



Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference



Aurore Avarguès-Weber*, Lars Chittka

Biological and Experimental Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, London, U.K.

ARTICLE INFO

Article history:

Received 10 March 2014
Initial acceptance 8 May 2014
Final acceptance 20 August 2014
Published online
MS. number: 14-00202R

Keywords:

associative learning
Bombus terrestris
bumblebee
demonstrators
foraging
observers
pollinating insect

Social learning is a widespread phenomenon allowing animals to use information provided by other animals when presented with a novel situation. A number of recent studies suggest that nonspecific Pavlovian conditioning may explain some forms of social learning, so that animals simply learn to use the presence of conspecifics as a predictor of reward. In this study, we investigated the conditions of flower choice copying behaviour in the bumblebee *Bombus terrestris*. We raised bumblebees in controlled laboratory conditions to compare the social learning performance of bees with different previous associative experiences. We investigated the influence of foraging experience with conspecifics on transferring the preference for a socially indicated flower type to flowers of the same species not occupied by conspecifics. Observers that had the opportunity to associate conspecifics with rewarding flowers instantly acquired the social flower preference and equally visited occupied and unoccupied flowers of the socially indicated flower type (stimulus enhancement). Such usage of social cues requires prior experience with live conspecifics (bees familiarized only with inanimate model bees did not display the same generalization from socially indicated flowers to other flowers of the same type). By contrast, nonsocial cues and immobile model bees, even if they had been previously associated with rewarding flowers, resulted in a wholly different pattern of preference, where observers preferred only those individual flowers with the nonsocial cue or model bee attached (local enhancement). This difference suggests a special salience of live social cues as information providers and results in different patterns of associative learning than nonsocial cues.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Using information inadvertently provided by other animals to decide where to forage, with whom to mate or which predator to avoid is widespread among animals from primates to insects (Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Leadbeater & Chittka, 2007b). The widespread nature of social learning processes reflects obvious advantages for the observers (Galef & Laland, 2005). Individual exploration of the environment is potentially costly, error-prone and possibly dangerous (Lima & Dill, 1990). For example, an assessment of the nutrient value and toxicity of a variety of available food sources often requires extensive sampling (Heinrich, 2004). Likewise, errors in an assessment of predation threat can be fatal (Dukas, 2001). Assessing the outcome of others' decisions allows animals to circumvent some of the costs of individual investigation (Dawson & Chittka, 2014; Galef & Laland, 2005).

Although the adaptive value and ecological relevance of social learning is often discussed (Giraldeau, Valone, & Templeton, 2002; Grüter, Leadbeater, & Ratnieks, 2010; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004; Rendell et al., 2010, 2011; Rieucou & Giraldeau, 2011), relatively little is known about the ontogeny of social learning in many species. In other words, how might such behaviour develop in an animal? What are the underlying cognitive mechanisms and the role of experience with conspecifics? It has been suggested that social learning behaviours may emerge from simple past associations between a relevant stimulus (unconditioned stimulus, US), such as a food reward or a predator threat, and a conspecific's presence or behaviour (conditioned stimulus, CS) (Avarguès-Weber, Deisig, & Giurfa, 2011; Giurfa, 2012; Heyes, 2011; Leadbeater & Chittka, 2007b). In this view, apparently complex 'copying' behaviour could be explained without requiring a specific salience of conspecifics as cue providers (Heyes, 2011). This proposition is supported by the existence of social learning capacities in solitary species (Fiorito & Scotto, 1992; Wilkinson, Kuenstner, Mueller, & Huber, 2010), for which there could not have been a selective pressure towards attaching special value to social information, given that they rarely interact with conspecifics. In

* Correspondence and present address: A. Avarguès-Weber, Université Toulouse 3—Centre de Recherches sur la Cognition Animale, Bat. IVR3, 118 Route de Narbonne, 31062 Toulouse Cedex 09, France.

E-mail address: aurore.avargues-weber@univ-tlse3.fr (A. Avarguès-Weber).

addition, positive correlations have been found in a few studies between individual and social learning performance across individuals or species (Boogert, Giraldeau, & Lefebvre, 2008; Bouchard, Goodyer, & Lefebvre, 2007; Heyes, 2011; Reader, Hager, & Laland, 2011), further supporting the notion that social learning relies on similar mechanisms as individual learning.

In a different scenario, social learning might be the consequence of a specific salience of conspecifics thus inducing a specific responsiveness towards social cues. In this case, social learning might not rely on the same mechanisms as basic Pavlovian conditioning (i.e. the simple association of a CS with a US). Instead, animals might have preconfigured sensory filters that lend special salience to conspecifics' appearance, facilitating their usage as predictors of reward and safety, and resulting in different patterns of associations than arbitrary sensory cues (Avarguès-Weber, Dawson, & Chittka, 2013; Heyes, 2011).

