

Category Difference Facilitates Oddity Learning in Honeybees (*Apis mellifera*)

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Performance of honeybees resembles that of vertebrates in a variety of associative learning experiments. Recent work has focused on relational learning phenomena not easily explained by associative principles, including same/different problems, the simplest of which is the oddity problem. Free-flying bees were trained to visit a laboratory window and were rewarded for choice of the odd stimulus among a set of stimuli. There were two stimulus categories, single-color solids and two-color patterns. The training was trial-unique, with new sets of stimuli on each trial. In Experiment 1, 4 groups were trained in a 3-stimulus oddity problem, 2 with solid odd and patterns nonodd and 2 with pattern odd and solids nonodd. For 1 group in each condition, the odd and nonodd stimuli shared a color. The performance of all groups was better than chance. The bees could solve the problem on the basis of oddity (same vs. different) or category (solid vs. pattern). These possibilities were unconfounded in Experiment 2 with 2 groups trained in a 4-stimulus oddity problem. Group 1 was trained with a category difference on each trial; the solid color was odd on half the trials and the pattern odd on the others. Group 2 was trained with no category difference; all stimuli were patterns. Both groups showed better-than-chance performance, and the irrelevant category difference facilitated oddity discrimination for Group 1. The results support previous findings of oddity learning in honeybees, the only invertebrate species for which any relational learning phenomena have been demonstrated.

Keywords: comparative cognition, category discrimination, honeybee, oddity discrimination, relational learning

In experiments that are analogous to those conducted with vertebrates, honeybees have shown an extensive array of associative learning phenomena (Bitterman, 1988, 1996). These include basic reward effects such as partial reinforcement, positive contrast, and negative contrast; complex choice phenomena such as dimensional transfer, conditional discrimination, ambiguous cue discrimination, and probability matching; as well as phenomena such as escape, avoidance, spontaneous recovery, US preexposure, within-compound association, and so forth. The training procedures included Pavlovian and instrumental with both appetitive and aversive outcomes. In most cases, the results for honeybees are nearly identical to those for vertebrates. Although such similarities could indicate similar biological mechanisms, convergent evolution is probably the more parsimonious view; “different phenom-

ena may be produced by the same processes, and what appear to be identical phenomena may be produced by different processes” (Bitterman, 1975).

There is much still to be discovered in studies of basic associative learning in honeybees, and there is a need also for more in-depth and theoretical analyses of apparent similarities. Nonetheless, it is compelling to continue to expand the breadth of the work with honeybees to include some of the more cognitively complex vertebrate learning phenomena. The phenomena of most interest are those not easily explained with basic associative learning principles and may require relational or conceptual interpretations.

Particularly well-studied in vertebrates are relational learning problems that can be viewed as variants of “same/different” paradigms including simultaneous matching- and nonmatching-to-sample, delayed matching- and nonmatching-to-sample, successive same/different discrimination, simultaneous same/different discrimination, and oddity learning. In recent years, there has been a growing interest in such studies with honeybees and bumblebees. For example, Giurfa, Zhang, Jenett, Menzel, and Srinivasan (2001) trained honeybees in matching-to-sample and nonmatching-to-sample problems in a Y maze; Brown and Sayde (2013) trained bumblebees in a same/different discrimination; and Muszynski and Couvillon (2015) trained honeybees in three-stimulus oddity problems.

It is “the oddity problem” that appears to be the first of the same/different paradigms to have been studied in vertebrates. The simplest, most straightforward form of the oddity problem is one

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in which a set of three stimuli is presented on each training trial with one different and the other two identical. Choice of the different or “odd” stimulus is rewarded. The first known oddity experiment was conducted by Robinson (1933) with a single macaque monkey as the subject. The monkey was presented with three stimuli on every trial, one odd object and two identical nonodd objects. The objects were plain gray boxes and gray boxes with a black disk on the front, and a set of three was presented on a tray for each trial. Rewarded for choosing the odd object, the monkey eventually solved the problem, although it took more than 400 training trials. Although Robinson interpreted the results of her experiment in terms of “abstraction” or relational learning, an associative explanation is possible. There were only two stimuli, say, A and B, and therefore only two trial types throughout the training, one with A as the odd stimulus and one with B as the odd stimulus. These two trial types, A+ B− B− and B+ A− A−, were presented during training in six different left-middle-right horizontal configurations (ABB, BAB, BBA, AAB, ABA, and BAA). As a result of such extensive training, it is quite possible that the monkey had learned the correct response for each of the six configurations.

Robinson’s (1933) experiment can be referred to as a traditional oddity problem to differentiate it from the several procedural variations that were developed later to address the possibility that the traditional oddity problem can be solved by simply learning all of the configurations over many, many training trials. These variations include multiple oddity problems presented either simultaneously or successively across training, traditional oddity problems with transfer tests to new stimulus sets, and oddity problems with unique stimulus sets on every training trial, the latter often referred to as a “trial-unique” procedure. To distinguish these variants from Robinson’s traditional oddity problem, Muszynski and Couvillon (2015) classified all of them as “multiple-stimulus-set” oddity problems.

Such multiple-stimulus-set oddity experiments have been conducted with a variety of vertebrate species, including goats (Roitberg & Franz, 2004), a sea lion (Hille, Dehnhardt, & Mauck, 2006), monkeys (Bromer, 1940; Davis, Leary, Stevens, & Thompson, 1967; Draper, 1965; Levine & Harlow, 1959; Meyer & Harlow, 1949), chimpanzees (Davenport & Menzel, 1960; Devine & Ivens, 1969), rats (Bailey & Thomas, 1998; Koronakos & Arnold, 1957; Thomas & Noble, 1988; Wodinsky & Bitterman, 1953), cats (Boyd & Warren, 1957; Strong & Hedges, 1966; Warren, 1960), and raccoons (Strong & Hedges, 1966). In general, these tasks proved difficult, but the performance usually reached levels better than expected by chance. Typically, as was the case with Robinson’s monkey, successful solution required hundreds, if not thousands, of trials. In contrast to the widespread use of the oddity problem to study relational learning in vertebrate species, there are only a few studies of oddity learning with invertebrate species. A study with octopus by Boal (1991) failed to provide evidence of oddity learning in a series of three-stimulus problems. However, in a recent series of experiments with honeybees, Muszynski and Couvillon (2015) found oddity learning in three-stimulus, trial-unique problems as well as *nonoddy* learning in three-stimulus, trial-unique problems where choice of either of the two *nonodd* stimuli was rewarded. As is the case for vertebrate species, the problems were difficult for honeybees. However, it is interesting that many fewer trials were required by the honeybees

to achieve a better-than-chance performance than might have been expected based on the vertebrate results. The authors speculated that the powerful training technique used in their experiments with honeybees may have promoted learning of the problems. Other bee researchers have also noted rapid learning rates in a variety of problems. See Chittka and Niven (2009) for a comparative discussion of learning and cognition in insects and vertebrates.

