

REPORT

COGNITION

Bumblebees show cognitive flexibility by improving on an observed complex behavior

Olli J. Loukola,*† Clint J. Perry,† Louie Coscos, Lars Chittka

We explored bees' behavioral flexibility in a task that required transporting a small ball to a defined location to gain a reward. Bees were pretrained to know the correct location of the ball. Subsequently, to obtain a reward, bees had to move a displaced ball to the defined location. Bees that observed demonstration of the technique from a live or model demonstrator learned the task more efficiently than did bees observing a "ghost" demonstration (ball moved via magnet) or without demonstration. Instead of copying demonstrators moving balls over long distances, observers solved the task more efficiently, using the ball positioned closest to the target, even if it was of a different color than the one previously observed. Such unprecedented cognitive flexibility hints that entirely novel behaviors could emerge relatively swiftly in species whose lifestyle demands advanced learning abilities, should relevant ecological pressures arise.

Insects can solve a range of cognitive tasks (1, 2), such as numerosity (3), basic forms of concept learning (4), and social learning (5, 6). However, most of these paradigms have analogs in bees' natural foraging routines (7), and bees might perform well at them simply because the learning processes involved might be used in tasks encountered by bees naturally. One approach to testing animal intelligence is to examine behavioral flexibility by using paradigms that are removed from problems encountered naturally by the species in question (8). To probe the limits of behavioral and cognitive flexibility in bees, we explored whether they can use a non-natural object in a task that is relatively far removed from bees' natural foraging activities.

We designed an experiment that required subjects to move an unattached object to a specified location in order to obtain a reward. Bumblebees were allowed to forage in an arena connected to their hive. In experiment 1, bees were pretrained (48 hours) to locate a small yellow-painted ball in the middle of a small circular blue platform (supplementary materials) and access a 30% sucrose solution through a hole in the ball. During the training phase, to obtain the reward, bees had to move the ball from the edge of the platform to the central designated area (Fig. 1A) within 5 min. In early trials, when a bee did not manage to accomplish the task, the experimenter would demonstrate how to solve it. While the bee was on the platform near the ball, the ex-

perimenter used a plastic model bee attached to a thin transparent stick to move the ball into the circular area around the hole (movie S1), at which point the experimenter would open the door using a button-operated servo mechanism, giving the bee access to sucrose solution (Fig. 1A). By using model bees (9–11), rather than live bee demonstrators, we ensured standardized demonstration. In later trials, the experimenter gave the bee access to the reward when it succeeded by itself. The first 10 trials of the training phase were done on a small circular platform (diameter = 7 cm). Individuals that failed to reach a minimum 60% success rate during the first training phase were removed from the study ($n = 4$ bees). During the next 20 trials, 14 bees (4, 4, and 6 from three colonies) continued the same training and demonstrations on a larger platform (diameter = 14.5 cm) (Fig. 1A). The test phase consisted of 10 trials, on the large platform, without any demonstrations (movie S2). Four bees died of natural causes during the training phase, and one bee died after only three test trials.

In all trials of the test phase, all nine remaining bees successfully gained access to reward by moving the ball to the central region (Fig. 1B). Bees also took progressively less time to solve the task over trials (Fig. 1C; generalized linear modeling analyses are provided in table S1). Bees travelled with the ball for significantly shorter distances between the first and last test phase trial (t test; $n = 14$ bees, $t_{12} = 3.07$, $P < 0.0096$) (Fig. 1D) and were more likely to enter the central region from the half of the platform where the ball started (Fig. 1E).

To determine the influence that social learning had on bees' performance, we first pretrained bees as in experiment 1, but on a square platform (supplementary materials, experiment 2). Subse-

quently, on a platform with three yellow balls placed at varying distances from the center, bees were trained over three trials in one of three conditions: (i) social demonstration, in which a previously trained conspecific moved the furthest ball to the center to gain a reward ($n = 10$ bees) (Fig. 2A and movie S3); (ii) "ghost" demonstration, in which a magnet hidden underneath the platform was used to move the furthest ball to the center to gain a reward, allowing us to examine whether movement of the ball alone was sufficient to solve the task ($n = 10$ bees) (Fig. 2A and movie S4); and (iii) no demonstration, in which bees found the ball already at the center of the platform with a reward, to explore whether bees could learn the task without any information regarding the movement of the ball, when it was found at displaced locations in later tests ($n = 10$ bees) (Fig. 2A and movie S5). During this training phase, the two balls closest to the center were glued down to prevent their movement and ensure that the demonstrator would only move the furthest ball. The balls were placed in three guiding lanes converging onto the center of the platform to facilitate the task (in experiment 1, bees took up to 5 days to learn the task). After training, bees were challenged to move any of the three balls (again positioned at three different distances from the target, but none glued) to the center. If a bee was successful, the experimenter placed 200 μ l of 30% sucrose solution within the central region (movie S6). If a bee failed within 5 min, she was moved back to the hive and allowed to return to try again.

