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The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*)

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Abstract Bumblebees (*Bombus terrestris*) are attracted to those particular inflorescences where other bees are already foraging, a process known as local enhancement. Here, we use a quantitative analysis of learning in a foraging task to illustrate that this attraction can lead bees to learn more quickly which flower species are rewarding if they forage in the company of experienced conspecifics. This effect can also be elicited by model bees, rather than live demonstrators. We also show that local enhancement in bumblebees most likely reflects a general attraction to conspecifics that is not limited to a foraging context. Based on the widespread occurrence of both local enhancement and associative learning in the invertebrates, we suggest that social influences on learning in this group may be more common than the current literature would suggest and that invertebrates may provide a useful model for understanding how learning processes based on social information evolve.

Keywords Bumblebee foraging · Social learning · Local enhancement

Introduction

Animal learning processes that are influenced by the inadvertent behavior of conspecifics have attracted a wealth of research attention because learning through the experience of others can sometimes offer an economical alternative to individual exploration (Boyd and Richerson 1985; Zentall and Galef 1988; Heyes and Galef 1996; Kendal et al. 2005). In some instances, mostly involving primates and birds (Dawson and Foss 1965; Atkins and Zentall 1996; Whiten 1998), it has been suggested that social learning processes may reflect highly evolved cognitive processing. However, in many of the cases described in the literature, social learning does not invoke specialized types of learning that are unique to social situations, but instead derives from learning processes that also occur when animals learn asocially (Galef 1995; Galef and Giraldeau 2001; Heyes 1994), shaped or directed by social behavior mechanisms.

In spite of this, studies of social learning have focused on animals with relatively large brains, and examples from the invertebrate literature remain few and isolated (but see Chittka and Leadbeater 2005; Coolen et al. 2005; Worden and Papaj 2005). In the social insects particularly, the spotlight has been on specialized signals that have been shaped by natural selection specifically for communication (e.g., the dances of honeybees or the complex recruitment systems of ants), rather than instances where animals learn through cues that others produce simply by going about their normal activities. In this study, we investigate a mechanism of social learning about food types in a classic insect model, the bumblebee *Bombus terrestris*. Our findings provide a model of how social learning can arise not through a specialized learning process, but rather through the combination of associative learning and a very simple social behavior mechanism, which is a widespread feature of insect behavior.

Bumblebees face the challenge of efficient nectar collection from a range of flower species whose reward levels change rapidly and unpredictably (Heinrich 1979). A worker's choice of focal species will reflect both unlearned

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color preferences (Chittka and Wells 2004) and learned information about current reward levels, gained through individual sampling (Menzel 1985; Chittka et al. 2004). Previous work has established that social information provided at the food source may also be important; when bees were allowed to remotely observe conspecifics foraging on green and avoiding orange flowers, they subsequently found green flowers more attractive than if no conspecifics had been observed or if the demonstrators were foraging from the alternative orange flowers (Worden and Papaj 2005). This may be an example of stimulus enhancement, a mechanism by which the presence of a conspecific at an object attracts an animal to objects of that type (Spence 1937; Galef 1988; Heyes 1994).

Thus, a bee's choice of which flower species to sample is clearly influenced by information that is provided inadvertently by conspecifics. However, most pollinating insects are rarely faced with wholly unfamiliar resources, as was the case in the above study. Insects typically have unlearned preferences for certain colors and shapes over others (Lehrer et al. 1995; Lunau and Maier 1995; Kelber 2002; Chittka and Wells 2004; Raine et al. 2006) possibly as an evolutionary response to higher nectar concentrations (Menzel and Shmida 1993; Giurfa et al. 1995; Chittka et al. 2004). Although such preferences can be modified by learning, they can be remarkably resilient under some conditions (Heinrich 1977; Banschbach 1994). In the above study (Worden and Papaj 2005), the flowers offered were of highly unusual colors that are rarely seen in bee-pollinated flowers, perhaps chosen, justifiably, because they are almost equally attractive to foragers (Chittka et al. 2004). However, the effect described is relatively weak, and was detectable for only one of the two flower colors, raising the question of how robust such a finding might be in a more ecologically realistic context, where bees have strong and consistent preferences which bias them towards some of the available floral options.