In this study, we used bumblebees, *Bombus terrestris*, to analyse the mechanisms underpinning flower choice copying in a foraging context. Bumblebees are useful models to explore the ontogeny of behaviour patterns, since they offer unique opportunities to control past experience and experimental conditions because they can be raised in completely controlled laboratory conditions. In addition, bumblebees possess impressive learning skills (Raine, Ings, Dornhaus, Saleh, & Chittka, 2006; Riveros & Gronenberg, 2009) and can be trained to use social cues as indicators of reward in classical associative paradigms (Dawson & Chittka, 2012; Leadbeater & Chittka, 2009). Importantly, bumblebees are also known to follow conspecific choices when deciding which flowers to visit, thus increasing their foraging efficiency (Avarguès-Weber & Chittka, 2014; Baude, Danchin, Mugabo, & Dajoz, 2011; Kawaguchi, Ohashi, & Toquenaga, 2006; Kawaguchi, Ohashi, & Toquenaga, 2007; Leadbeater & Chittka, 2005; Worden & Papaj, 2005).

The observed preference of bumblebees for the flowers visited by conspecifics may reflect an attraction for conspecifics' features themselves (local enhancement). Such attraction could be acquired through experience of the positive relation between the presence of conspecifics (CS) and profitable flowers (US). However, there are two complications with this scenario. One is of an ultimate nature: in many typical flower species it might not make adaptive sense for a pollinator to visit a flower that is currently being drained by another visitor. Instead, it would be useful to steer towards unvisited flowers of the same plant species where visits by others indicate that the flower type is profitable. The other complication is that such local enhancement is not consistent with the observation that flower preferences can be acquired by observing other bees foraging at a distance through a screen (Avarguès-Weber & Chittka, 2014; Dawson, Avarguès-Weber, Leadbeater, & Chittka, 2013). In this particular social learning situation, the demonstrators are no longer present when the observer makes its choice, which implies that the positive value of conspecifics is transferred to the associated flowers themselves (stimulus enhancement). In that case, an explanation based on associative rules requires an additional associative step (second-order conditioning). Bees should thus have the opportunity to learn a positive association between a conspecific (CS1) and a food reward (US), as a result of past shared foraging experience on the same resources (Dawson et al., 2013). When a bee observes a conspecific feeding from an unknown flower, the close association between the CS1 (conspecifics) and the flower induces the bee to consider the flower cues themselves as indicative of reward (CS2) (Pavlov, 1927). Such a mechanism would lead to a socially acquired preference for all flowers sharing the same characteristics (stimulus enhancement) and not only for the occupied flowers (local enhancement) (Dawson et al., 2013; Leadbeater & Chittka, 2007b).

Although bumblebees behave in a manner consistent with stimulus enhancement when social cues are no longer present (Avarguès-Weber & Chittka, 2014; Worden & Papaj, 2005), attraction to conspecifics (local enhancement) is considered a common pathway for social transmission of flower preference. Many previous studies have therefore focused on landings on flowers occupied by a conspecific as an indicator of social learning (Dawson & Chittka, 2012; Kawaguchi et al., 2006, 2007; Leadbeater & Chittka, 2005; Leadbeater & Chittka, 2007a, 2009; Plowright et al., 2013). Under such conditions, bees often display a preference for the occupied flowers (Kawaguchi et al., 2006; Leadbeater & Chittka, 2005; Leadbeater & Chittka, 2009; Plowright et al., 2013). However, without comparing bees' preference for unoccupied flowers of the demonstrated flower species and for flowers of an alternative species, it is impossible to distinguish between local enhancement and stimulus enhancement.

To dissect the mechanisms underlying flower choice copying in bumblebees, we analysed the bees' choice between two types of artificial flowers, one of which was visited by conspecifics, after being reared in different conditions. Both types of flowers were unfamiliar to the tested bees. We investigated the role of past experience and associative learning processes as well as the social learning strategies (local versus stimulus enhancement) elicited by the different cues and rearing conditions.

METHODS

Three bumblebee, *B. terrestris*, colonies provided by Syngenta Bioline Bees (Weert, The Netherlands) were used. The colonies were housed in bipartite wooden nestboxes (28 × 16 cm and 11 cm high) connected to a flight arena (117 × 72 cm and 30 cm high) covered by a UV-transparent Plexiglas ceiling. One chamber of the nestbox contained the actual nest structure; the other chamber (front chamber) was connected to the flight arenas via a Plexiglas tube with sliding doors allowing controlled individual access to the arena. In the front chamber, we provided bees with a 30% (volume/volume) sucrose solution in perforated plastic tubes outside periods of experimentation. Pollen was provided directly onto the nest in the back chamber. The nest was kept in darkness when food was supplied to avoid association of food with the visual cues provided by nestmates. Outside of the feeding periods, the front chamber of the nest was illuminated. Light conditions in the arena and front chamber mimicked the natural daylight spectrum and the light flicker frequency was set beyond bumblebees' flicker fusion frequency (Skorupski & Chittka, 2010). Individual bees were identified by numbered tags or paint marks, and were removed from the colony after testing.

Treatment Groups

Four different groups of 20 bees each were tested. Each bee was trained and tested individually. Each group of bees experienced different pretesting conditions allowing us to pinpoint the respective learning mechanisms.