When faced with live demonstrators, observers had, on average, more successful trials ($99 \pm 1\%$) and took less time (47 ± 8 s) to solve the task than did ghost demonstration ($78 \pm 5.5\%$, 84 ± 7 s) or no demonstration ($34 \pm 7.0\%$, 96 ± 21 s) groups (Fig. 2, B and C; generalized linear modeling analyses are provided in tables S2 to S5), showing that the behavior of the demonstrator was vital for the observer's level of success. Bees receiving the ghost demonstration had, on average, more successful trials than those of bees receiving no demonstration, suggesting that observation of a moving ball was enough for bees to solve the task.

Demonstrators always moved the furthest ball to the center, and always from the same spatial location, because they had been trained under conditions in which the more proximate balls were immobile (Fig. 2A). Observers thus had the option of copying the demonstration (moving the furthest ball) or moving one of the balls closer to the center. This design allowed us to test whether social learning in bees, in our task, was due to common associative mechanisms. In most of the successful trials, bees used the closest ball to the center ($\chi^2 = 158.94$, $df = 2$, $P < 2.2 \times 10^{-16}$) (Fig. 2B), indicating that bees were not attracted to the location where conspecifics were observed and that local enhancement (increased attention to the spatial location and movement of the demonstrator) did not play a role in how bees solved the task. Most bees solved the

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task on their very first test trial (25 of 30 bees). In addition, bees did not simply copy the instruction of “moving a yellow ball.” On a generaliza-

tion test, with a black ball in the position nearest the center, bees chose to move the black ball in most of the successful trials ($\chi^2 = 16$, $df = 2$, $P =$

3.36×10^{-4}) (Fig. 2D and movie S7), suggesting that bees were not attracted to the color of the ball during training and that stimulus enhancement (increased attention to the yellow ball) played no role in how the bees solved the task.

The behavioral flexibility required in these experiments extends substantially beyond that typically encountered by bees in nature. Foraging bees learn to handle a variety of complex-shaped flowers (12), but in these scenarios, continuous pushing toward the goal (nectar or pollen source) is required, immediate access to reward is present, and objects manipulated are all attached to the flower. In our paradigm, bees commonly faced away from the reward location because they rolled the ball in a pulling manner backward toward the hole, with reward delayed until the ball was positioned within the central area (movie S2). The best examples of cognitive flexibility involve actions that are not within the animals’ heritable inventory of behaviors to ecologically frequent problems (13). We present here an example in which an insect displays a goal-directed behavior for which evolution has not provided them with a rigid adaptation.

Insects have been trained on complex behaviors such as pushing a cap (14), rotating a lever (15), and pulling a string (16) to gain a reward. Although these works have added to our understanding of operant conditioning, such behaviors required shaping with simple associations, in which subjects are trained on a series of tasks that increase in difficulty (17). In our experiment 1, bees could have learned through shaping. However, in experiment 2 our bees were not trained in a stepwise manner. Only three bees in the social demonstration group and two in the ghost demonstration group attempted to move the ball as they followed the demonstration. However, the success of both social and ghost demonstration groups were significantly above that of the no demonstration group when accounting for this effect (Fig. 2B; generalized linear modeling analyses are provided in tables S2 and S3). Further, in all instances of bees following the demonstrations, they did so walking forward. During test trials, however, bees pulled the ball while walking backward toward the center, indicating that their behavior was not the result of shaping during the demonstration.

In most of the aforementioned studies on operant conditioning (14, 15), bees had to remove an obstacle that blocked their access to a known rewarding location. By approaching a stimulus associated with reward, they moved this obstacle until reward was accessible. In contrast, our bees could directly reach the rewarding location but instead moved a displaced object while walking backward to that location to receive reward.

Previous works also trained bees on tasks that relied on local and stimulus enhancement to solve the task (14–16). In our current work, on most successful trials, bees used the closest ball instead of the furthest ball (which they had seen the demonstrator moving) and in the generalization test used a differently colored ball than previously encountered, suggesting that bees did