In this study, we examine the extent to which social information influences learning when its use must interact with the color preferences that typically shape bee foraging behavior, over the course of three experiments. We begin by presenting bees with the task of learning to avoid an initially preferred species and switch to a more rewarding, but less attractive, alternative. Through a quantitative analysis of learning performance, we illustrate that foragers learn the task more quickly when accompanied by experienced demonstrator bees than when alone, not because the learning process itself is any more rapid, but because bees are initially more attracted to the target species.

Our second study focuses on the mechanism by which bees are attracted to the rewarding flower species. We have previously found that when bees visit unfamiliar flower species, they tend to land on those flowers that are already occupied by a foraging conspecific (Leadbeater and Chittka 2005; see also Brian 1957; Kawaguchi et al. 2006), which we propose may explain why subjects in the current study sampled the rewarding species more quickly. Thus, we go on to compare the alternative hypotheses that bees may be attracted to *all* the rewarding flowers equally (as described previously by Worden and Papaj 2005) or that they may be attracted only to those particular inflorescences where others are foraging. The former would represent stimulus enhancement, whereby conspecific presence at an object attracts an individual to all other objects of that type (Spence 1937), while the latter would imply local enhancement, whereby conspecific presence attracts individual to a particular location (Thorpe 1956; Heyes et al. 2000).

Finally, we investigate whether local enhancement occurs specifically in a foraging context or whether it is a general feature of bumblebee behavior. Based on the widespread occurrence of both local enhancement (Raveret Richter 2000; Prokopy and Roitberg 2001; D'Adamo et al. 2003; Otis et al. 2006; Sontag et al. 2006) and associative learning about resource properties (Menzel 1985; Giurfa 2003; Dukas 2006; Menzel et al. 2006) in the invertebrates, we suggest that this form of social learning is unlikely to be limited to bumblebees, but may be found in many other contexts where individuals must choose between resources.

Materials and methods

Experiment I

We presented bees with an individual foraging task that required them to learn that a blue flower species was unrewarding, and an alternative yellow species provided sugar solution. Individuals of the chosen subspecies (commercially obtained *B. terrestris dalmatinus*) have a strong unlearned preference for the blue over the yellow flowers (Chittka and Briscoe 2001; Raine et al. 2006). Hence, the task facing each bee was to learn to avoid her initially preferred blue flowers and focus her efforts on the yellow only.

Subjects were allocated to one of five treatment groups. Bees in the "individual" group (T1, $n=20$) were controls and completed the task entirely alone. For bees in the "olfaction only" and "vision only" groups (T2 and T3, $n=10$ in each treatment), the rewarding yellow flowers were associated with either the scent of conspecifics or with model bees made from inorganic materials, as described below. Both model bees and olfactory cues were available for bees in the fourth group, "vision and olfaction" (T4, $n=10$), while the fifth group completed the task in the presence of live conspecific demonstrators from a different colony who had previously learned to visit the yellow flowers only ("live", T5, *n*=10).

Set-up

Two wooden nest boxes, housing an "observer" and a "demonstrator" bee colony, were connected using transparent tubing to two large flight arenas (Fig. 1a). One arena was used solely for foraging under non-test conditions and contained only a transparent elevated group feeder dispensing 0.2-M sucrose solution ad libitum. The other arena (the test arena) contained an array of ten yellow and ten blue artificial flowers (5-mm radius plastic-based craft foam circles, height 5 cm), randomly placed in a grid formation. The yellow flower type (henceforth species) was always rewarding, each flower dispensing 20 µl of 0.2-M sucrose solution, while the blue species provided no reward. All flowers were connected via flexible transparent tubing to syringes placed outside the arena and so could be refilled during the test period. Flowers were thoroughly washed with 50% alcohol solution and allowed to dry before each trial.

For those treatments that required visual conspecific cues (T3 and T4), we pinned model bees to the rewarding flowers in the test arena. Models were created from odorless adhesive sticks and roundheaded pins using a Hot Melt™ glue gun (Fig. 1b). Each was painted with the yellow, black, and white coat patterns of *B. terrestris dalmatinus*. We chose paint colors by measuring the spectral reflectance of a range of paints and selecting those that differed from the reflectance spectra of real bees by the least distance in the bee color hexagon (Chittka 1992).