The main purpose of the series of experiments reported here was to build on the demonstration of oddity learning in honeybees (Muszynski & Couvillon, 2015) to determine its robustness and generality as a necessary next step in the analysis of mechanism. Specifically, there were two aims. The primary aim was to expand the stimulus set to include the 6 two-color patterns used in the original studies by including four solid colors, almost doubling the size of the stimulus set. The solid colors and the two-color pattern stimuli also might be viewed as two stimulus categories. Therefore, they can be used to add a category difference to oddity problems. The expectation was that the bees’ oddity performance might be improved with the addition of the category difference by increasing the discriminability of the stimuli on each trial. Honeybees easily discriminate the 6 two-color patterns from each other and show no evidence of a preference. When only the two-color patterns were used in oddity experiments, the bees were able to learn to choose the odd pattern. Nonetheless, there was room for improvement in the asymptotic oddity performance.

A secondary aim was to increase the number of exemplars in the oddity problem from a set of three to a set of four. There was no a priori basis for making a prediction about whether or not the bees could learn a four-stimulus oddity problem, although there is some evidence from work with pigeons that adding distractor stimuli improves visual search for a target stimulus in discrimination problems (Blough, 2001; Zentall, Hogan, Edwards, & Hearst, 1980). There is work with honeybees that shows they can process five or six items simultaneously (Howard, Avarguès-Weber, Garcia, Greentree, & Dyer, 2018). The stimuli in the current experiments were presented simultaneously, three stimuli in Experiment 1 and four stimuli in Experiment 2, with the relative distance between the stimuli the same in both experiments. Although the bees in both cases tended to fly over the horizontal line of stimuli before making a choice, the bees might process the stimuli in rapid succession rather than simultaneously. There is evidence that successive discrimination is more difficult for honeybees than simultaneous discrimination because of a very small (on the order of milliseconds) memory decay (Dyer & Neumeyer, 2005). However, in a previous symbolic matching-to-sample experiment, honeybees were able to retain information about the sample for at least 5 s to make a choice in the absence of the sample (Cooke, Couvillon, & Bitterman, 2007). Therefore, it will be interesting to see whether or not honeybees can solve a four-stimulus oddity problem and, if so, whether performance appears to be facilitated with the additional stimulus.

In Experiment 1, four groups of bees were trained in a three-stimulus oddity problem with the difference in category defining the odd stimulus. In Experiment 2, two groups of bees were trained in a four-stimulus oddity problem. For one group, the stimulus sets contained a mix of two-color patterns and solids, and for the other group, the stimulus sets were all two-color patterns.

Experiment 1: Three-Stimulus Oddity With a Category Discrimination

Muszynski and Couvillon (2015) conducted both oddity and nonoddy experiments with honeybees. In all of their experiments, bees were trained with a set of three two-color pattern stimuli on each trial, one odd and two nonodd. They used a trial-unique procedure; that is, there was a unique set of stimuli on every trial. (See Figure 1 for a sample trial sequence.) In their oddity experiments, bees were rewarded for choosing the odd stimulus, and in their nonoddy experiments, bees were rewarded for choosing either of the two nonodd stimuli. For example, on the first trial of the sequence shown in Figure 1, the bees in the oddity group were rewarded for choice of the white–green pattern and punished for choice of either of the two yellow–purple patterns. Bees in the nonoddy group were rewarded for choice of either of the yellow–purple patterns and punished for choice of the white–green pattern. The performance in both kinds of problems reached levels above chance, and the results were interpreted as evidence of relational learning in honeybees.

The results of Muszynski and Couvillon's series of experiments provided the first evidence of oddity learning in honeybees. Although performance was better than chance, there was still room for improvement. Previous pilot work in this laboratory indicated that the two-color patterns were easily discriminated, even with one color in common. Nonetheless, it is possible that there was substantial generalization between the two-color pattern stimuli in the earlier experiments, and it seemed reasonable to expand the stimulus set to improve discriminability in oddity problems. Therefore, in the experiment presented here, the stimulus set included solid colors as well as the two-color patterns. Previous work in this laboratory suggested that bees can readily discriminate solid colors from two-color patterns.

The primary purpose of this experiment was to determine if honeybees could solve oddity problems with a mix of solid colors and two-color patterns on each trial. Four groups of bees were trained in a three-stimulus oddity problem with choice of the odd stimulus rewarded. For two of the groups (Solid Odd), the odd stimulus was always a solid color, and for two of the groups (Pattern Odd), the odd stimulus was always a two-color pattern. The preliminary work in this laboratory on the discrimination of solids and patterns as categories found no evidence of a preference for either and provided no basis in general to expect a difference in difficulty between the Solid Odd and Pattern Odd groups. For half of the bees in each condition (Solid Odd and Pattern Odd), there was a shared common color between the odd and nonodd stimuli, and for the other half of the bees, there was no shared common color (Table 1). One possible outcome was that the groups with no common color would learn the problem more quickly than the groups that had one common color. In other words, it was possible that the common color could interfere with the discrimination of oddity.

The design is reminiscent of feature-positive and feature-negative discriminations. In a feature-positive discrimination, the training is $AB+ A-$, and in a feature-negative discrimination, the training is $A+ AB-$ ($+$ = reward and $-$ = no reward or punishment). In such experiments, A and B represent single stimuli, and feature-positive discrimination is typically easier than a feature-negative discrimination (cf., Pace, McCoy, & Nallan,

Oddity & Nonoddy

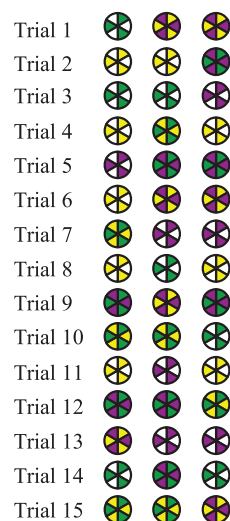


Figure 1. A sample training sequence from the study by Muszynski and Couvillon (2015). See the online article for the color version of this figure.

1980). The typical feature-positive and feature-negative discriminations use only one set of stimuli. In our oddity experiments, there is a new stimulus set on every training trial; that is, the colors change on every trial. Nonetheless, the Pattern Odd Group with one common color ($AB+ A- A-$) may learn the oddity discrimination more easily because of the rewarded feature (B) than the Solid Odd Group with one common color ($A+ AB- AB-$).

The design of the experiment was explicitly an oddity problem because there were three stimuli on every trial, one odd and the other two identical. The category difference, solids versus patterns, was introduced to try to improve on the oddity performance shown in the previous work with only patterns. To maximize the possibility of improvement, the category difference defined the odd stimulus; in other words, the bees could solve the discrimination on the basis of oddity or category discrimination. As the experiment progressed, it was clear that the bees in all groups could solve the problems. Therefore, it seemed prudent to add a control group of bees trained only with a category discrimination. The expectation was that the performance of the control group with only a category discrimination might provide a clue as to whether the "oddity" groups were solving the problem relationally or simply as a category discrimination.

Method

Subjects. The subjects were 36 forager honeybees (*Apis mellifera*) never used in previous experiments, with nine bees trained in each of the four oddity groups. Four additional bees were trained in a category discrimination control group. All bees were captured at feeders containing a 10% to 20% sucrose solution, which were located near the hives in the back of the Békésy Laboratory at the University of Hawai'i at Mānoa. Each subject was trained individually in a single daily session lasting up to several hours.