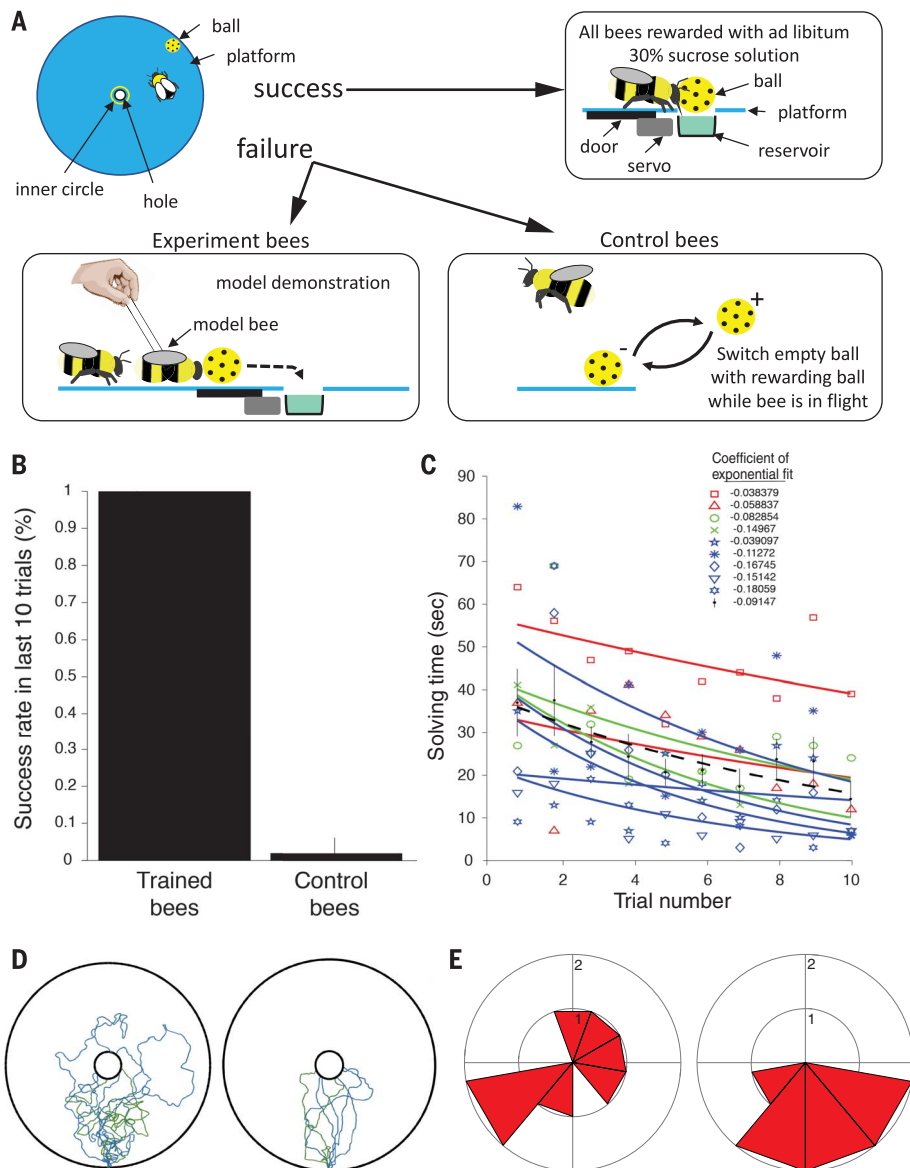
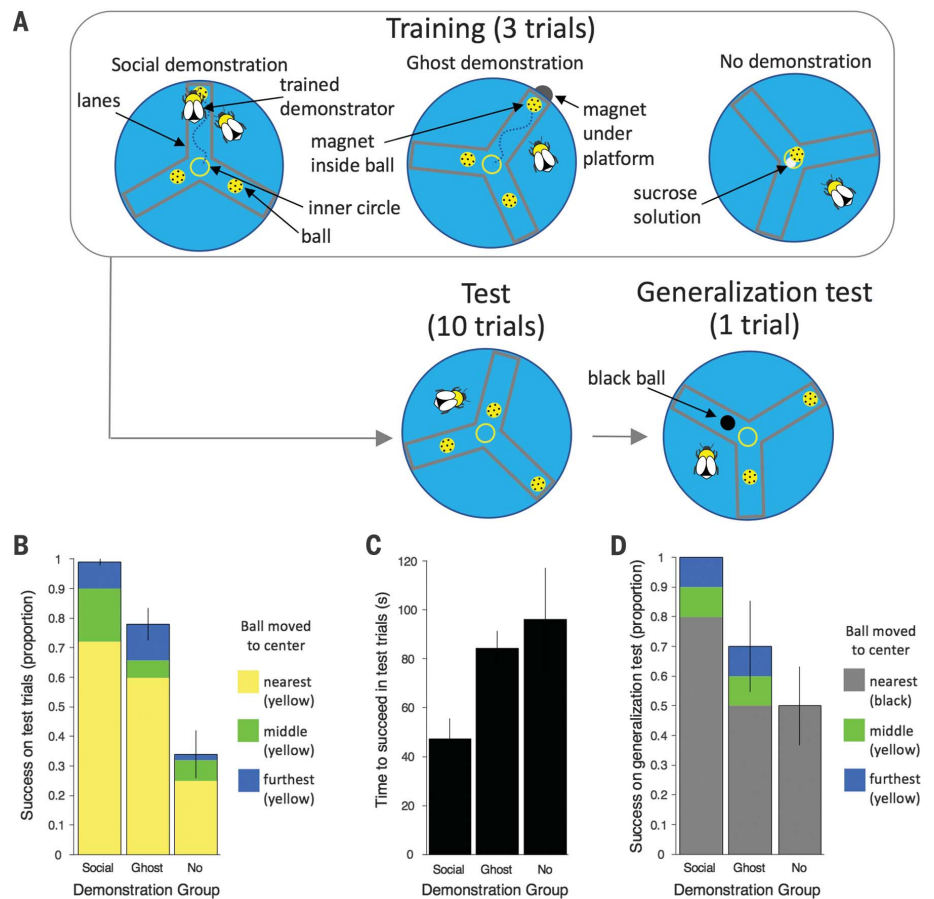