Naive group (control group)

In the pretesting phase, each bee was trained to forage from coloured Perspex artificial 'flowers' (25 × 25 mm and 5 mm thick squares with a small hole with a diameter of 5 mm in the centre to hold 'nectar' rewards) randomly placed in the arena on top of transparent supports (Fig. 1a). In this phase, six green (Green 6205 Perspex from Hamar Acrylic Fabrications Ltd, London, U.K.) flowers filled with 40 µl of a 30% (volume/volume) sucrose solution were offered to the bee at each foraging bout (consisting of a full trip from the nest, visiting flowers and return to the nest). During such a

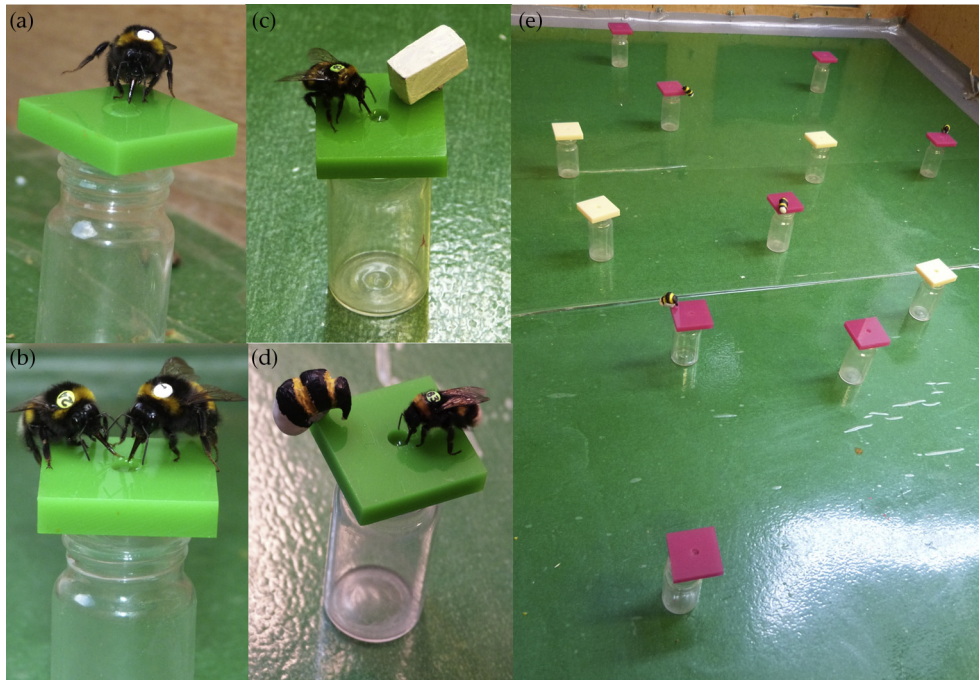


Figure 1. Set-up, the artificial flowers and the different pretraining procedures. (a)–(d). Illustrations of the pretesting condition for each test group. (a). Bees from the ‘control group’ foraged only in isolation before the test. (b). Bees from the ‘socially experienced group’ were allowed to forage simultaneously with conspecifics thus allowing the association between live social cues and nectar. (c). Bees from the ‘nonsocial cue experienced group’ were familiar with the association of nonsocial cues, i.e. white wooden blocks pinned on flowers, and nectar. (d). Bees from the ‘model bees experienced group’ never foraged with live conspecifics and were familiar with the association of models of bees and nectar. (e). Example of a flower arrangement in the test. In this example, the socially demonstrated flower colour was fuchsia. Only half of the fuchsia flowers (four out of eight) were associated with models of bees. Four flowers from the alternative colour were also displayed. All flowers were filled with 20 μ l of a 50% (volume/volume) sucrose solution.

bout, visits to three to four flowers were typically necessary for the bee to collect a full crop of sucrose solution. The bee then returned to the nest to deposit the sucrose solution, before resuming foraging. After five successful foraging trips, the bee was presented with the social learning test (see below).

The bees from this group were thus prevented from forming an association between visual properties of conspecifics and the sucrose reward as they only foraged individually during the pretesting phase on the green artificial flowers.

Socially experienced group

The bees from this group foraged with a second bee during the pretraining phase (Fig. 1b). Thus, the bees had the opportunity to associate a conspecific with a reward when foraging from the same flower. Joint visits to the same flowers occurred in all tested bees with a mean \pm SEM of 8.7 ± 0.5 times and a minimum of five times over the five pretraining foraging bouts.

Nonsocial cues experienced group

The nonsocial cues were cuboid, white wooden blocks (15 \times 7 mm and 7 mm high) of a size similar to worker bumblebees of the species tested here. Nonsocial cues were attached to half of the green flowers in the pretesting phase (Fig. 1c). Pilot experiments demonstrated that these white blocks can be detected by the bees and used as a predictor of a reward.

Model bees experienced group

Inanimate model bees were attached to half of the green flowers in the pretesting phase (Fig. 1d). The bees from this group could associate social cues with rewarding flowers but without being influenced by olfactory or behavioural (movement) cues from live bees. Model bees were shaped using oven-hardening modelling clay (Fimo Soft, Staedtler, Nürnberg, Germany) and painted with a

colour pattern matching that of the species. We used the following paints: yellow (Rheotech Acrylics Bright Yellow, Arkema, Colombes, France); black (Winsor & Newton, London, U.K.), Griffin fast drying oil painting, ivory black) and white (unpainted modelling clay) to reflect natural *B. terrestris* colour properties as assessed through bumblebee photoreceptors (Skorupski, Döring, & Chittka, 2007; Stelzer, Raine, Schmitt, & Chittka, 2010) and quantified in a bee colour space model (Chittka, 1992; Fig. 1d).