Apparatus. The bees were trained in a wooden enclosure, shown in Figure 2, that was 61 cm wide, 61 cm high, and 61 cm

Table 1
The Design of the Training of Each Group in Experiment 1

Solid Odd: One common color	A+ AB- AB-
Pattern Odd: One common color	AB+ A- A-
Solid Odd: No common color	C+ AB- AB-
Pattern Odd: No common color	AB+ C- C-

Note. A, B, and C represent different colors. Note that the training was trial-unique, and examples of the actual training sequences for each oddity group are shown in Figure 3.

deep, which was recessed in a window on the exterior wall of the laboratory. A 15-in. NEC computer monitor (model FE700) with a flat glass surface (not LCD) was mounted in the floor of the enclosure. The surrounding floor area was covered by a piece of plywood (painted gray) with an opening cut out to expose the monitor screen such that the visible display surface was recessed by 1.5 cm below the gray floor covering. The visible surface of the monitor was 21 cm by 29 cm, with the longer dimension parallel to the window opening. The enclosure was open to the outside and on the inside was fitted with two sliding Plexiglas panels. The transparent panels allowed the experimenter access to the enclosure and permitted observation of the bee during training trials. They also served to prevent unwanted entrance of the bee into the laboratory.

Stimuli. Stimuli were generated in Microsoft PowerPoint and projected as slides. The digital stimuli were circles approximately 5.5 cm in diameter composed of either solid colors or two-color patterns arranged in a “pinwheel” pattern of six equal segments (Figure 3). The colors used for the stimuli were purple, green, yellow, and white. The two-color pattern stimuli consisted of two of those colors in an alternating sequence. The combination of two different alternating colors allowed for six unique two-color patterns: white and green, white and yellow, white and purple, purple and yellow, purple and green, and green and yellow. The solid colored stimuli consisted of the same four colors. Note that all four colors had been used in previous simple discrimination experiments and in previous oddity experiments conducted in this laboratory with computer-generated images; the colors are discriminable and equally preferred.

The colors were created in Microsoft Paint by specifying values for yellow, white, green, and purple. The values are as follows: yellow (red = 255, green = 255, blue = 0; hue = 40, saturation = 240, luminosity = 120), white (red = 255, green = 255, blue = 255; hue = 160, saturation = 0, luminosity = 240), green (red = 0, green = 153, blue = 0; hue = 80, saturation = 240, luminosity = 60), purple (red = 153, green = 0, blue = 153; hue = 200, saturation = 240, luminosity = 72). To facilitate the bees’ detection of the stimuli, the background of the Microsoft PowerPoint slides was black, which maximized contrast with the colored stimuli.

Pretraining. Each subject in the experiment was collected in a matchbox at one of the feeders and brought to the window enclosure for pretraining. To ensure that the bees were exposed to all four colors to be used in training, the pretraining stimulus was constructed of four equally divided segments of the four colors (purple, green, white, and yellow). The pretraining stimulus was projected in the middle of the visible display surface of the computer monitor, and a 100- μ l drop of 50% sucrose was placed

in the center of the stimulus, directly on the monitor. A bee was placed at the drop on the stimulus, began to drink, and was marked on its thorax with colored enamel for identification purposes. The bee drank until replete and then flew to the hive to unload the sucrose. If the bee returned to the enclosure, it again found the pretraining stimulus with a 100- μ l drop of 50% sucrose, drank, and flew again to the hive to unload. If a marked bee did not return to the enclosure, it was recaptured at the feeder and replaced on the pretraining stimulus. If the marked bee still did not return on its own, another bee was selected from the feeder. Pretraining ended after a bee had returned on its own to the pretraining stimulus. When the bee next returned to the enclosure, the oddity training began.

Training of oddity groups. The design of the training for the four groups is shown in Table 1. For the bees in the two Solid Odd groups, the odd stimulus was always a solid color, and the two nonodd stimuli were identical two-color patterns. For one of the Solid Odd groups, the patterns included the color of the odd solid stimulus (A+ AB- AB-); that is, there was one common color. For the other Solid Odd group, the patterns did *not* include the color of the odd solid stimulus (C+ AB- AB-); that is, there was *no* common color. For the bees in the two Pattern Odd groups, the odd stimulus was always a two-color pattern, and the two nonodd stimuli were identical solid colors. For one of the Pattern Odd groups, the pattern included the color of the solid stimuli (AB+ A- A-); that is, there was one common color. For the other Pattern Odd group, the pattern did *not* include the color of the solid stimuli (AB+ C- C-); that is, there was *no* common color. For



Figure 2. The wooden enclosure used in Experiment 1. A computer monitor was mounted, display side up, in the floor of the enclosure. See the online article for the color version of this figure.

Experiment 1: Oddity Groups

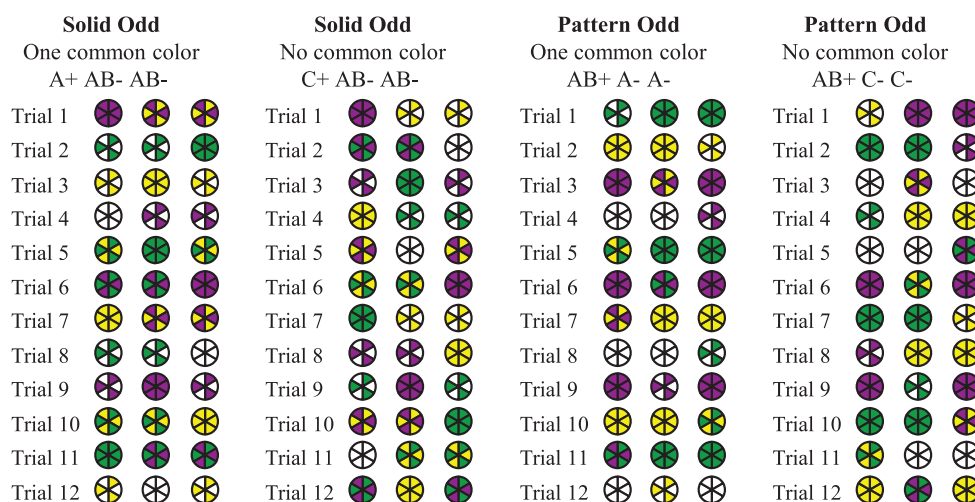


Figure 3. Sample training sequences for each of the four oddity groups of Experiment 1. See the online article for the color version of this figure.

all groups, there were 12 training trials, each with a set of three stimuli, two identical and one odd. The six possible two-color patterns and the four solid colors could be combined to form 12 unique stimulus triads, one for each of the 12 training trials. Because the training procedure was trial-unique, every trial was a transfer test with new stimuli.

The stimuli were presented simultaneously and positioned horizontally in the center of the visible area of the computer screen, about 1.5 cm apart edge-to-edge. A 100- μ l drop of 50% sucrose was placed directly on top of the odd stimulus and served as reward. A 100- μ l drop of 15% salt solution was placed on top of each of the nonodd stimuli and served as punishment. (Results of previous experiments from this laboratory indicate that salt solution is highly aversive to honeybees. When presented on the computer screen, the drop of salt solution cannot be discriminated from the drop of sucrose except by taste. In pilot work with nondifferentially reinforced discriminations [A+ A- or A+ B- and B+ A-], bees failed to discriminate the drops of solutions. [See Couvillon, Ferreira, and Bitterman (2003) for a test with sucrose vs. water.]).