To create olfactory cues for treatments 2 and 4 (olfaction only/olfaction and vision), the foam-based heads of the yellow flowers were removed and placed inside a wire mesh tube that was left inside the nest chamber of another colony for at least 1 week before each test. Note that this is intended to mimic the scent of a bee, rather than any scent-marking pheromones applied by bees to flowers. Bees carry

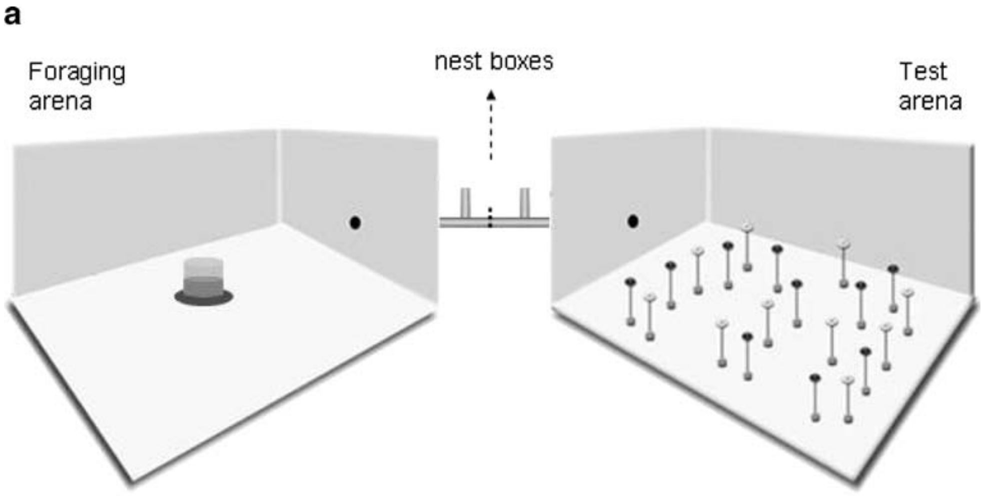

Fig. 1 **a** The test arena contained a mixed-species flower array, while the pretest arena contained a colorless colony feeder dispensing sugar solution ad libitum. **b** Model bee on artificial flower

in their tarsal glands (Schmitt et al. 1991) many of the hydrocarbons present in the nest air.

Bees in T5 (live demonstrators) were accompanied in the test arena by bees from the demonstrator colony. Demonstrators had been allowed 2 days of unrestricted access to the flower array before testing and had, hence, learned to focus their foraging effort on the yellow species, visiting blue flowers only very rarely.

Testing

At the beginning of each test, a marked observer bee was directed into the test arena using a shutter system. Demonstrator bees were retained inside their nest box, with the exception of tests in treatment T5 (live demonstrators), when they were released into the test arena alongside the observer bee at the beginning of each trial.

We recorded the test bee's first 100 flower visits, allowing return trips to the colony to offload sugar solution when required. Bees required between two and five foraging bouts to complete the task, which took between 15 and 90 min. In treatment T5, demonstrator bees were given the opportunity to enter or exit the arena approximately every 2 min during testing, so the number of demonstrators present was not constant but, nevertheless, did not exceed 13 or drop below 8. Observer bees were removed from the colony after testing.

To ensure that rewards were consistently available from the yellow species, we refilled yellow flowers every minute. In treatment T5 (live demonstrators), yellow flowers may have been less consistently rewarding than in the other treatments because demonstrator bees were also collecting sucrose in these trials. However, if this lowered reward level was perceptible to the bees, we would expect the rate of learning to be slower, rather than faster; thus, any resulting bias in learning performance should serve to make the test more conservative, rather than more lenient.

Data analysis

We created a learning curve for each of the 60 bees. For every individual, our raw data consisted of 100 successive choices between yellow and blue flowers. From this binary variable, we created an inaccuracy index for every one of the 100 flower visits, by calculating the average proportion of incorrect (blue) choices in the ten visits up to and including that visit. For example, if a bee chose a yellow flower on her 15th flower visit, but had previously chosen only blue, her inaccuracy index would fall from 1 to 0.9 between the 14th and 15th visits.

