RESEARCH ARTICLE

Feature-positive and feature-negative learning in honey bees

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SUMMARY

Honey bees (*Apis mellifera anatolica*) were subjected to sequential trials where they were given the choice between a feature-positive and a feature-negative feeding plate. The 'feature' being manipulated is the presence of a single blue circle among three circles marking the location of a small sucrose reward. That is, a 'feature-negative' target had three white circles, while a 'feature-positive' target had two white circles and one blue one. Two experiments were performed. In both experiments, each bee was tested under two different reward scenarios (treatments). In the first experiment, during the feature-positive treatment bees received 4 μl of 2 mol l^{-1} sucrose when choosing the feature-positive plate, but received 4 μl of saturated NaCl solution (saltwater) when choosing the feature-negative plate. During the feature-negative treatment, bees were rewarded when visiting the feature-negative plate, while visitation to the feature-positive plate only offered bees the saltwater. The second experiment was a repeat of the first except that pure water was offered instead of saltwater in the non-rewarding feeding plate. As an experimental control, a set of bees was offered sequential trials where both the feature-positive and feature-negative plates offered the sucrose reward. Bee feeding plate choice differed between the feature-positive and feature-negative treatments in both experiments. Bees favored the feeding plate type with the sucrose reward in each treatment, and never consumed the saltwater or pure water when encountered in either treatment. Further, behavior of bees during both the feature-positive and feature-negative treatments differed from that of control bees. However, neither feature-positive nor feature-negative learning reached high levels of success. Further, a feature-positive effect was seen when pure water was offered; bees learned to solve the feature-positive problem more rapidly. When we tested bees using simply the choice of blue *versus* white targets, where one color held the sucrose reward and the other the saltwater, a bee's fidelity to the color offering the sucrose reward quickly reached very high levels.

Key words: *Apis mellifera*, feature-positive, feature-negative, discrimination conditioning.

INTRODUCTION

Discrimination among stimuli is perhaps one of the most fundamental cognitive abilities an animal possesses after simple Pavlovian conditioning. This ability is not limited to vertebrates. Indeed, honey bees are extremely good at discrimination problems involving odor choices (reviewed by Wells et al., 2010). Using odors, their success rate reaches nearly 90% after being given the discrimination choice just three times (e.g. Abramson et al., 2010). Similar rates of learning have been observed when honey bee foragers have been required to discriminate between colors such as blue and yellow (Hill et al., 1997; Hill et al., 2001). Not only can honey bees learn rapidly to respond to only one of several conditioning stimuli, they can also readily learn to emit an appropriate response to alternative conditioned stimuli (Collett and Baron, 1995).

A more complex discrimination task is recognizing that a feature of a conditioning stimulus differs when presented with alternatives. This can involve association of a reward with the presence of a feature (feature-positive problem) or with the absence of a feature (feature-negative problem). Indeed, this is considered such an important developmental step that these two tasks are prominent parts of children's television shows funded by the US Department of Education (e.g. 'Moose and Zee' and 'Dora the Explorer').

The terms feature-positive and feature-negative were first used by Jenkins and Sainsbury (Jenkins and Sainsbury, 1969; Jenkins and Sainsbury, 1970) to describe an interesting phenomenon in the area of discrimination learning. If two stimuli presented successively or simultaneously are differentiated by a distinctive feature located on one of the stimuli, the learning of the discrimination is faster if the distinctive feature is associated with the rewarded stimulus (feature-positive effect) and hindered if it is associated with the unrewarded stimulus (feature-negative effect). The term 'feature' refers to one aspect of a complex cue; the basic cue remains the same, but some aspect of the cue is altered. For example, children are shown sailboats and the correct

answer is associated with whether the color of any of the sails is different (Nick Jr's 'Lesson plans with Moose and Zee').

Experimental comparison of addition and deletion tasks for animals other than humans has been notably rare (reviewed by Hearst and Wolff, 1989), and this problem continues to be understudied (Miranda et al., 1992; Abramson and Buckbee, 1995). However, it is clear that at least some species in a variety of vertebrate groups can solve both feature-positive and feature-negative problems. These groups include primates (Pace et al., 1980), rodents (Crowell and Bernhardt, 1979) and birds (Jenkins and Sainsbury, 1969).