The odd stimulus occurred four times in each position (left, middle, and right) in a quasi-random sequence over the 12 training trials. There were three unique sequences for each group, and each sequence was used for three subjects in the group. Sequences were constructed so that successive trials did not share any identical stimuli, and each pattern or solid could be rewarded only two or three times over the training trials, but never more than once in any position. A sample training sequence for each of the four groups of bees is shown in Figure 3.

All choices were recorded on each of the 12 training trials for all bees. A correct initial choice was defined as landing on the odd stimulus and making contact with the sucrose drop. An incorrect initial choice was defined as landing on a nonodd stimulus and making contact with the salt solution. A correction procedure was used, so if the bee chose incorrectly, it was allowed to choose again until it made contact with the drop of sucrose on the odd

stimulus. The bee drank the sucrose, flew to the hive to unload, and then returned to the window (usually within 3min) for the next trial. After the bee completed 12 training trials, it was captured and sacrificed to ensure that it did not return to the enclosure during the training of subsequent bees.

Training of a discrimination control group. As noted in the introduction to this experiment, although all four groups were explicitly trained in an oddity problem, the problem could be solved either as an oddity problem or as a category discrimination, or both. The training of the control group was a simple category discrimination. A group of four bees was run with the same procedures as the oddity groups but with only a pair of stimuli in a choice discrimination problem. One bee was trained A+ AB-, one bee was trained C+ AB-, one bee was trained AB+ A-, and one bee was trained AB+ C-. The training was trial-unique, with different stimulus pairs on every trial, and the training procedure was exactly the same as described for the oddity groups. The stimuli were presented simultaneously and positioned horizontally in the center of the visible area of the computer screen, about 3 cm apart edge-to-edge. Again, there were 12 training trials. The actual trial sequences for the four bees are shown in Figure 4, and in all sequences, the position (left and right) of the rewarded stimulus was balanced across trials.

In all of our previous relational experiments with honeybees, the reward for correct choice was sucrose, and the punishment for an incorrect choice was an aversive solution, here a salt solution. In previous pilot work in our laboratory, there has been no evidence that the bees can discriminate the solutions without tasting. Nonetheless, it seemed reasonable to test these control subjects with an unreinforced extinction test with the same solution on both stimuli. The 12th trial, therefore, was an unreinforced preference test with a new stimulus in the previously rewarded category and a new stimulus in the previously unrewarded category. There was a 100- μ l drop of plain water placed on top of each stimulus. All landings on both stimuli were recorded for a 10-min test. Note that the extinction test with water provides a measure of the bees'

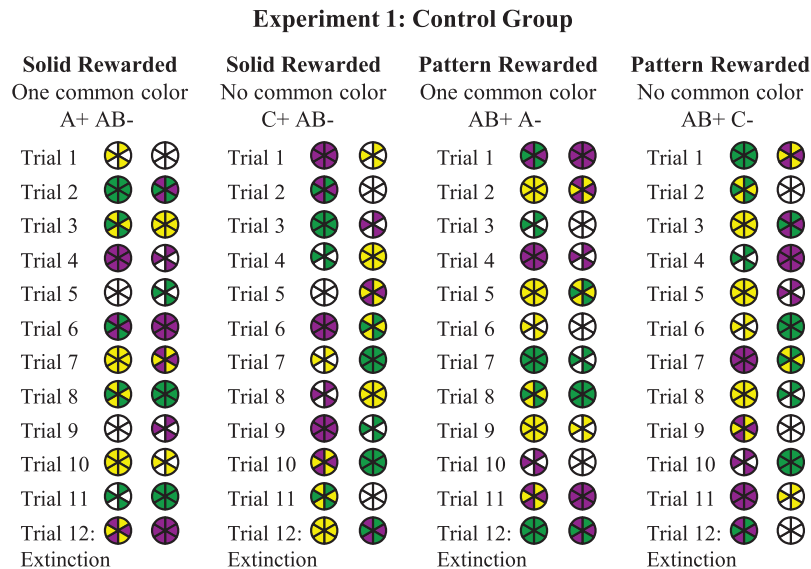


Figure 4. The training sequences used for each of the four control subjects in Experiment 1. See the online article for the color version of this figure.

preference for the rewarded category (solid or pattern) in the absence of sucrose and salt solutions.

Results for the Oddity Groups

The performance of the four oddity groups is plotted in Figure 5 as the proportion of bees with a correct initial choice on each trial. Inspection of the curves suggests that all groups learned the oddity task, but there is considerable trial-to-trial variability. For analysis of the data, the proportion of correct choice for all trials was computed for each bee in each of the groups. The group means were tested in a one-sample t test with a hypothesized mean of .33 (chance). The results for all groups were significantly greater than chance. For the Solid Odd Group with a common color, the mean proportion correct was .55, with a range of .33 to .83, and $t(8) = 3.99$, $p = .004$, with a standard error of the mean (SEM) of .05, $d = 1.38$. For the Solid Odd Group with no common color, the mean proportion correct was .50, with a range of .33 to .66, and $t(8) = 4.59$, $p = .002$, $SEM = .04$, $d = 1.55$. For the Pattern Odd Group with a common color, the mean proportion correct was .49, with a range of .42 to .58, and $t(8) = 7.37$, $p < .001$, $SEM = .02$, $d = 2.66$. For the Pattern Odd Group with no common color, the mean proportion correct was .59, with a range of .5 to .66, and $t(8) = 12.52$, $p < .001$, $SEM = .02$, $d = 4.33$.

It is interesting to note that the initial data point is slightly above chance for all four groups. A close inspection of the choices of individual bees indicated that 4 of the nine subjects in each group chose correctly on the first trial, that is, a proportion of .44 which is higher than the proportion of .33 expected by chance. This slight tendency seems to be due to the fact that the bees whose training sequence began with the odd stimulus in the middle position had a tendency to choose the middle stimulus on the first trial. It is likely that this tendency was an unexpected consequence of the placement of the pretraining stimulus in the middle of the computer display which may have given a slight "associative edge" to the middle position on

the first trial. No such tendency appears after the initial trial. Analyses of the choices of the individual bees on all subsequent trials revealed no systematic position or color preferences, nor any position reward following. Color reward following was explicitly not possible given the restrictions on the training sequences (discussed above). Therefore, although there is considerable variability in the acquisition curves, there appears to be no systematic explanation for high or low variations in the points of the curves.

In addition to the overall analyses of proportion of correct choice for each group, performance was analyzed by comparing the mean proportion of correct choice in the first half of training (the first six trials pooled for each bee) and the last half of training (the last six trials pooled for each bee). It should be noted that there was no a priori expectation about the speed of learning, the shape of the learning curve, or, indeed, that any learning would occur at all. Consequently, there is no basis for a decision about where the curves should have diverged from chance nor for comparing learning curves between groups. In addition, options for pooling data are limited with only 12 training trials. Therefore, the most conservative approach is to analyze the differences in proportion correct choice between the first half and last half of training for each group. For each group, a repeated measures analysis of variance (ANOVA) was conducted using the mean proportion correct choice in the first six trials and in the last six trials for each of the nine bees in each of the groups. For Group Solid Odd with one common color, there was a significant difference in the proportion of correct choice between the first and last halves of training, $F(1, 8) = 6.659$, $p = .033$. For Group Solid Odd with no common color, the difference between the first and last halves of training did not quite reach the conventional level of significance, $F(1, 8) = 4.888$, $p = .058$. For the two Pattern Odd Groups, there was no significant difference between the first and last half, $F < 1$. A close look at Figure 4 shows that the variability was quite high for both of those groups.