For those data points that had not been preceded by ten visits (i.e. visits 1 to 9), we assumed that all previous visits would have been to blue flowers, a reasonable assumption because data from bees that did not show an initial blue preference were removed from the analysis (n=2).

We plotted this moving inaccuracy index against flower visit number. Presenting the data in this way creates a moving average, allowing each bee's performance to be fitted by the sigmoid decay function

$$F(x) = 1 + \left[\frac{g - 1}{1 + e^{(\nu 50/x) - s}} \right]$$

where x is the flower visit number (curves fitted using Prism 4, GraphPad Software, San Diego). This provides three fitted parameters that provide separate measures of each individual's learning performance. g is the final asymptotic inaccuracy index attained by the subject, a measure of the outcome of learning—how well the bee finally learned the task. s is the slope of the learning curve, a measure of learning speed. ν_{50} is the value of x, i.e., the flower visit number, at which the bee has attained one half of her maximal accuracy. See Fig. 2 for an example. Subsequent analyses of these parameters, and data collected in the two subsequent experiments, were carried out using R statistical software (version 2.2.1).

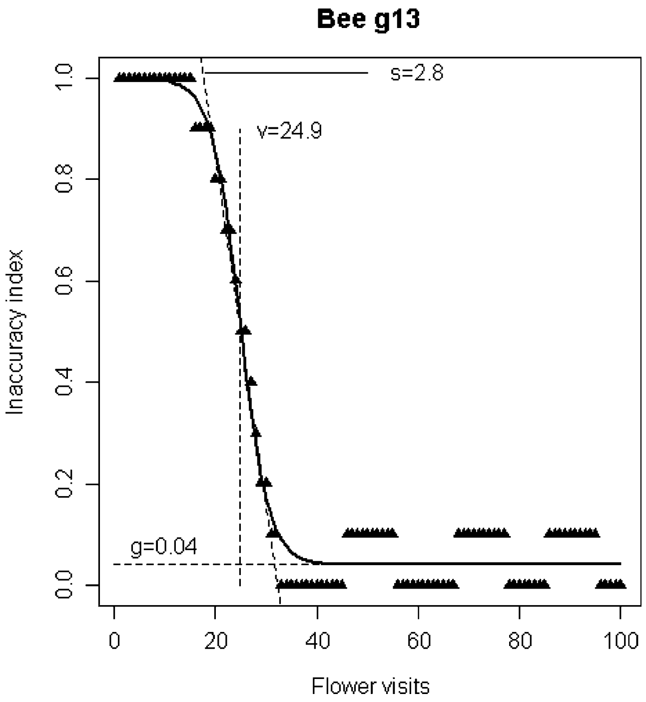

Fig. 2 An example learning curve for one individual bee (g13). *Black triangles* represent raw data (inaccuracy index for each of 100 flower visits); *smooth line* indicates the fitted function. s is a logarithmic parameter representing learning speed, the gradient of the learning curve. g is the final asymptotic inaccuracy level or saturation performance. ν_{50} is the flower visit number at which a bee attains half of her maximal performance. In this data set, this provides a measure of latency to begin learning

Experiment II

We found in Experiment I that bees probe an unfamiliar rewarding species more quickly when conspecific demonstrators are visually present on that species, and as a result, they learn which species to forage on more quickly than they otherwise would. In Experiment 2, we went on to examine the nature of this mechanism which initially attracts observers to the rewarding species. We compared the alternative hypotheses that bees that observe conspecifics on yellow flowers may be attracted to *all* yellow flowers or only to those inflorescences that are occupied by a foraging bee. The former would be consistent with stimulus enhancement, the latter with local enhancement.

We allowed bees to complete the same task as described above, but in which only half of the rewarding flowers were occupied by conspecifics. If local enhancement is indeed the mechanism that leads bees to probe the rewarding species more quickly, we expected that bees should show a preference for those inflorescences that are occupied over their vacant counterparts.