Most of the literature related to addition *versus* deletion problems has shown what has come to be known as the feature-positive effect. The feature-positive effect is manifested as better discrimination performance when stimulus features are added. That is, discrimination problems in which the response was based on the presence of a feature (feature-positive) were learned rapidly, whereas discrimination problems where the response was based on the absence of a feature (feature-negative) were learned slowly and subjects reached poorer performance levels. The feature-positive effect (superiority of feature-positive over feature-negative learning) has been found to occur in pigeons (Jenkins and Sainsbury, 1969), rats (Crowell and Bernhardt, 1979), monkeys (Pace et al., 1980) and even humans (Neisser, 1963; Sainsbury, 1971; Newman et al., 1980; Healy, 1981).

The cognitive abilities of honey bees enter the realm of that originally thought to be limited to the more complex vertebrates (Giurfa et al., 2001). This includes the ability to categorize stimuli (Srinivasan et al., 1998; Zhang et al., 1999), solve delayed matching-to-sample and non-matching-to-sample problems, master sameness and difference inter-relationships of spatial objects (Giurfa et al., 2001), learn contextual information (Collett and Baron, 1995; Collett et al., 1997) and categorize visual information (van Hateren et al., 1990; Horridge and Zhang, 1995; Giurfa et al., 1996, Hill et al., 1997). These abilities that mirror those of the more complex vertebrates suggest that honey bees should also be able to master both feature-positive and feature-negative problems. It also suggests that the feature-positive effect should be prominent in these insects.

However, unlike vertebrates, insects do not appear to be able to recognize the gap in background 'noise' as a conditioning stimulus. Several vertebrate groups have been shown to be able to associate the removal of a stimulus with an impending event, although this is much more difficult than associating the presentation of a stimulus with a reward or punishment [e.g. pigeons (Jenkins and Sainsbury, 1969), rats (Crowell and Bernhardt, 1979), monkeys (Pace et al., 1980) and humans (Newman et al., 1980; Healy, 1981)]. In contrast, honey bees are unable to associate the offset of an odor stimulus with the presentation of a sucrose reward in either a simple conditioning or a discrimination-learning situation (Abramson et al., 2010). This suggests that a very different cognitive architecture is used by invertebrates to deal with some environmental situations (Suddendorf and Corballis, 2007), which would include signaled avoidance. Indeed, this prediction agrees with signaled avoidance studies using honey bees (Abramson, 1986), crabs (Abramson et al., 1988) and earthworms (Abramson and Buckbee, 1995).

Here we present results of experiments testing whether honey bees can solve a feature-positive and also a feature-negative problem. If consistent with vertebrates, we would expect a feature-positive effect. Further, if the studies of Abramson (Abramson, 1986; Abramson et al., 2010) on the offset of a signal and on signal avoidance are predictive, bees may be completely unable to solve feature-negative problems.

MATERIALS AND METHODS

Free-flying honey bee foragers (*Apis mellifera anatolica* Maa 1953) were used as the experimental organism. Foragers from a nine-frame hive were trained to fly 50 m to the experiment location where there was a clear Petri dish containing clove-scented $1\,mol\,l^{-1}$ sucrose solution ($5\,\mu l\,l^{-1}$ clove oil) located on a $60\times60\,cm$ square brown table, which served as the experiment platform.