Experiment 1: Oddity Groups

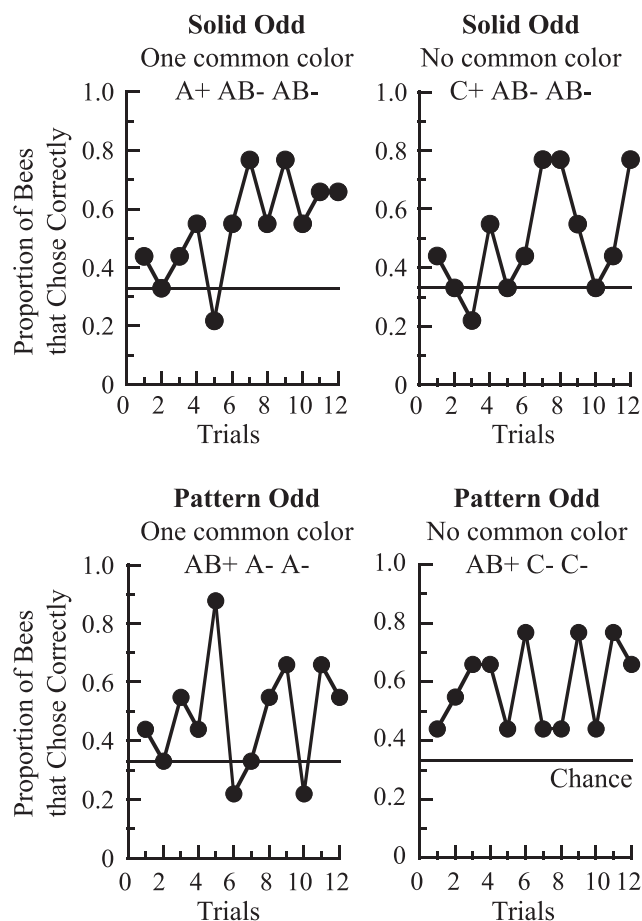


Figure 5. The results for the four oddity groups in Experiment 1. Note that the solid line at 0.33 represents chance performance.

One anticipated outcome was that the two groups trained with the common color would find the oddity discrimination more difficult than the groups trained with no common color. Another anticipated outcome was that there would be no difference between the groups that had solid stimuli odd and the groups that had pattern stimuli odd. An overall ANOVA was conducted. The analysis was a 2×2 design with condition as one factor (one common color vs. no common color) and stimulus category as another factor (solid odd vs. pattern odd). There was no effect of condition, $F(1, 35) = .54, p = .47$, a finding that suggests that the common color had no effect on discrimination. There also was no effect of stimulus category, $F(1, 35) = .26, p = .61$, a finding that suggests that the category of the odd stimulus (solid or pattern) had no effect on discrimination. Although no main effects of condition or category were found, there was a barely significant condition by category interaction, $F(1, 35) = 4.16, p = .05$. The interaction is difficult to explain but may be due to the slightly better performance of the pattern odd group that had no common color. Perhaps that context produced a small perceptual “pop-out” (Blough, 2001) of the pattern that facilitated performance.

As noted earlier, the design of the two groups with a common color is reminiscent of a feature-positive and feature-negative

discrimination. Even though the training, here, was trial-unique, it seemed reasonable, nonetheless, to determine if the “feature-positive group” (AB+ A- A-) found the discrimination easier than the “feature-negative group” (A+ AB- AB-). A two-sample t test found no difference between the two groups, $t(16) = .946, p = .358, SEM = .06$. If anything, the “feature-negative group” had slightly better performance.

Results for the Control Group

The training performance of the four bees in the pattern versus solid discrimination control group is plotted in the left panel of Figure 6 as the proportion of bees with a correct initial choice on each trial. All four bees easily learned the discrimination; the average proportion correct was .94 for the last four training trials. The overall mean proportion correct was 0.78, and a t test against the chance value of 0.5 was significantly greater than chance, $t(3) = 6.76, p = .006, SEM = .04, d = 3.29$.

On the 12th trial, instead of sucrose and salt solutions, drops of water were placed on both stimuli. The first choice on that trial was recorded. Once the bee had tasted the water, the trial became an extinction test, and all choices to both stimuli were recorded during this 10-min unreinforced preference test. The extinction performance is shown in the right panel of Figure 6 as the mean total responses to the stimulus of the previously rewarded category (S+) and to the stimulus of the previously nonrewarded category (S-). The mean number of responses to the S+ was 20.25, and the mean number of responses to the S- was 10.5. All four bees responded more to the rewarded category than to the unrewarded category. A dependent sample t test of the mean total responses to both stimuli showed a significant difference, $t(3) = 7.181, p = .006, SEM = 1.32, d = 1.21$.

Experiment 1: Control Group

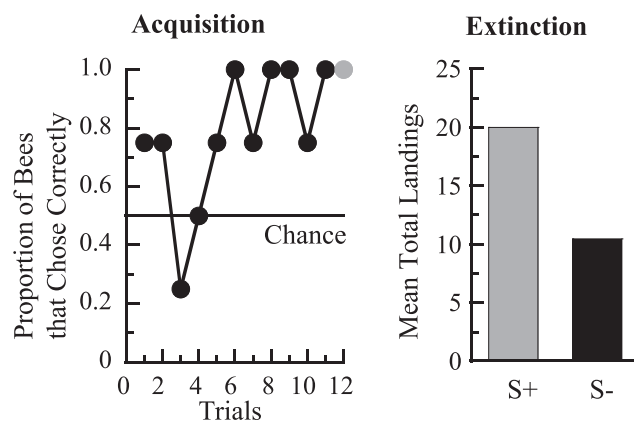


Figure 6. The results for the control group of Experiment 1. The results for acquisition training are shown in the left panel. Note that the solid gray circle at Trial 12 shows the proportion of bees whose first choice was correct at the beginning of the extinction test. The results for extinction with a novel pair of stimuli are shown in the right panel. One of the stimuli was from the previously rewarded category (S+) and the other from the previously nonrewarded category (S-).

Discussion

All four of the oddity groups chose correctly at levels above chance. Although the experimental design was explicitly an oddity problem, it also was a category discrimination. For two groups, on every trial, a solid color was odd and rewarded, and the two patterns were nonodd and not rewarded. For the other two groups, on every trial, a pattern was odd and rewarded and the two solid colors were nonodd and not rewarded. Therefore, it is possible that instead of learning an oddity problem, the bees in all groups were learning a solid versus pattern category discrimination. Although the trial-unique procedure ensured that the actual stimuli on every trial were different, there likely are features of solids and patterns that are independent of the individual stimuli, for example, simple versus complex, larger area of a color versus smaller area of a color, and so forth. If the bees, in fact, made a category discrimination, the results can be understood in associative terms with no need to assume relational learning. In the extreme, if the bees did not discriminate the color of the stimuli, then the oddity problems and the control discrimination problem reduce to a simple discrimination of solid versus pattern. However, color is highly salient for honeybees, so that possibility is unlikely. Furthermore, the performance of the control group was qualitatively better than that of the oddity groups, and that would not have been the case if the control and oddity problems essentially reduce to the same simple discrimination (e.g., A+ B− vs. A+ B− B−).