The bees were randomly allocated to the experimental groups (three colonies being tested sequentially). There was no significant colony effect on the data within treatment groups (Kruskal–Wallis ANOVA: $P > 0.1$ in all cases).

Tests

The social learning test consisted of the presentation of two types of artificial flowers distinguished by colour, i.e. fuchsia (red 4415 Perspex) and cream (cream 128 Perspex) flowers (from human perception; Fig. 1e). These colours were novel for the bee and were easily discriminable from each other (0.3 hexagon units) and from the green flowers (0.3 and 0.4 hexagon units, respectively) 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 under absolute (not differential) conditioning procedures, in which bees generalize fairly broadly (Dyer & Chittka, 2004). All flowers were filled with 20 μ l of a 50% (volume/volume) sucrose solution. Across bees and following a balanced design, one type of flower was defined as the socially indicated ‘flower species’; we pinned a bee model on four of the eight flowers of this colour, thus mimicking conspecifics’ choice towards this particular flower colour (Fig. 1e). In the case of the nonsocial cue experienced group, white blocks were pinned on flowers in the test instead of model bees. There were four flowers of

the alternative colour, so that a total of 12 flowers were randomly placed in the flight arena (Fig. 1e). The bee's landing choices for each category of flowers (occupied flower type, unoccupied flowers of the same colour, alternative flower type) were recorded once the test bee had approached an occupied flower to within 3 cm, therefore having the opportunity to detect the presence of demonstrators (Dyer, Spaethe, & Prack, 2008), and until the bee returned to the nest. Two bees from the nonsocial cue experienced group were discarded from the analysis as they never approached flowers presenting the cue during the whole foraging trip, so they did not have the opportunity to use the cue for future foraging decisions.

Statistical Analysis

Preference during the test was analysed in terms of the proportions of landings for each flower category. Comparisons of the proportion of landing between flower categories were performed by nonparametric Friedman tests and post hoc tests for dependent variables. The potential colour preference (for cream or fuchsia flower types) was analysed with nonparametric Wilcoxon signed-ranks tests for dependent samples. Statistics were run with SPSS Statistics version 22.0.

RESULTS

Social Learning Requires Prior Exposure to Foraging with Conspecifics

The bees from the 'control group' (Fig. 1a) were not permitted to form any positive association between the visual pattern of bees and a reward. Their choices were dependent on the flower colours ($80.2 \pm 8.7\%$ of total landings on cream flowers versus $19.8 \pm 8.7\%$ on fuchsia flowers; Wilcoxon test: $T = 15$, $Z = 3.36$, $N = 20$, $P < 0.001$). When comparing preferences for the different flower categories, we observed a significant preference for the cream flowers irrespective of the flower colour associated with the demonstrator bees (demonstrators on fuchsia flowers: $N = 10$; $15.6 \pm 7.2\%$ of landings on the flowers associated with the model bees, $13.4 \pm 5.2\%$ of landings on the other flowers of the same indicated colour and $71.0 \pm 8.6\%$ of landings on the flowers of the alternative colour (cream); Friedman's test: $N = 10$, $df = 2$, $P = 0.007$; comparison between flower categories: post hoc tests: occupied versus unoccupied flowers of the same colour: $N = 10$, $P = 0.81$; occupied versus alternative flowers: $N = 10$, $P = 0.01$; unoccupied flowers of the indicated colour versus alternative flowers: $N = 10$, $P = 0.02$; demonstrators on cream flowers: $N = 10$; $50.6 \pm 5.4\%$ of landings on the flowers associated with the model bees, $36.2 \pm 6.5\%$ of landings on the other flowers of the same indicated colour and $13.2 \pm 7.8\%$ of landings on the flowers of the alternative colour (fuchsia); Friedman's test: $N = 10$, $df = 2$, $P = 0.009$; comparison between flower categories: post hoc tests: occupied versus unoccupied flowers of the same colour: $N = 10$, $P = 0.18$; occupied versus alternative flowers: $N = 10$, $P = 0.003$; unoccupied flowers of the indicated colour versus alternative flowers: $N = 10$, $P = 0.01$).

The pooled data confirmed that the bees landed on flowers independently of the presence of conspecific cues during the test, with no significant choice level difference for the different categories of flowers ($33.1 \pm 5.9\%$ ($N = 20$) of landings occurred on the flowers associated with the model bees, $24.8 \pm 4.8\%$ of landings were observed on the other flowers of the same indicated colour and $42.1 \pm 8.7\%$ of landings on the flowers of the alternative species; Friedman's test: $N = 20$, $df = 2$, $P = 0.59$; Fig. 2).