The Petri dish was removed and replaced with two disks that each had a $4\,\mu l\,2\,mol\,l^{-1}$ sucrose reward in the center. Each disk was a flat 85 mm diameter circular plate of clear 2 mm Plexiglas. Each feeding disk had three 20 mm diameter color circles, the centers of each placed 12 mm from the center of the plate. The circles were either all painted white (Testors enamel no. 1245, Testors Corporation, Rockford, IL, USA), or two of the circles were painted white and the third was painted blue (Testors enamel no. 1208) as depicted in Fig. 1. This arrangement eliminated a position effect (e.g. blue in the center position indicated the presence of a reward). After a disk was visited, it was removed and replaced with a new disk with the same reward. Disk placement was random. Each disk was washed after each bee visit. One bee was followed at a time. Additional bees were removed from the system. Each bee was allowed to freely choose disks to visit. Those bees that had been used in an experiment were uniquely marked. Disk and experimental design were modifications of those used by Pace et al. (Pace et al., 1980) for tests with monkeys and pigeons. Here, addition of a blue
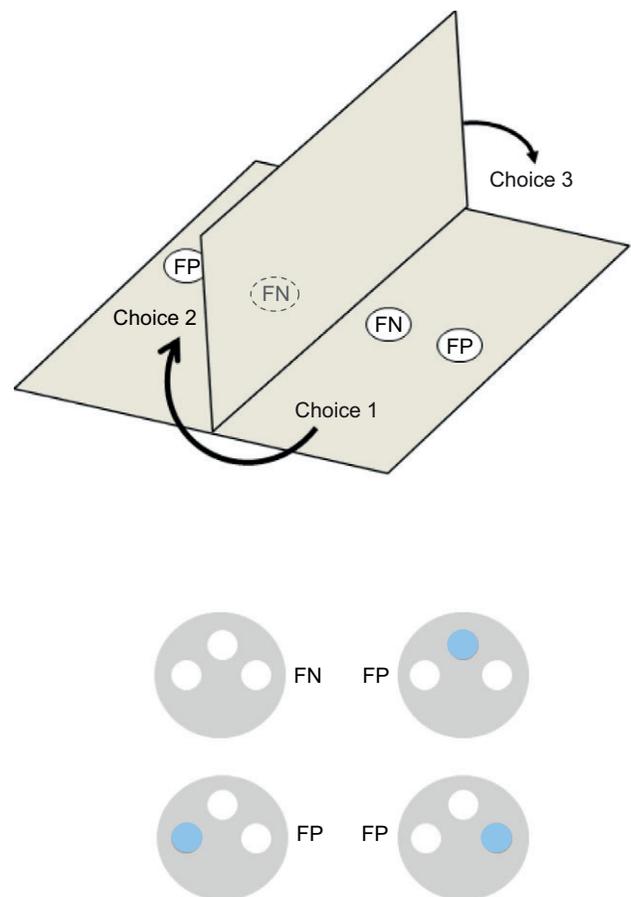

Fig. 1. Experimental design. Top: diagram of the partition with a choice between a feature-positive (FP) and a feature-negative (FN) disk on each side of the partition. Whether the feature-positive or feature-negative disk was closest to the partition was random. Bottom: arrangement of white and blue circles on the feature-positive and feature-negative disks.

circle (while controlling for number of circles and the location effect of the blue circle) represents the feature-positive disk, while replacement of the blue circle with a white circle represents the feature-negative disk. Two experiments were performed.

Saltwater experiment

Once the test bee was freely moving back and forth between disks (~10 min), a 60 cm tall barrier the length of the table was placed between the disks. The bee had to fly around the barrier to visit the next feeding disk each time (Fig. 1). An experiment had three treatments, which were performed sequentially and without break. The first treatment (initiation treatment) was a session to demonstrate that bees would readily visit all disks and fly around the barrier. The initiation treatment had one feeding disk on each side of the barrier. Each disk had a $4\,\mu l$ $2\,mol\,l^{-1}$ sucrose unscented reward. After visitation of the test bee to a side of the table, the disk was replaced with another disk with the same reward regardless of whether the bee chose to consume the reward. Each of the four color patterns occurred in equal frequency, and the order of presentation was random. The disk color pattern and whether the bee consumed the reward were recorded each time the bee visited a side of the barrier. Each bee took part in six trials over the course of the initiation treatment, where a trial consisted of a trip from the hive in which all of the feeding disks were visited by a bee (~10).

The order of the second [feature-positive (FP)-rewarding] and third [feature-negative (FN)-rewarding] treatments was randomized so that half of the bees received the FN-rewarding treatment before the FN-rewarding treatment. In both the FP-rewarding and FN-rewarding treatments, each side of the barrier gave the bee a choice between two disks: one of the disks always had three white circles (feature-negative: missing the blue circle) and the other disk always had two white circles and one blue circle (feature-positive: with a blue circle). Each of the three patterns with a blue circle occurred in equal frequency during the FP-rewarding and FN-rewarding treatments. Each bee invariably went around the side of the barrier rather than over it. Thus, the two-disk set was presented in a line perpendicular to the barrier with the feature-negative disk placed next to the barrier approximately half of the time (random placement).