The training of the control group was trial-unique, and on every trial, the bees had a choice between a novel combination of a solid stimulus and a pattern stimulus. The results shown in Figure 6 for both acquisition and extinction suggest that such a category discrimination is very easy for bees. That result raises an interesting question about the oddity groups. The good performance of the control group demonstrates that the category discrimination is easy for bees. Nonetheless, the performance of the four oddity groups indicates that the oddity problems were quite difficult (cf., Figure 5). It is possible that the bees in the oddity problems responded on the basis of oddity and were not simply discriminating solid versus pattern categories. However, it is also possible that adding a third stimulus to a simple category discrimination increased its difficulty because (a) the bees needed to compare three stimuli instead of only two as in the control group, (b) there were three stimulus positions instead of only two stimulus positions, and (c) although the stimuli were exactly the same size for the control group and the oddity groups, they were closer together for the oddity groups due to the limit of the display size on the computer monitor. It would be interesting to further explore category learning, per se, in honeybees with manipulation of these parameters. Nonetheless, our interest here is in oddity learning, and therefore in the next experiment, the two possible interpretations were unconfounded.

Experiment 2: Four-Stimulus Oddity—Role of an Irrelevant Category Difference

The general purpose of the experiments reported here was to increase the discriminability of the odd stimulus in oddity problems. In Experiment 1, a category difference was incorporated in the stimulus set with the expectation that discriminability of the odd stimulus could be improved. However, the results resembled those for the previous studies with bees trained only with pattern

stimuli (Muszynski & Couvillon, 2015), with no indication that the category difference facilitated discrimination of the odd stimulus. Nonetheless, the results of the oddity training as well as those of the control group do indicate that the bees are capable of discriminating solid colors versus two-color patterns in trial-unique problems. Although Experiment 1 was ostensibly an oddity problem, the design was confounded. Therefore, the interpretation of the results is ambiguous; instead of choosing on the basis of oddity, the bees may have chosen on the basis of category. The present experiment includes an experimental group (Group 1) trained much like the bees in Experiment 1, except the odd stimulus was a solid on half of the trials and a pattern on the other half of the trials. Therefore, successful solution of the problem cannot be based on category discrimination.

A comparison group (Group 2) also was trained in a four-stimulus oddity problem but with no category difference, that is, with only two-color patterns, one of which was odd on each trial. The main purpose of Group 2 was to serve as a control to determine if the addition of the category difference in Group 1 improves oddity performance relative to training with only patterns. The expectation was that the irrelevant category difference would increase the discriminability of the odd stimulus for Group 1, which then should improve overall performance relative to Group 2. As in Experiment 1, the training procedure for both groups was trial-unique; that is, there was a novel set of stimuli on every training trial. The design of Experiment 2 is shown in Table 2.

In addition, the bees in both groups were trained with four stimuli instead of the traditional three stimuli used in all of the previous oddity experiments with honeybees. There is some evidence from work with vertebrates (cf., Zentall et al., 1980) that adding exemplars improves oddity discrimination performance. Another purpose of this experiment was to determine whether honeybees could in fact solve a four-stimulus oddity problem. Therefore, if the bees in Groups 1 and 2 are able to solve the oddity problem, then it will be the first evidence that honeybees can solve oddity problems with more than three stimuli.

Method

Subjects. The subjects were 24 honeybees (*Apis mellifera*) never used in previous experiments with 12 bees in each of the two oddity groups. The subjects were selected in the same way as those used in Experiment 1.

Apparatus. The training situation is similar to that used in Experiment 1. However, instead of using a computer monitor for display of the stimuli, the bees in the present experiment were trained with stimuli mounted on Petri dishes that were set on the floor of the wooden enclosure, as shown in Figure 7. Note that the

Table 2
The Design of the Training of the Two Groups in Experiment 2

Group 1: Solids and Patterns	A+ AB− AB− AB− & AB+ A− A− A−
Group 2: Patterns only	AB+ AC− AC− AC−

Note. A, B, and C represent different colors. Note that the training was trial-unique, and examples of the actual training sequences for each oddity group are shown in Figure 8.



Figure 7. Apparatus used in Experiment 2. See the online article for the color version of this figure.

display area of the computer monitor used for the three-stimulus problems of Experiment 1 was not large enough for the presentation of the four stimuli to be used in Experiment 2. Muszynski and Couvillon (2015) had conducted one of their three-stimulus oddity experiments using a computer monitor and the other using the three-dimensional stimulus presentation used here. The results of both experiments were much the same.

Stimuli. The stimuli used also were similar to those in Experiment 1. However, in Experiment 1, the solid color stimuli and the two-color pattern stimuli were digitally created, and here they were created from colored vinyl plastic that had a matte finish. The solid color stimuli and the two-color pattern stimuli consisted of six equal segments arranged in a pinwheel pattern and mounted on the surface of a Petri dish, 5.5 cm in diameter. For the solid colors, all six segments were of the same color, and for the two-color pattern stimuli, the color of the segments alternated in the pinwheel arrangement. The set of solid stimuli consisted of the following colors: blue, green, orange, and yellow. The set of pattern stimuli consisted of two of those colors in alternating sequence. The combination of two different alternating colors allowed for six unique two-color patterns: yellow and green, yellow and orange, yellow and blue, blue and orange, blue and green, and green and orange. All four colors have been used in many previous experiments from this laboratory and are highly discriminable and equally preferred.

Pretraining. The pretraining procedure was exactly the same as that used in Experiment 1. However, in this case, the pretraining stimulus was a Petri dish with equal segments of the four colors to be used in training mounted on the top surface. The pretraining stimulus was placed in the middle of the floor of the wooden enclosure.

Training. The design of the training of the two groups is shown in Table 2. For the bees in both groups, there were four stimuli presented on every training trial, one of the four stimuli

was odd and the other three were nonodd. For the bees in Group 1 (solids and patterns), on half of the trials, the odd stimulus was a solid colored stimulus and the three nonodd stimuli were identical two-color patterns. On the other half of the trials, the odd stimulus was a two-color pattern and the three nonodd stimuli were identical solid color stimuli. For the bees in Group 2 (patterns only), all four stimuli were two-color patterns. The odd stimulus was a different pattern than the three nonodd patterns.