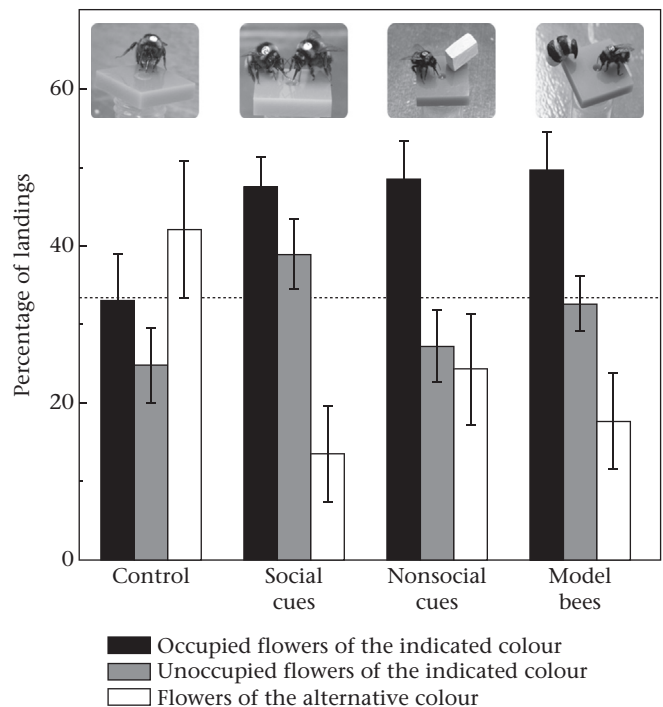


Figure 2. Behavioural results depending on previous experience. The percentage of choices (mean \pm SEM) is plotted for each flower category. The dashed line indicates random choice level. Before the test, bees were either naïve (control) or had the opportunity to associate rewarding flowers with live conspecifics (social cues), nonsocial cues or model bees.

Behavioural Specificity Triggered by Social Visual Cues

Social cues induce preference for all flowers of the indicated colour

Bumblebees that were allowed to forage together with other bees prior to the test ('socially experienced group'; Fig. 1b), showed a significant preference towards the socially indicated flower colour.

No significant colour influence was found for this group ($63.5 \pm 6.1\%$ of total landings on cream flowers versus $36.6 \pm 6.1\%$ on fuchsia flowers; Wilcoxon test: $T = 60.5$, $Z = 1.66$, $N = 20$, $P = 0.10$), so the data were pooled for further analysis.

There was a significant difference of choices between the different flower categories (Friedman's test: $N = 20$, $df = 2$, $P < 0.001$). In particular, the percentage of landings on the occupied flowers ($47.5 \pm 3.9\%$) was significantly higher than on the alternative flower colour ($13.5 \pm 6.1\%$ of landings; post hoc test: $N = 20$, $P < 0.001$; Fig. 2). The percentage of choices for the occupied flowers was not significantly different from that for the unoccupied flowers of the same indicated colour ($39.0 \pm 4.4\%$: $N = 20$, $P = 0.21$; Fig. 2). The comparison between the percentage of landings on the unoccupied flowers of the socially indicated colour and on the flowers of the alternative colour was also significant ($N = 20$, $P = 0.003$; Fig. 2).

The bees thus extracted the characteristics of the flowers visited by conspecifics to generalize their preference to all flowers of the same species.

Nonsocial cues induce attraction to the cues exclusively

Bumblebees from the 'nonsocial cue experienced group' foraged on flowers occupied by nonsocial cues (white wooden blocks; Fig. 1c) prior to the social learning test.

No significant colour influence was found for this group ($55.3 \pm 7.1\%$ of total landings on cream flowers versus $44.7 \pm 7.1\%$

on fuchsia flowers; Wilcoxon test: $T = 65$, $Z = 0.54$, $N = 18$, $P = 0.59$) so the data were pooled for further analysis.

These bees showed a significant preference to land specifically on 'occupied' flowers, i.e. those with the wooden block attached ($N = 18$; Friedman's test: $df = 2$, $P = 0.04$; $48.5 \pm 4.8\%$; comparison with percentage of landings on unoccupied flowers of the indicated colour: $27.2 \pm 4.6\%$; post hoc test: $N = 18$, $P = 0.03$; Fig. 2), thus showing an attraction towards the nonsocial cues. In addition, there was no significant preference for unoccupied flowers of the indicated colour over flowers of the alternative colour (comparison with percentage of landings on flowers of the alternative species: $24.3 \pm 7.1\%$; $N = 18$, $P = 0.58$; Fig. 2). The difference in choices between the occupied flowers and the flowers of the alternative colour was significant ($N = 18$, $P = 0.006$).

Social Learning Specificity Requires Visual Experience of Live Conspecifics

For bees from the 'model bee group' no significant colour influence was found ($60.2 \pm 6.1\%$ of total landings on cream flowers versus $39.8 \pm 6.1\%$ on fuchsia flowers; Wilcoxon test: $T = 68$, $Z = 1.38$, $N = 20$, $P = 0.17$) so the data were pooled for further analysis.

The bees showed a significant preference to land on occupied flowers ($N = 20$, Friedman's test: $df = 2$, $P = 0.001$; $49.7 \pm 4.8\%$ of choices for the occupied flowers; comparison with the percentage of choices for the unoccupied flowers of the socially indicated colour: $32.6 \pm 3.5\%$; post hoc test: $N = 20$, $P = 0.04$; with the percentage of choices for the flowers of the alternative colour: $17.7 \pm 6.1\%$; $N = 20$, $P = 0.007$; Fig. 2). These bees chose the unoccupied flowers of the indicated colour at the same level as the flowers of the alternative colour ($N = 20$, $P = 0.53$; Fig. 2). Their behaviour was therefore comparable to that of bees subjected to the nonsocial cues, that is, they showed a simple Pavlovian pattern of associative learning.