Subjects (n=10) derived from two different colonies. Dead bees were used as demonstrators, in preference to models with associated scent, simply to achieve consistency with a previous, associated experiment. Demonstrators did not originate from the same colonies as the observer individuals and had been killed 1 day before testing by rapid freezing to −18°C. On the morning of the test, they were placed in a dish in the laboratory for 3 h to ensure return to room temperature. New demonstrator bees were used every day.

Experiment III

In the preceding two experiments, we established that bees begin to learn to focus their foraging effort on yellow flowers more quickly if demonstrators are present because they are attracted to occupied inflorescences through local enhancement. In Experiment III, we examine whether local enhancement is confined to a foraging context in bumblebees or whether it might reflect a general attraction to conspecifics, which also occurs in other contexts of bee behavior.

We marked out a 4×5 grid of 20 squares (5×5 cm) on the floor of a bumblebee flight arena identical to those described above, using black tape. In every second square,

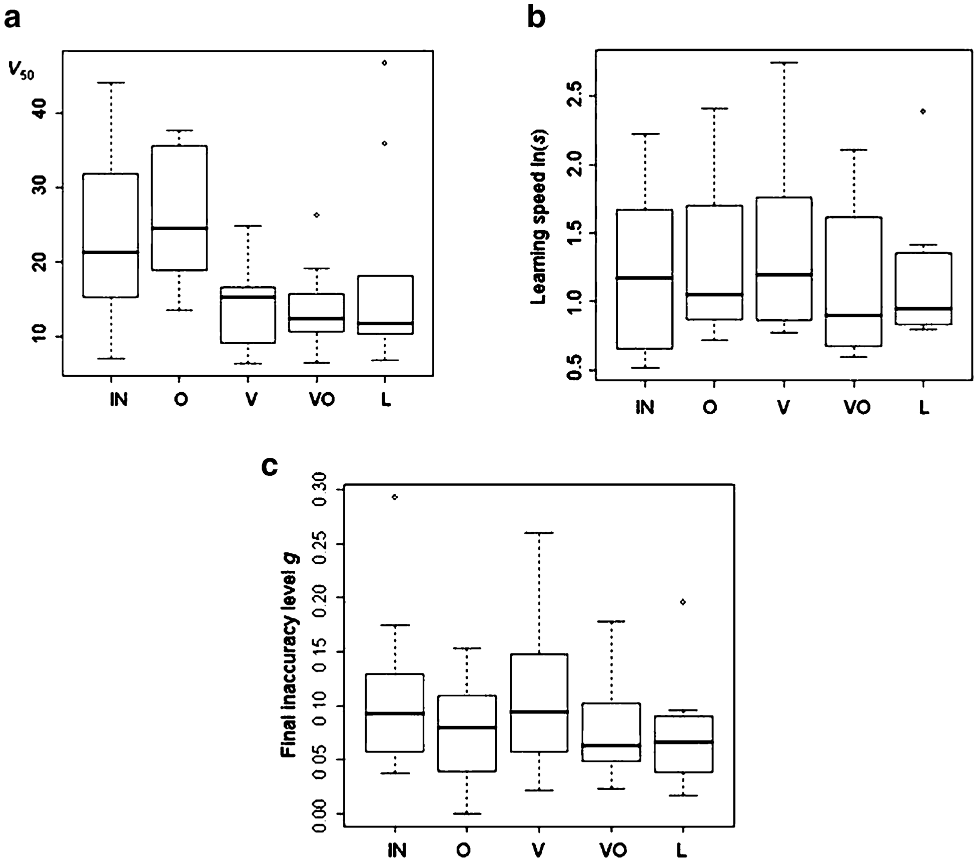

Fig. 3 Learning performance in the various treatment groups: *IN* Individual (T1), *O* olfaction only (T2), *V* vision only (T3), *VO* vision and olfaction (T4), *L* live demonstrators (T5). Learning parameters: **a** ν_{50} flower visit at which half of maximal performance has been attained; **b** ln(s) learning speed; **c** g final performance. *Boxes* indicate inter-quartile range, *thick lines* represent mean values

we pinned a dead bumblebee (as described in "Experiment III") to the green matting floor.