Because Group 1 had both solid odd and pattern odd trials, the six possible two-color patterns and the four solid colors could be combined to create 24 unique stimulus sets with a common color in each set, 12 with a solid color odd and 12 with a two-color pattern odd. Four training sequences of 16 trials each were created from these possible sets, and three subjects were trained with each sequence. A sample sequence is shown in Figure 8. The odd stimulus for Group 1 occurred four times in each position (far-left, middle-left, middle-right, far-right) and two times for each trial-type (solid odd and pattern odd). The position of the odd stimulus was balanced quasi-randomly over the 16 trials such that the odd stimulus was never in the same position for more than two trials in succession. (On the few occasions in which the odd position was the same on two trials in succession, the trial types were different; that is, one was a solid odd and the other a pattern odd type.) Each of the two types of trials also never occurred more than twice in succession. Because there were only four solid colors in the stimulus set, each was odd on two of the eight solid-odd trials and always in a different position and always with different two-color patterns as the nonodd stimuli. Because there were six different two-color patterns, each was odd on one or two of the eight pattern odd trials and always in a different position and always with different solid nonodd stimuli.

For Group 2, sets of pattern stimuli were used on every trial, each with one odd pattern and three identical nonodd patterns.

Experiment 2

Group 1				Group 2			
Solids & Patterns				Patterns Only			
Trial 1				Trial 1			
Trial 2				Trial 2			
Trial 3				Trial 3			
Trial 4				Trial 4			
Trial 5				Trial 5			
Trial 6				Trial 6			
Trial 7				Trial 7			
Trial 8				Trial 8			
Trial 9				Trial 9			
Trial 10				Trial 10			
Trial 11				Trial 11			
Trial 12				Trial 12			
Trial 13				Trial 13			
Trial 14				Trial 14			
Trial 15				Trial 15			
Trial 16							

Figure 8. Sample training sequences for the two groups of Experiment 2. See the online article for the color version of this figure.

There were only 15 unique sets that could be created from a combination of two of the 6 two-color pattern stimuli. Four different training sequences were created, and three subjects were trained with each sequence. A sample sequence is shown in Figure 8. The odd stimulus occurred three to four times in each position in a quasi-random sequence over the 15 trials. The rewarded position of the odd stimulus was never the same on two successive trials.

On every trial, for both groups, the four stimuli were presented horizontally in the center of the wooden apparatus, 2.5 cm apart edge-to-edge. A 100- μ l drop of 50% sucrose was placed directly on top of the odd stimulus and served as reward. A 100- μ l drop of 10% stevia solution was placed on top of each of the nonodd stimuli and served as punishment. (In Experiment 1, salt solution was used as punishment, but, here, stevia solution was used. Both are highly aversive to honeybees. As discussed for the salt solution used in Experiment 1, pilot work in this lab found that bees could not learn a discrimination problem that was solvable only by discriminating drops of sucrose from drops of stevia solution. Stevia was used instead of salt in this experiment to be consistent with the procedure used by Muszynski and Couvillon (2015) in the three-stimulus noncomputer oddity problems. Interestingly, quinine solution also has been used as an aversive substance in a difficult visual discrimination with bumblebees [Chittka, Dyer, Bock, & Dornhaus, 2003]).

As in Experiment 1, all choices were recorded on each training trial for all bees. A correct initial choice was defined as landing on the odd stimulus and making contact with the sucrose drop. An incorrect initial choice was defined as landing on a nonodd stimulus and making contact with the stevia drop. A correction procedure was used, so if the bee chose incorrectly, it was allowed to choose again until it made contact with the drop of sucrose on the odd stimulus. Then, the bee drank the sucrose, flew to the hive to unload, and returned to the window (usually within 3–5 min) for the next trial. Again, after the bee finished training, it was captured

and sacrificed to ensure that it did not return to the enclosure during the training of subsequent bees.

Results

The performance of the two groups of bees is plotted in Figure 9 as the proportion of bees with an initial correct choice on each trial. The acquisition curves indicate that the bees in both groups learned the oddity problem. For analysis of the data, the proportion of correct choice across all training trials was computed for each bee in both of the groups. The group means were tested in one-sample *t* tests with a hypothesized mean of 0.25 (chance). The performance for both groups was greater than chance. For Group 1, with the category difference, the overall mean proportion correct was 0.67, with a range of 0.44 to 0.81, $t(11) = 11.14$, $p < .0001$, $SEM = .04$, $d = 3.23$. It is interesting to note that there was no difference in performance on the two trial types, solid odd and pattern odd, $t(22) = 1.7$, $p = .1029$, $d = .695$. For Group 2, with all patterns (no category difference), the overall mean proportion correct was 0.47, with a range of 0.33 to 0.6, $t(11) = 8.72$, $p < .0001$, $SEM = .03$, $d = 2.53$. Both groups were able to solve a four-stimulus oddity problem.

As was the case for the groups in Experiment 1, the initial data point is somewhat above chance for both groups. Again, this tendency may be a function of the center location of the pretraining stimulus because half of the bees in each group chose one of the two center positions on the very first trial. Analysis of all subsequent trials revealed no such position preferences. Inspection of the trial-by-trial data of individual bees revealed no systematic explanation for high or low variations in the points of the curves, even for the two low points at Trials 10 and 11 for Group 1.

To determine if the category difference facilitated oddity learning, the performance of Group 1, trained with a category difference, was compared with that of Group 2, trained with all patterns (no category difference). The data for both groups were blocked in two-trial blocks.

Experiment 2

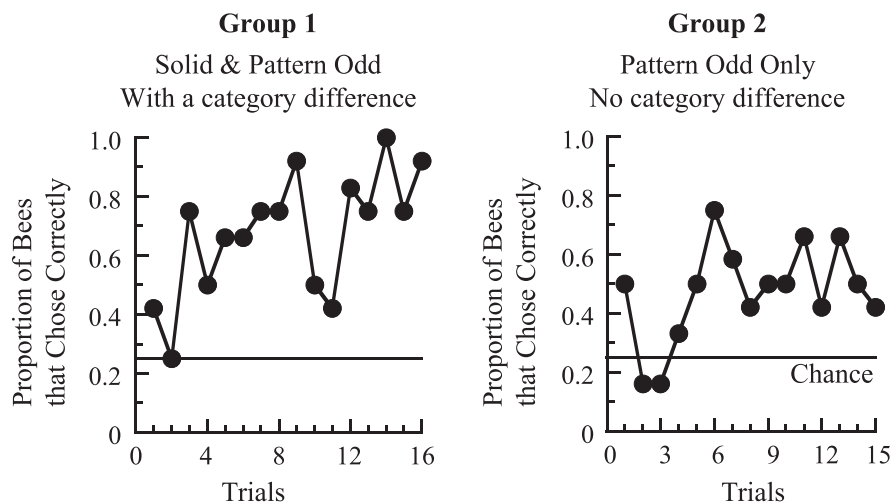


Figure 9. The results for the two groups in Experiment 2. Note that the solid line at 0.25 represents chance performance.

However, because the two groups had different numbers of training trials, it was necessary to equate the number of blocks to compare acquisition rates. The procedure used was to drop the first block from Group 1 and the first trial from Group 2, leaving both groups with 7 two-trial blocks. This approach is conservative because early performance might be expected to be more sensitive to differences between the two groups. An ANOVA showed a significant group effect, $F(1, 22) = 27.08$, $p < .001$, a significant block effect, $F(6, 132) = 2.65$, $p = .018$, but no group by block interaction, $F(6, 132) = 1.28$, $p = .271$. The group effect reflects the higher level of correct choice in Group 1, trained with the category difference. The absence of a group by block interaction indicates there was no difference in rate of learning between the two groups. Therefore, the category difference in the training of the bees in Group 1 affected the asymptotic level of the oddity performance.