The FP-rewarding treatment presented the reward in the feature-positive disk. Thus bees received $4\,\mu l$ of $2\,mol\,l^{-1}$ sucrose when choosing the feeding plate with one blue and two white circles, but received $4\,\mu l$ of saturated NaCl solution when choosing the feeding plate with three white circles. The FN-rewarding treatment presented the reward in the feature-negative disk. Thus bees received $4\,\mu l$ of $2\,mol\,l^{-1}$ sucrose when choosing the feeding plate with three white circles, but received $4\,\mu l$ of saturated NaCl solution when choosing the feeding plate with one blue and two white circles. After visitation of the test bee to a side of the table, the two-disk set was replaced with another set with the same rewards regardless of whether the bee chose to consume the reward. Each bee was presented six trials over the course of treatment 2 and six trials over the course of treatment 3, where a trial consisted of a trip from the hive in which all of the feeding disks were visited by a bee (~10). Each time the bee was presented with a two-disk choice, we recorded whether the bee chose either of the disks and, if so, the initial color pattern chosen. The disks chosen by 20 bees were recorded throughout the three treatments of the experiment.

Pure-water experiment

In the pure-water experiment, the experiment described above was repeated exactly except that pure water was used in the disk type without the reward rather than saturated saltwater. Thus, there was no punishment for choosing the non-rewarding disk type. As in the saltwater experiment, in the FP-rewarding treatment, the feature-positive disk offered $4\,\mu l$ of $2\,mol\,l^{-1}$ sucrose and the feature-negative disk offered $4\,\mu l$ of pure water. In the FN-rewarding treatment, the feature-negative disk offered $4\,\mu l$ of $2\,mol\,l^{-1}$ sucrose and the feature-positive disk offered $4\,\mu l$ of pure water. Again, the order of the FP-rewarding and FN-rewarding treatments was randomized. A new set of bees was used for this experiment. The disks chosen by 20 bees were recorded throughout the three treatments of the experiment.

Negative experimental control

A negative experimental control in which bees were expected to show no preference was performed using the design of treatments 2 and 3 in terms of presentation of feeding disks, but where both feature-positive and feature-negative disks in a set offered a $4\,\mu l$ $2\,mol\,l^{-1}$ sucrose reward. Only one treatment was performed after the training treatment, and it contained six trials, as did the experimental treatments. This tested for bees innately favoring either feature-positive or feature-negative disks. Each time the bee was presented with a two-disk choice, we recorded whether the bee chose either of the disks and, if so, the initial color pattern chosen. A new set of bees was used for the negative experimental control. The disks chosen by 20 bees were recorded throughout the two treatments of the negative experimental control.

Positive experimental control

A second experimental control where bees were expected to make few mistakes was performed using disks that presented a simple target – either blue or white. Here each disk had a single 35 mm diameter circle in the center, which was the same area as the three circles in the feature-positive/feature-negative experiments. The same three-treatment experimental design described above was used, except that instead of feature-positive and feature-negative disks being paired, blue and white disks were paired, with blue rewarding in the second treatment and white rewarding in the third treatment. A new set of bees was used for the positive experimental control. The disks chosen by 20 bees were recorded throughout the three treatments of the positive experimental control.

Statistical analysis

First, we tested for differences in behavior between the FP-rewarding and FN-rewarding treatments in each feature-positive/feature-negative experiment (saltwater and pure water). The test was performed separately for the saltwater and pure-water experiments, in each case using a repeated-measures MANOVA. The arcsine square root transformed mean relative frequency (over six trials of a treatment) of feature-positive disk choice for each bee was used (Sall and Lehman, 1996; Sokal and Rohlf, 1995). The MANOVA tested for treatment (feature-positive or feature-negative with the reward), order (whether the feature-positive treatment came before or after the feature-negative treatment) and treatment × order interaction effects.

Next, a repeated-measures MANOVA was used to test whether behavior differed in the FP-rewarding treatment between the saltwater and pure-water experiments, where the feature-positive disk held the reward. The arcsine square root transformed relative frequency of feature-positive disk-type choice for each bee was used (Sall and Lehman, 1996; Sokal and Rohlf, 1995). The MANOVA tested for experiment (saltwater or pure water), trial (1 through 6) and experiment × trial interaction effects. The statistical test was

repeated for the FN-rewarding treatment of the saltwater and pure-water experiments, where the feature-negative disk held the reward.