Subjects ($n=17$) came from two colonies tested in succession. In each test, we released one individual worker from the single nest box that was connected to the arena and recorded whether the first ten squares that she chose to land in were occupied by dead bees or vacant. After testing, bees were removed from the colony. We cleaned the arena floor with 50% alcohol solution between tests to remove any scent deposited and replaced any dead bees that had been in contact with live subjects.

Results

Experiment I

Each bee's learning performance was closely fitted by the sigmoid decay function (mean $R^2=0.9$, range=0.67–0.99). We found a significant difference in ν_{50}, the flower visit at which a bee has attained half of her maximal accuracy, between the five treatment groups (Fig. 3a; general linear model: $F_{4,55}=4.07$, $p=0.006$). Post hoc (LSD) tests indicate that this difference reflected the availability of visual cues because there were no significant differences ($p>0.05$) between T1 (individual) and T2 (olfaction only) or between T3, T4, and T5 (vision only, vision and olfaction, and live demonstrators), but significant differences ($p<0.05$) were found between all other groups. We therefore recalculated the model using the presence of visual cues and the presence of olfactory cues as the two predictors of ν_{50}. The availability of visual cues was associated with significantly lower ν_{50} ($F_{1,56}=15.46$, $p<0.01$), but olfactory cues were not ($F_{1,56}=0.38$, $p=0.54$).

We found no significant differences between bees in the five treatment groups in either learning speed s (Fig. 3b; Kruskal–Wallis test, chi-square=1.88, $p=0.76$), or final saturation level g (Fig. 3c; general linear model, square root transformation, $F_{4,54}=1.21$, $p=0.32$). The mean shape of the learning curves of bees for which visual cues were available, compared with those for which they were not, can be seen in Fig. 4.

What does a significantly lower value of ν_{50} indicate? ν_{50} is the value of x at which the bee has attained one half of her maximal accuracy index. Here, there is no significant difference between the slopes of the learning curves for the five different treatments, so ν represents how long a bee persists with visiting blue flowers before choosing a yellow flower for the first time. It is hence the latency for learning to begin. Those bees for which visual cues were present probed yellow flowers earlier than bees that had only olfactory cues or foraged alone.

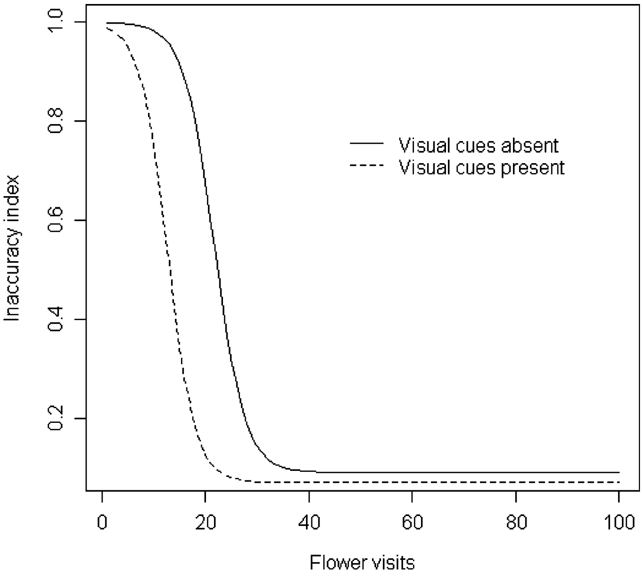

Fig. 4 Learning curves derived from the mean learning parameters (ν_{50}, s, and g) obtained for bees in the presence (T1 and T2 combined data) or absence (T3, T4, and T5 combined) of visual cues

Experiment II

When only half of the yellow flowers were associated with conspecific cues, subjects significantly preferred those yellow flowers that were occupied over their vacant counterparts (Wilcoxon signed-rank test, $V_9=52$, $p=0.014$; mean preference for occupied flowers=0.6±0.04).

Experiment III

Bees landed in occupied squares significantly more often than chance expectations of 0.5 (Wilcoxon signed-rank test, $V_{27}=132$, $p<0.001$). The mean preference (±1 SE) for occupied over unoccupied squares was 0.72±0.05. We observed that, before landing in occupied squares, subjects typically approached the conspecific from the air several times and then landed right next to or on top of it.

