^2_1 = 16.48$, $P < 0.001$). The bees preferred the unoccupied flowers in the nonrewarded test (mean ± SEM = 1.5 ± 4.8% of landings on the flowers of the appropriate colour; $Z = 3.23$, $P = 0.01$; Fig. 2b). Thus, adding colour information as a cue for the highly rewarding flowers seems to allow the bees to restore performance by comparison with having only the social model as an available cue even if direct comparison is not possible as different colonies were used for these treatment groups.

DISCUSSION

Bumblebees continued to visit flowers occupied by conspecifics even when this led to suboptimal foraging choices. While bees learned to avoid poorly rewarding flowers when they were indicated by nonsocial cues, they failed to do so when poorly rewarding flowers were only indicated by the presence of a model bee. Thus, this result does not reflect an incapacity to repress attraction for demonstrated flowers but rather a selective difficulty to use conspecifics as an avoidance cue. However, when a cue was provided (flower colour) in addition to the social cue, the bees then successfully learned to avoid the less profitable flower type. This is equivalent to a natural scenario with either one or two flower species available in a patch. When two flower species are available, and only one is foraged upon by other bees, a newcomer will initially be drawn to the popular species, but learn to reverse its preference when experience shows that this is a maladaptive option. Conversely, if only one flower type is available, but some flowers are occupied but poorly rewarding, bees may visit occupied and unoccupied flowers indifferently, indicating that when conspecific presence is the sole indicator of poor reward, bees do not display readiness to learn this as a cue to stay clear of these flowers.

Socially induced maladaptive foraging choices have been demonstrated previously in various animal species: in insects such as *Temnothorax albipennis* ants (Franks & Richardson, 2006) and honeybees, *Apis mellifera* (Dechaume-Moncharmont, et al., 2005; see Grüter & Leadbeater, 2014 for a review), guppies, *Poecilia reticulata* (Laland & Williams, 1998), dogs, *Canis familiaris* (Pongrácz, Miklósi, Kubinyi, Topál, & Csányi, 2003) and nutmeg mannikins, *Lonchura punctulata* (Rieucau & Giraldeau, 2009), for example, have all been shown to preferentially join others in exploiting a demonstrated food source or foraging route even when more profitable options were available with individual investigation. While these results demonstrate costs involved when social learning takes precedence over individual learning, it is crucial to highlight that the attraction to conspecifics, or to resources indicated by them, is likely to be beneficial in many settings, for example for naïve individuals to locate suitable food sources faster than they would by individual exploration, and also for the potential reduction in predation risk. Indeed, the selective pressure to stay in the group may often outweigh energetic considerations, particularly in the case of gregarious species such as guppies living in shoals or nutmeg mannikins forming flocks. In our bumblebee species, conspecifics may also indicate safety from predators, thus favouring preference for socially occupied flowers (Dawson & Chittka, 2014).

Beyond the question of the optimality of social learning, our results contribute to the debate about the specificity of social learning mechanisms. It has been suggested that social learning may not differ from nonsocial associative learning except for the nature of the cues (Giurfa, 2012; Heyes, 2011; Leadbeater & Chittka, 2007b). Thus, preference for socially exploited food sources could be explained by previous experience. When conspecifics have been associated with profitable food sources, their presence becomes attractive through basic Pavlovian mechanisms. Indeed, naïve bees with no previous social foraging experience tend to ignore conspecific choices in their foraging decisions (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b; Dawson, et al., 2013) suggesting the decisive role of prior associations between social cues and a reward. In addition, the preference for socially demonstrated flowers can be changed into an avoidance if the tested bees formed an association between conspecifics and a bitter aversive solution beforehand (Dawson, et al., 2013). Our results here, however, add to other recent findings (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b; Dawson & Chittka, 2012; Smolla, et al., 2016) suggesting that social cues have special meaning in guiding choices of foraging options.

Indeed, even though we controlled the bees' experience with both conspecifics in the foraging context and the nonsocial objects (wooden blocks), the bees behaved differently when faced with social versus nonsocial indicators in our experiment, suggesting a specific and different treatment of social information that cannot be explained solely by the individual's history.

This conclusion, that social cues play a privileged role as information providers, confirms and expands our previous findings with the same bumblebee species, *B. terrestris*. In an earlier study (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b), bumblebees followed different flower choice strategies when model bees (social cues) or wooden white blocks (nonsocial cues) provided an indicator of high-quality food resources. While bees from the social experimental groups, which had foraging experience with conspecifics, were attracted equally by all flowers of the same colour whether or not they were occupied by a model bee ('stimulus enhancement'), no generalization of preference between occupied and unoccupied flowers of the same type was observed when nonsocial cues were used as indicators ('local enhancement'; Avarguès-Weber, A. & L. Chittka, 2014a, 2014b). This difference in flower choice strategies is reflected by the bumblebees' initial behaviour in our current study when confronted with our training situation. In the nonsocial group, bees were attracted preferentially to the flowers with cues (i.e. by the cues themselves due to their positive association with reward in the pretraining phase) while no bias between categories of flowers was found in the social group, as predicted by a stimulus enhancement strategy (see results from the first foraging bout, Fig. 2a). Importantly, when socially occupied flowers differed in their colour from the unoccupied flowers (social and colour cue group), an initial preference was observed for the occupied flowers. The pretraining situation was identical in the social cue and the social and colour cue groups but led only to an observed preference for the occupied flowers in the second case while no generalization was possible between pretraining and training flowers without additional cues, due to the pronounced colour difference. Such social learning about a flower type rather than a specific individual flower might be an adaptive behaviour to reduce local competition and to minimize visits to depleted flowers.

The different strategies exhibited by the bees in social versus nonsocial learning may also help explain the selective difficulty they showed in the current study in repressing their attraction to conspecific-occupied flowers. Learning information about the characteristics of the flowers visited by conspecifics instead of their individual location only leads the bees to treat as equivalent all flowers of the same colour, independent of the presence or absence of social cues. As a result, bees appear to only consider flower characteristics in their foraging decisions, while ignoring the presence of conspecifics. This induces a difficulty in learning a new reward rule based on the categorization of conspecific-occupied versus unoccupied flowers, at least in the time frame of our

experiments. It is plausible that extending the experiment length or introducing a penalty for visiting occupied flowers would have allowed the bees to succeed in the task.

The current study extends our knowledge about how bumblebees use social cues in a foraging context. Social attraction has a clear influence on bumblebees' decisions and this social attraction does not have the same degree of plasticity as nonsocial associative learning. The origin of the special nature of social learning that we demonstrated, however, remains unresolved. It may be the consequence of a perceptual bias in bees' visual template for conspecific bees. Such classification of model bees as live animals may prevent bees from processing these social cues as features of the flowers themselves. Through previous experience with live nestmates, bees could also have learned to associate the visual patterns of conspecifics with mobility and movement, an association that would not be possible with nonsocial cues. Indeed, in a previous study (Avarguès-Weber, A. & L. Chittka, 2014a, 2014b), when the bees only had foraging experience with model bees (not with other bees), they showed an intermediate behaviour between the social and the nonsocial groups. These bees were first attracted by the model bee itself but generalized to a certain extent their preference towards the flowers of the same species with no model bee attached. The similarity between live nestmates visible in the nest and model bees might consequently induce the bees to process the models as mobile objects, and therefore independent of flowers. Further investigations should therefore attempt to decipher which conspecifics' characteristics are innately recognized by the bumblebees and which characteristics could be learned and stored by simple familiarization processes within the nest and its surroundings.

Acknowledgments

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