MANOVAs were used to test for overall differences in the rate of choosing a feature-positive disk in the FP-rewarding treatment of the experiment (feature-positive disks had the reward) and in the negative experimental control, and separately for choosing a feature-negative disk in the FN-rewarding treatment of the experiment (feature-negative disks had the reward) and in the negative experimental control (Sall and Lehman, 1996). Arcsine square root transformed relative frequency of choosing the positive disk-type was used (Sokal and Rohlf, 1995). The MANOVAs tested for category (experiment *versus* control), trial and interaction effects. Data from the saltwater and pure-water experiments were tested separately.

For the positive experimental control, MANOVAs (Sall and Lehman, 1996) were used to test for overall differences in the rate of choosing a feature-positive disk in the FP-rewarding treatment of the experiment (feature-positive disks had the reward) and a blue disk in the control (blue rewarding of the control), and separately for choosing a feature-negative disk in the FN-rewarding treatment of the experiment (feature-negative disks had the reward) and a white disk in the control (white rewarding of the control). Arcsine square root transformed relative frequency of choosing the positive disk-type was used (Sokal and Rohlf, 1995). The MANOVAs tested for a category (experiment *versus* control), trial and interaction effect. Data from the saltwater and pure-water experiments were tested separately.

RESULTS

In the saltwater experiment, where saltwater was presented in the non-rewarding disk type, forager behavior differed between treatments 2 and 3 (treatment effect: $F_{1,18}$=41.608, P<0.0001). However, neither order of treatment ($F_{1,18}$=0.0054, P=0.9424) nor interaction ($F_{1,18}$=0.0187, P=0.0893) effect were significant. Bees favored feature-positive disks in treatment 2 and feature-negative disks in treatment 3. Bees never consumed the saltwater (Fig. 2).

In the pure-water experiment, where water was presented in the non-rewarding disk type, forager behavior differed between treatments 2 and 3 (treatment effect: $F_{1,18}$=19.035, P=0.0003). However, neither order of treatment ($F_{1,18}$=1.8483, P=0.1908) nor interaction ($F_{1,18}$=1.4161, P=0.2495) effect were significant. Bees favored feature-positive disks in the FP-rewarding treatment and feature-negative disks in the FN-rewarding treatment (Fig. 2). Bees never consumed the water in this experiment. However, bees will collect water to cool the hive, and so the water cannot be considered a punishment.

Behavior in the FP-rewarding treatment did not differ between the saltwater and pure-water experiments. There was not a significant experiment ($F_{1,38}$=0.8718, P=0.3565), trial ($F_{5,34}$=2.0557, P=0.0955) or interaction effect ($F_{5,34}$=2.0092, P=0.1023). Learning was rapid, as has been reported in artificial flower patch studies (e.g. Hill et al., 1997). However, foragers never became very proficient at choosing the rewarding disk type (Fig. 2).

In contrast, behavior in the FN-rewarding treatment did differ between the saltwater and pure-water experiments. Although there was not a significant experiment effect ($F_{1,38}$=0.8386, P=0.3659), both significant trial ($F_{5,34}$=4.2152, P=0.0043) and experiment × trial ($F_{5,34}$=2.6101, P=0.0421) effects occurred. Response in the saltwater experiment resembled that of FP-rewarding treatment, where what learning occurred happened within the first few choice situations of trial 1, but where bees never became very proficient in solving the task. However, learning was slower in the pure-water
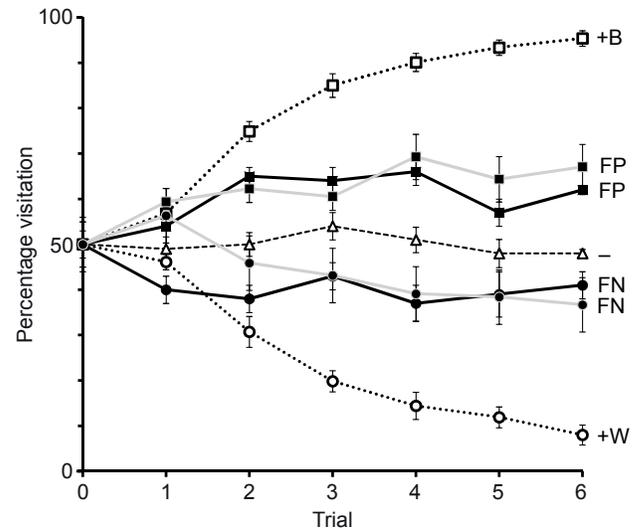