Discussion

Bees were quicker to begin learning which of two flower species was currently producing nectar when accompanied by experienced conspecifics than when alone. Inanimate models, which provided only visual conspecific cues, produced the same outcome, but olfactory cues alone did not. Thus, the visual cues associated with conspecific presence are sufficient to elicit this effect.

We considered three learning parameters: the point at which bees achieved half of their maximal accuracy (ν_{50}), the speed of the learning process itself (s), and the outcome of learning (g). Bees that could see others foraging on the rewarding flower species achieved half of their maximal accuracy sooner, but the learning process itself was no quicker than when bees completed the task alone, nor was the eventual outcome of learning different. This strongly implies that the learning process itself was the same in the presence and absence of social cues, but the learning curve is shifted to the left when social cues are available (Fig. 4). Thus, learning begins earlier, with bees abandoning their initially preferred blue flowers to probe a yellow sooner if conspecifics are foraging on the yellow species.

What mechanism is responsible for initially attracting bees to the yellow flowers? We consider four possibilities. Firstly, joining behavior might be observed if individuals had previously learned to associate conspecific presence with rewarding flowers. In the context of the current study, however, we can rule out this explanation because bees had no prior experience of such a situation, having fed only from a single, continuously rewarding colony feeder in the past. Secondly, bees may be attracted to the yellow flowers through observational conditioning, by which we mean that observation of foraging behavior directed towards those flowers by conspecifics might elicit the same behavior in observer bees (Galef 1988; Whiten and Ham 1992). We find this explanation unlikely, as neither the model bees or the dead demonstrators actually exhibited foraging behavior, and yet, similar effects were observed as with live demonstrators. This leaves the two explanations that we compared experimentally: Bees that observed conspecifics foraging on yellow flowers may have been attracted to *all* yellow flowers via stimulus enhancement, as described in bumblebees by Worden and Papaj (2005), or they may have been attracted only to those specific flowers where conspecifics were physically present (Leadbeater and Chittka 2005; Kawaguchi et al. 2006), via local enhancement.

When only half of the yellow flowers are occupied by demonstrators, bees landed significantly more often on those yellow inflorescences on which a conspecific had been placed than on their vacant counterparts, especially on their first visit. Thus, although we do not rule out the possibility that stimulus enhancement also occurs to some extent, local enhancement is likely to be the dominant cause of the effect observed here. Our findings indicate that bees were attracted to the rewarding inflorescences because they were occupied by conspecifics, and as a consequence, they sampled these flowers and learned to focus their efforts on that flower species more quickly than they otherwise would. This complementary combination of individual learning and social influences is typical of many instances of vertebrate social learning. As Galef (1995) puts it, “Social learning might best be described as socially-biased individual learning.”

In the scenario that we investigated, local enhancement proved to influence learning in a manner that had beneficial (and hence potentially adaptive) consequences, causing bees to learn more quickly about their environment and partly bypass the time investment of individual exploration. Nonetheless, we do not suggest that local enhancement has evolved specifically because it promotes faster learning. Bees also showed a strong attraction to conspecifics in a context that was not associated with foraging, and it seems more likely that local enhancement during foraging may reflect a general attraction to conspecific presence. In certain environmental contexts, joining others at a resource would not lead individuals to those resources that are the most optimal (Beauchamp et al. 1997), and further research is underway to investigate how social cues influence learning under these circumstances.

Local enhancement is a common feature of invertebrate behavior, occurring in a variety of contexts from sexual behavior to foraging (Prokopy and Roitberg 2001; D’Adamo et al. 2003; Slaa et al. 2003). Most of these species also learn about aspects of their environment, and recent decades have revealed that some have surprisingly complex cognitive abilities (Giurfa et al. 2001; Giurfa 2003; Menzel et al. 2006). The data that we present here provide evidence of a straightforward mechanism by which social behavior can significantly influence insect learning, and the simplicity of this mechanism suggests that it may well occur in other invertebrate species. Invertebrate systems have the advantage of being relatively easy to manipulate in the lab and providing results that are straightforward to interpret. Hence, we suggest that, although insect models cannot compete with many vertebrate social learning systems in terms of complexity, they may prove an excellent system for understanding the processes by which social learning begins to evolve.

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