Fig. 1. Bees learn to move a ball to a specific location to gain reward through model-bee demonstration. (A) After pretraining all bees to find 30% sucrose solution in a hole under a ball (supplementary materials), bees were trained to move a ball from the edge of a platform to the center within 5 min in order to obtain a reward. For experiment bees, on early unsuccessful trials the experimenter used a model bumblebee attached to a transparent stick to move the ball to the hole and gain the reward. When control bees were unsuccessful, and off the platform, the empty ball was switched for a ball containing a reward. In the testing phase, the task was the same, but no demonstration occurred. When bees were successful in moving the ball to the center in the training or test phases, the experimenter would immediately open a door using a button-operated servo mechanism, giving access to 30% sucrose solution. (B) Experiment bees ($n = 9$) succeeded in significantly more test trials than did control bees ($n = 10$) (supplementary materials) (t test; $n = 19$ bees, $t_{17} = -69.52$, $P < 2.57 \times 10^{-22}$). (C) Learning curves show that all experiment bees increased efficiency with experience (coefficients of exponential fit for all learning curves are negative). Symbol shapes indicate individual bees. Colors indicate colonies. The black dashed line shows exponential fit to the mean solving times across bees. (D) Paths of experiment bees during first (left) and last (right) trials of test phase ($n = 7$ bees; two bees were not filmed) (supplementary materials, materials and methods). Colors indicate colonies. All paths’ origins (where the ball was randomly placed along the edge) are fixed at the 6 o’clock position. (E) Ball entrance into the center circle during the first trial (left) and last trial (right) of the test phase. Angles of entrance were binned into nine 40° sectors. Sector length indicates the number of bees entering the center circle from within that sector.

Fig. 2. Analysis of social and movement aspects of learning a complex behavior. (A) After pretraining all bees to find 30% sucrose solution in a hole under a half-ball in a square blue platform, bees were allocated to three demonstration groups for training (three trials). The social group received demonstrations by a live conspecific moving the furthest of three balls located at various distances from the center of a large blue platform, to the center to gain reward. Balls were placed in lanes (sided by 1-mm-high plastic walls) to facilitate the task. The nonsocial group received a ghost demonstration via moving the furthest ball with a hidden magnet. The bees that did not receive demonstration (No) found one ball at the center of the platform already with reward. Bees were then tested (10 trials) with the same platform, where three balls were placed at varying distances from the center. Bees were required to move any ball to the center for the reward. The generalization test required bees to move any ball to the center for reward, but the closest ball was black.

(B) Social demonstration bees had, on average, more successful test trials than those of other groups. All groups tended to use the nearest ball to solve the task. (C) Social demonstration bees took less time on average than did bees of other groups. (D) When a black (unfamiliar) ball was placed nearest the center, all groups tended to use the black ball to solve the task, but performance on the generalization task by bees that received social demonstration was better than that of other groups. In (B) to (D), the vertical black lines indicate SE. In (B) and (D), colored portions of bars indicate proportions of each ball used relative to successes.



not simply copy the behavior of the demonstrator but rather improved on the observed behavior by using a more optimal route. That bees solved this novel, complex goal-directed problem—and solved it via observation and using a better strategy than originally demonstrated—shows an unprecedented degree of behavioral flexibility in an insect.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/355/6327/833/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 and S2
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Editor's Summary

Very clever bees use tools

One hallmark of cognitive complexity is the ability to manipulate objects with a specific goal in mind. Such "tool use" at one time was ascribed to humans alone, but then to primates, next to marine mammals, and later to birds. Now we recognize that many species have the capacity to envision how a particular object might be used to achieve an end. Loukola *et al.* extend this insight to invertebrates. Bumblebees were trained to see that a ball could be used to produce a reward. These bees then spontaneously rolled the ball when given the chance.

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