Fig. 2. Honey bee response to different experimental conditions. Solid symbols are the feature-positive (FP; filled squares; treatment 2) and feature-negative (FN; filled circles; treatment 3) experimental results. Percentage visitation to feature-positive disks is shown for each trial of the FP-rewarding and FN-rewarding treatments. Black lines represent the experiment where the non-rewarding disk offered concentrated saltwater. Gray lines represent the experiment where the non-rewarding disk simply offered pure water. Open symbols are the experimental controls. Percentage visitation to feature-positive disks is shown for the negative experimental control (–; open triangles). Percentage visitation to blue disks is shown for the positive experimental control, with blue rewarding in the second treatment (+B; open squares) and white rewarding in the third treatment (+W; open circles). Half the bees had the FN-rewarding treatment before the FP-rewarding treatment in the feature-positive/feature-negative experiments, and half the bees had the white-rewarding treatment before the blue-rewarding treatment in the positive experimental control. Data are means ± s.e.m. for each trial. Trial 0 is the mean percentage during the training session of each experiment (initiation treatment).

experiment, but by trial 3 reached the same level of proficiency as saltwater (Fig. 2).

The negative experimental control demonstrated that the FP-rewarding and FN-rewarding treatments in both the saltwater and pure-water experiments had an effect on behavior when compared with random disk selection (Fig. 2). In the saltwater experiment, the test of the FP-rewarding treatment *versus* the control showed that there was a significant category (control *versus* experiment) effect ($F_{1,38}$=40.3145, P<0.0001) but not trial ($F_{5,34}$=1.6638, P=0.1700) or interaction ($F_{5,34}$=0.5406, P=0.7441) effects. Results were the same for the FP-rewarding treatment of the pure-water experiment when tested against the control (category: $F_{1,38}$=33.4039, P<0.0001; trial: $F_{5,34}$=1.4602, P=0.2285; interaction: $F_{5,34}$=1.8073, P=0.1378). Similarly, in the saltwater experiment, the test of the FN-rewarding treatment *versus* the control showed that there was a significant category (control *versus* experiment) effect ($F_{1,38}$=25.5185, P<0.0001) but not trial ($F_{5,34}$=0.5771, P=0.7171) or interaction ($F_{5,34}$=0.3326, P=0.8897) effects. Results for the FN-rewarding treatment of the pure-water experiment when tested against the control differed in that there was not only a category effect ($F_{1,38}$=4.3101, P=0.0447) but also a trial effect ($F_{5,34}$=2.9121, P=0.0271) and an interaction effect ($F_{5,34}$=2.5063, P=0.0491). Learning was slower for the feature-negative problem.

The positive experimental control demonstrated that bees did not do as well at solving feature problems as they did at solving a simple

discrimination problem (Fig. 2). In the positive control experiments, in which the targets were solid blue or white, the bees chose the rewarded targets at significantly higher rates than they chose the feature-positive disks when these were rewarded in the feature experiments (FP-rewarding saltwater *versus* blue-rewarding positive control – category: $F_{1,38}=175.5486$, $P<0.0001$; trial: $F_{5,34}=17.9046$, $P<0.0001$; interaction: $F_{5,34}=18.2681$, $P<0.0001$; FP-rewarding pure-water *versus* blue-rewarding positive control – category: $F_{1,38}=68.1638$, $P<0.0001$; trial: $F_{5,34}=29.0587$, $P<0.0001$; interaction: $F_{5,34}=11.1476$, $P<0.0001$; FN-rewarding saltwater *versus* white-rewarding positive control – category: $F_{1,38}=97.9964$, $P<0.0001$; trial: $F_{5,34}=28.4310$, $P<0.0001$; interaction: $F_{5,34}=24.5204$, $P<0.0001$; FN-rewarding pure-water *versus* white-rewarding positive control – category: $F_{1,38}=48.1120$, $P<0.0001$; trial: $F_{5,34}=24.6910$, $P<0.0001$; interaction: $F_{5,34}=2.3453$, $P=0.0622$).