DISCUSSION

We found that observing other live bees foraging from an unknown flower species had a specific influence on bumblebees' foraging decisions, which differs from simple associative behaviours elicited by conditioned nonsocial cues or by stationary model bees. While in the first case, the flowers chosen by live conspecifics became attractive by themselves (stimulus enhancement), the bees were attracted exclusively by the conditioned cues in the other cases (local enhancement). Thus, only social demonstration of rewarding flowers triggered a generalization to other flowers of the same colour.

Individual bumblebees face the challenge of ensuring the survival and growth of the colony by finding the most profitable food sources from scattered flower patches (Goulson, 2010; Heinrich, 1979, 2004). This task is challenging because different flower species vary in reward quality and some flower species deliver nectar or pollen only at certain times of day. In this context, a strategy based on monitoring other foragers' success when visiting a given type of flower is likely to be favourable (Kawaguchi et al., 2006; Leadbeater & Chittka, 2007b). Bumblebee pollinators range too far from their colonies, and colony densities are often too high, for sibling encounters in flower patches to be a more common occurrence than encounters with members of different colonies (Chapman, Wang, & Bourke, 2003; Knight et al., 2005; Thomson & Chittka, 2001). Thus, social learning behaviours observed in bumblebees often benefit the observers exclusively. The value of resource information

provided by conspecifics is likely to be particularly high. Different pollinator species differ in nutritional needs and morphological equipment in relation to flower morphology. For example, it might make relatively little sense for members of a short-tongued species such as *B. terrestris* to copy the foraging choices of the longer tongued *Bombus pascuorum*, which sometimes exploits long-tubed flowers whose nectar is harder to reach for workers of *B. terrestris* (Goulson, 2010).

Therefore, specific social learning mechanisms might have evolved to promote efficient information use in flower foraging. However, a simple innate attraction to conspecifics might be counterproductive, leading the bees to visit drained flowers; thus, mechanisms inducing better exploitation of the pool of available flowers should be developed (Giraldeau et al., 2002). Learning the characteristics of a flower species from conspecifics, rather than just attraction to particular locations at which conspecifics are observed could be one such mechanism.

In this sense, bumblebee foragers might have an innate preparedness to respond to conspecific cues on flowers, and their appearance induces a switch from a local enhancement type of strategy (as seen with the nonsocial cues and stationary model bees) to a stimulus enhancement scenario, in which observer bees extrapolate the value of a conspecific-occupied flower to all members of the same flower species. However, our results show that to trigger social learning of this type, bumblebees first need to experience the association of social cues with a positive reinforcement. Indeed, without having the opportunity to learn that flowers occupied by a conspecific could offer a nectar reward, the tested bees ('control group') did not show any interest in conspecifics when choosing between both flower options, demonstrating the decisive influence of previous experience with conspecifics. Thus, social learning behaviour reported in previous studies (Baude, Dajoz, & Danchin, 2008; Leadbeater & Chittka, 2005; Plowright et al., 2013) may have been facilitated by group feeding prior to the experiment allowing the bees to learn the association between conspecifics and reward.

Our results also reveal the importance of prior co-feeding experience with live bees. Although model bees were efficient at triggering social learning behaviour in the test phase, prior exposure to live bees was a necessary condition for a stimulus enhancement social learning strategy to occur.

It is, however, also possible that there is no special role of conspecifics in the pattern of stimulus enhancement observed when demonstrators indicate rewarding flowers. It was in the nature of our training protocol with live demonstrators that the socially indicated flower species would sometimes be occupied by demonstrators and sometimes not, occasionally in rapid succession, and the situation might change while the observer was on the flower. Thus, observers had exposure to mobile demonstrators physically dissociated from the flowers, and this in turn may have favoured future generalization to unoccupied but socially indicated flowers. Unfortunately, our results do not allow us to tell whether stimulus enhancement resulted from the specific salience of conspecific cues or whether their mobility could by itself have favoured the transfer of the social cue's positive value to the visited flower species. Indeed, the nonsocial cues and model bees used in this study were never perceived as mobile objects, and preventing the bees from experiencing live, moving conspecifics in the pretesting phase led to a simple attraction to the cue instead of a stimulus enhancement strategy. The observation of moving cues may facilitate the dissociation between the cue and the associated flowers, thus favouring the subsequent transfer of the positive acquired value between them.

Conclusion

Bumblebees responded to live conspecifics differently from nonsocial static cues on flowers, so that only the former induced stimulus enhancement in flower foraging decisions. This indicates that associations made between floral rewards and the cues that indicate them are not entirely arbitrary, and that bees might have an innate preparedness to respond differently to social and nonsocial cues (where this preparedness, however, needs to be reinforced through visual exposure to conspecifics' appearance). Whether the specificity came from social cues or from live, mobile cues remains unresolved, but it is clear that at the behavioural output level the response patterns differ between situations in which live conspecific and nonsocial cues or stationary model bees indicate the most rewarding flowers. Many aspects of pollinator social learning behaviour are specific to certain settings (namely generalization towards all similar flowers described here, restriction to low competitive contexts (Baude et al., 2011; Plowright et al., 2013) and choice situations for which no individual information is available (Leadbeater & Chittka, 2005; Kawaguchi et al., 2007)). Such specificities might reflect an intricate interplay between evolutionary adaptation to attend to conspecific cues and individual experience with such cues and their contingencies with salient aspects of the environment.