DISCUSSION

Foragers were able to solve both feature-positive and feature-negative problems to some degree when the non-rewarding disk type offered saltwater. However, neither feature-positive nor feature-negative learning reached very high levels of success. Selection of feature-positive disks when they were rewarding averaged ~60% over the six trials of the FP-rewarding treatment (mean ± s.e.m.: 61.3±1.5%). Selection of feature-negative disks when they were rewarding also averaged ~60% over the six trials of the FN-rewarding treatment (mean ± s.e.m.: 60.3±1.6%). Random visitation in each case would have resulted in choosing the feature-positive disk 50% of the time, which is what was observed in the negative experimental control (mean ± s.e.m.: 50.3±1.4%). Bees failed to make a choice less than 1% of the time, and never drank the saltwater solution when it was chosen, which occurred ~40% of the time.

Responses were very similar for the feature-positive problem when the non-rewarding disk type offered simply water. Selection of feature-positive disks when they were rewarding averaged ~64% over the six trials of the FP-rewarding treatment (mean ± s.e.m.: 63.6±2.0%). Although selection of feature-negative disks when they were rewarding reached similar levels in trial 6 of the FN-rewarding treatment (mean ± s.e.m.: 62.3±2.1%), bees took much longer to reach that level of proficiency than when saltwater was associated with the non-rewarding disk (Fig. 2).

The success rate in feature problems was quite low in comparison to that reported for simple discrimination problems and in our positive experimental control. Although performance may improve with more trials in the saltwater and pure-water experiments, it seems unlikely that it will improve significantly based on the flatness of the curves between trials 2 and 6, and because the six trials represent approximately 60 binary choices made by each bee (~10 choice situations per trial). In the positive experimental control, selection of blue disks when they were rewarding averaged ~80% over the six trials (mean ± s.e.m.: 82.6±1.3%), and selection of white disks when they were rewarding also averaged ~80% over the six trials (mean ± s.e.m.: 78.2±1.5%). By trial 6 in each treatment, bees chose the rewarding disk over 90% of the time (Fig. 2). These results are comparable to success rates of bees visiting artificial flower patches where the choice is between blue flowers and white flowers; they choose the rewarding flower color 80 to 90% of the time (Wells and Wells, 1986; Hill et al., 1997; Cakmak et al., 2009). Similar success rates have been observed using harnessed bees discriminating between odors such as cinnamon and lavender oils as conditioning stimuli (Bitterman et al., 1983; Abramson and Boyd, 2001; Abramson et al., 2010). Furthermore, these success rates are

achieved in both types of studies (odor and color) in what is equivalent to one trial (~10 test choices) in our study. This shows how much more difficult feature problems are to honey bees than simple discrimination problems.

As in vertebrate groups, the feature-positive effect was observed in the honey bees in the present study, but only when water was associated with the non-rewarding disk type. Thus, saltwater in the non-rewarding disk type acted as a punishment that enhanced learning rate. Nevertheless, honey bee forager success rate by trial 6 was not better when given the feature-positive rather than the feature-negative problem, with performance highly variable in each trial. Thus, foragers never seemed to consolidate learning, and seemed to be continually reassessing the problem presented to them. It is possible that only short-term memory is involved. Because the general experimental design and the use of a series of colored circles (either all being the same color or one different in color) follow the study of Pace et al. (Pace et al., 1980) with monkeys and pigeons, the vertebrate and honey bee results should be broadly comparable. However, both birds and primates reach a much higher success rate than honey bees, although there was considerable variability between subjects for each species.

The difficulties we observed in learning feature problems and the feature-positive effect, combined with the honey bees' inability to use the removal of a cue in learning either to expect a reward or punishment, may represent a fundamental aspect of the cognitive architecture of bees that differs from vertebrates, and is worth exploring not only in other insects but also in other invertebrates. Although the end result in vertebrates and honey bees may appear to be the same in terms of behavior, honey bees seem to reach this point by very different cognitive processes.

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