Acknowledgments

We are grateful to Sébastien Weber for his program to help analyse the video recordings and to Adrian Dyer, Ellouise Leadbeater and Erika Dawson for helpful comments on the manuscript. A.A.-W. was funded by a postdoc fellowship from the Fyssen Foundation.

References

- Avarguès-Weber, A., & Chittka, L. (2014). Observational conditioning in flower choice copying by bumblebees *Bombus terrestris*: influence of observer distance and demonstrator movement. *PLoS One*, 9(2), e88415. <http://dx.doi.org/10.1371/journal.pone.0088415>.
- Avarguès-Weber, A., Dawson, E. H., & Chittka, L. (2013). Mechanisms of social learning across the species boundaries. *Journal of Zoology*, 290(1), 1–11. <http://dx.doi.org/10.1111/jzo.12015>.
- Avarguès-Weber, A., Deisig, N., & Giurfa, M. (2011). Visual cognition in social insects. *Annual Review of Entomology*, 56, 423–443. <http://dx.doi.org/10.1146/annurev-ento-120709-144855>.
- Baude, M., Dajoz, I., & Danchin, E. (2008). Inadvertent social information in foraging bumblebees: effects of flower distribution and implications for pollination. *Animal Behaviour*, 76(6), 1863–1873. <http://dx.doi.org/10.1016/j.anbehav.2008.08.010>.
- Baude, M., Danchin, É., Mugabo, M., & Dajoz, I. (2011). Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. *Proceedings of the Royal Society B: Biological Sciences*, 278(1719), 2806–2813. <http://dx.doi.org/10.1098/rspb.2010.2659>.
- Boogert, N. J., Giraldeau, L.-A., & Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, 76(5), 1735–1741. <http://dx.doi.org/10.1016/j.anbehav.2008.08.009>.
- Bouchard, J., Goodyer, W., & Lefebvre, L. (2007). Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10(2), 259–266. <http://dx.doi.org/10.1007/s10071-006-0064-1>.
- Chapman, R. E., Wang, J., & Bourke, A. F. G. (2003). Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. *Molecular Ecology*, 12(10), 2801–2808. <http://dx.doi.org/10.1046/j.1365-294X.2003.01957.x>.
- Chittka, L. (1992). The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *Journal of Comparative Physiology A*, 170(5), 533–543. <http://dx.doi.org/10.1007/BF00199331>.
- Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305(5683), 487–491. <http://dx.doi.org/10.1126/science.1098254>.
- Dawson, E. H., Avarguès-Weber, A., Leadbeater, E., & Chittka, L. (2013). Learning by observation emerges from simple associations in an insect model. *Current Biology*, 23(8), 727–730. <http://dx.doi.org/10.1016/j.cub.2013.03.035>.
- Dawson, E. H., & Chittka, L. (2012). Conspecific and heterospecific information use in bumblebees. *PLoS One*, 7(2), e31444. <http://dx.doi.org/10.1371/journal.pone.0031444>.
- Dawson, E. H., & Chittka, L. (2014). Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. *Proceedings of the Royal Society B: Biological Sciences*, 281(1785), 20133174. <http://dx.doi.org/10.1098/rspb.2013.3174>.
- Dukas, R. (2001). Effects of predation risk on pollinators and plants. In L. Chittka, & J. D. Thomson (Eds.), *Cognitive ecology of pollination* (pp. 214–236). Cambridge, U.K.: Cambridge University Press.
- Dyer, A. G., & Chittka, L. (2004). Biological significance of distinguishing between similar colours in spectrally variable illumination: bumblebees (*Bombus terrestris*) as a case study. *Journal of Comparative Physiology A*, 190(2), 105–114. <http://dx.doi.org/10.1007/s00359-003-0475-2>.
- Dyer, A. G., Spaethe, J., & Prack, S. (2008). Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *Journal of Comparative Physiology A*, 194(7), 617–627. <http://dx.doi.org/10.1007/s00359-008-0335-1>.
- Fiorito, G., & Scotto, P. (1992). Observational learning in *Octopus vulgaris*. *Science*, 256(5056), 545–547. <http://dx.doi.org/10.1126/science.256.5056.545>.
- Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61(1), 3–15. <http://dx.doi.org/10.1006/anbe.2000.1557>.
- Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *BioScience*, 55(6), 489–499. [http://dx.doi.org/10.1641/0006-3568\(2005\)055\[0489:sliaes\]2.0.co;2](http://dx.doi.org/10.1641/0006-3568(2005)055[0489:sliaes]2.0.co;2).
- Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1427), 1559–1566. <http://dx.doi.org/10.1098/rstb.2002.1065>.
- Giurfa, M. (2012). Social learning in insects: a higher-order capacity? *Frontiers in Behavioral Neurosciences*, 6, 57. <http://dx.doi.org/10.3389/fnbeh.2012.00057>.
- Goulson, D. (2010). *Bumblebees: Behaviour, ecology, and conservation*. Oxford, U.K.: Oxford University Press.
- Grüter, C., Leadbeater, E., & Ratnieks, F. L. W. (2010). Social learning: the importance of copying others. *Current Biology*, 20(16), R683–R685. <http://dx.doi.org/10.1016/j.cub.2010.06.052>.
- Heinrich, B. (1979). Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia*, 40(3), 235–245. <http://dx.doi.org/10.1007/bf00345321>.
- Heinrich, B. (2004). *Bumblebee economics*. Cambridge, MA: Harvard University Press.
- Heyes, C. M. (2011). What's social about social learning? *Journal of Comparative Psychology*, 126(2), 193–202. <http://dx.doi.org/10.1037/a0025180>.
- Kawaguchi, L. G., Ohashi, K., & Toquenaga, Y. (2006). Do bumble bees save time when choosing novel flowers by following conspecifics? *Functional Ecology*, 20(2), 239–244. <http://dx.doi.org/10.1111/j.1365-2435.2006.01086.x>.
- Kawaguchi, L. G., Ohashi, K., & Toquenaga, Y. (2007). Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. *Proceedings of the Royal Society B: Biological Sciences*, 274(1626), 2661–2667. <http://dx.doi.org/10.1098/rspb.2007.0860>.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35, 333–379. [http://dx.doi.org/10.1016/s0065-3454\(05\)35008-x](http://dx.doi.org/10.1016/s0065-3454(05)35008-x).
- Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A., et al. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, 14(6), 1811–1820. <http://dx.doi.org/10.1111/j.1365-294X.2005.02540.x>.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4–14. <http://dx.doi.org/10.3758/BF03196002>.
- Leadbeater, E., & Chittka, L. (2005). A new mode of information transfer in foraging bumblebees? *Current Biology*, 15(12), R447–R448. <http://dx.doi.org/10.1016/j.cub.2005.06.011>.
- Leadbeater, E., & Chittka, L. (2007a). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behavioral Ecology and Sociobiology*, 61(11), 1789–1796. <http://dx.doi.org/10.1007/s00265-007-0412-4>.
- Leadbeater, E., & Chittka, L. (2007b). Social learning in insects—from miniature brains to consensus building. *Current Biology*, 17(16), R703–R713. <http://dx.doi.org/10.1016/j.cub.2007.06.012>.
- Leadbeater, E., & Chittka, L. (2009). Bumble-bees learn the value of social cues through experience. *Biology Letters*, 5(3), 310–312. <http://dx.doi.org/10.1098/rsbl.2008.0692>.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. <http://dx.doi.org/10.1139/z90-092>.
- Pavlov, I. P. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex*. New York: Dover.
- Plowright, C. M. S., Ferguson, K. A., Jellen, S. L., Xu, V., Service, E. W., & Dookie, A. L. (2013). Bumblebees occupy: when foragers do and do not use the presence of others to first find food. *Insectes Sociaux*, 60(4), 517–524. <http://dx.doi.org/10.1007/s00040-013-0318-2>.
- Raine, N. E., Ings, T. C., Dornhaus, A., Saleh, N., & Chittka, L. (2006). Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Advances in the Study of Behavior*, 36, 305–354. [http://dx.doi.org/10.1016/S0065-3454\(06\)36007-X](http://dx.doi.org/10.1016/S0065-3454(06)36007-X).

- Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1017–1027. <http://dx.doi.org/10.1098/rstb.2010.0342>.
- Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., et al. (2010). Why copy others? Insights from the social learning strategies tournament. *Science*, 328(5975), 208–213. <http://dx.doi.org/10.1126/science.1184719>.
- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15(2), 68–76. <http://dx.doi.org/10.1016/j.tics.2010.12.002>.
- Rieucau, G., & Giraldeau, L.-A. (2011). Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 949–957. <http://dx.doi.org/10.1098/rstb.2010.0325>.
- Riveros, A. J., & Gronenberg, W. (2009). Learning from learning and memory in bumblebees. *Communicative & Integrative Biology*, 2(5), 437–440. <http://dx.doi.org/10.4161/cib.2.5.9240>.
- Skorupski, P., & Chittka, L. (2010). Differences in photoreceptor processing speed for chromatic and achromatic vision in the bumblebee, *Bombus terrestris*. *The Journal of Neurosciences*, 30(11), 3896–3903. <http://dx.doi.org/10.1523/jneurosci.5700-09.2010>.
- Skorupski, P., Döring, T., & Chittka, L. (2007). Photoreceptor spectral sensitivity in island and mainland populations of the bumblebee, *Bombus terrestris*. *Journal of Comparative Physiology A*, 193(5), 485–494. <http://dx.doi.org/10.1007/s00359-006-0206-6>.
- Stelzer, R. J., Raine, N. E., Schmitt, K. D., & Chittka, L. (2010). Effects of aposematic coloration on predation risk in bumblebees? A comparison between differently coloured populations, with consideration of the ultraviolet. *Journal of Zoology*, 282(2), 75–83. <http://dx.doi.org/10.1111/j.1469-7998.2010.00709.x>.
- Thomson, J. D., & Chittka, L. (2001). Pollinator individuality: when does it matter? In L. Chittka, & J. D. Thomson (Eds.), *Cognitive ecology of pollination* (pp. 191–213). Cambridge, U.K.: Cambridge University Press.
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6(5), 614–616. <http://dx.doi.org/10.1098/rsbl.2010.0092>.
- Worden, B. D., & Papaj, D. R. (2005). Flower choice copying in bumblebees. *Biology Letters*, 1(4), 504–507. <http://dx.doi.org/10.1098/rsbl.2005.0368>.