Discussion

The bees in both groups were able to solve these trial-unique four-stimulus oddity problems. The higher asymptotic performance of Group 1 suggests that the irrelevant category difference among the stimuli facilitated the learning of oddity. Note that the problem could not be solved as a discrimination of category (solids and patterns) because the solid was odd on half the trials and the pattern was odd on the other half. It is possible that the category difference on each trial promoted a discrimination of the perceptual features of the stimuli, such as, more or less of a stimulus type, that is, three patterns versus one solid or three solids versus one pattern.

If the bees of Group 1 were using more or less of a stimulus type to solve the oddity problem, it might be expected that the performance on trials where the odd stimulus is at the end of the set of four (e.g., A+ AB- AB- AB- or A- A- A- AB+) would be better than performance on trials where the odd stimulus is in one of the middle positions (e.g., AB- A+ AB- AB- or A- A- AB+ A-). Analysis of these two kinds of trials found no difference in correct choice, $t(22) = .44$, $p = .662$. For trials with the odd stimulus at the end of the set, the proportion correct choice was 0.69, and for trials with the odd stimulus in the middle of the set, the proportion correct choice was 0.66. A perceptual grouping of stimuli by type does not appear to be controlling the bees' choices.

For Group 2, all the trials are of the same type, but it is still possible that the odd stimulus is more easily detected (Moon & Harlow, 1955) on the ends of the four-stimulus set than in the middle. Therefore, it seemed reasonable also to compare the performance of the bees in Group 2 on trials where the odd stimulus was at the end of the set with trials where the odd stimulus was in the middle of the set. Analysis of these two kinds of trials did find a difference in correct choice, $t(22) = 2.65$, $p = .0146$. Surprisingly, performance was better on trials where the odd stimulus was in the middle of the set. For trials with the odd stimulus at the end of the set, the proportion correct choice was .38, and for trials with the odd stimulus in the middle of the set, the proportion correct choice was .57. This result actually suggests that when the odd stimulus is in the middle it may produce a perceptual pop-out (cf., Zentall et al., 1980). Interestingly, Muszynski and Couvillon (2015) found no better performance on trials where the odd stimulus was in the middle in a three-stimulus oddity problem. Therefore, the increase in the number of stimuli, as in vertebrate studies (Pastore, 1954; Zentall et al., 1980) may have produced a percep-

tual pop-out effect, at least on trials where the odd stimulus was in one of the middle positions.

The purpose of the experiment was to determine if performance could be enhanced by the addition of an irrelevant category difference and that seems to be the case for the performance of Group 1. The other purpose was to explore the bees' performance in four-stimulus oddity problems, as all of the previous studies of the oddity learning of honeybees have been with three-stimulus problems. The performance of both Groups 1 and 2 indicate that they can solve four-stimulus oddity problems. It will be interesting in future experiments to follow up the all-pattern results by further increasing the number of stimuli, which might enhance the perceptual pop-out effect of the odd stimulus.

General Discussion

The main purpose of this set of experiments was to further explore oddity learning in honeybees, first by expanding the stimulus set to include a category difference, two-color patterns and solid colors, and second to increase the number of exemplars. In Experiment 1, four groups of honeybees were trained in a three-stimulus oddity problem using a trial-unique procedure, that is, different stimulus-sets on every trial. For two of the groups, solid was odd, and, for two of the groups, pattern was odd. See Table 1 in Experiment 1 for more details. All four groups solved the oddity problem, although the results suggest that the problems are difficult. The confounded design raises the possibility that the bees were making a category discrimination between solids and patterns rather than an oddity discrimination. A control group easily discriminated solids versus patterns (Figure 6). Therefore, the relative difficulty of the oddity problems suggests that the bees did not treat them as solid versus pattern discriminations but as oddity problems.

Experiment 2 was conducted to unconfound the relational and category explanations of the results of Experiment 1. Two groups of honeybees were trained in a four-stimulus oddity problem, again with a trial-unique procedure. For Group 1, on half of the trials, the odd stimulus was a solid color, and on the other half of the trials, the odd stimulus was a two-color pattern. Unlike in Experiment 1, the bees could only solve the problem on the basis of oddity, not as a solid versus pattern category discrimination. For Group 2, on all trials, there were four two-color patterns, one of which was odd. In other words, there was no category difference for this group. See Table 2 for more details. Both groups solved the oddity problems. However, the bees in Group 1 (category difference) reached a higher asymptotic level of correct choice than the bees in Group 2 (no category difference). Thus, an irrelevant category difference seems to facilitate oddity learning.

These experiments do not provide a direct comparison of performance in three- and four-stimulus oddity problems, but it is interesting to note that the performance of Group 2, in Experiment 2, trained with only two-color patterns is not qualitatively better than the performance in any of the previous three-stimulus oddity problems with only two-color patterns (Muszynski & Couvillon, 2015). Nonetheless, there was evidence that the increase in the number of stimuli facilitated the discrimination of oddity when the odd stimulus was in one of the middle positions. This result is worth further study to determine the extent to which honeybees respond to the arrangement of stimuli in an oddity problem.

These are the first oddity experiments with honeybees to incorporate a category difference in an oddity learning problem. There is some interesting work with vertebrates that incorporates categories of

stimuli to determine the effect of stimulus variability on same/different judgments by both humans and pigeons (Wasserman & Castro, 2012a). Also, there is some work with pigeons that explored categorical matching-to-sample (Wasserman & Castro, 2012b). On some trials, for example, pigeons were shown a photograph of Dog A and then were rewarded for choosing the photograph of Dog A from a set of three photographs that included Dog A, a flower, and a fish (identity matching). On other trials, the pigeons were shown the photograph of Dog A and then rewarded for choosing a photograph of Dog B from a set of three photographs that included Dog B, a flower, and a fish (category matching). The pigeons' performance was better than chance on both kinds of trials, indicating that they could solve the problem on the basis of identity matching or category matching. However, there was no attempt to determine if the addition of the categorical matching trials improved performance relative to a group trained with only identity matching.

The honeybee experiments presented here were not designed to explicitly study category learning in honeybees. The aim instead was to further study oddity learning in honeybees, which is not easily explained with associative learning principles. On the other hand, category discrimination can be explained by generalization of associative learning based on stimulus features unique to each category or based on configurations of features. There is a growing number of studies of honeybee category learning. Horridge and Zhang (1995) found that honeybees can discriminate radial and concentric black and white patterns. Giurfa, Eichmann, and Menzel (1996) found that honeybees can discriminate black and white patterns on the basis of symmetry and asymmetry. Zhang, Srinivasan, Zhu, and Wong (2004) found that honeybees can discriminate four categories of projected images including landscapes and flowers. Avarguès-Weber, Portelli, Benard, Dyer, and Giurfa (2010) found that honeybees could discriminate face-like and nonface-like stimuli. Wu, Moreno, Tangen, and Reinhard (2013) found that honeybees could discriminate Monet and Picasso paintings. The focus of all of these studies was primarily to determine the mechanisms of the perception of the categories, that is, feature-based or configuration-based. It might be instructive to analyze how the bees are discriminating the solid and pattern colored stimuli used here, but the aim was not to study category learning, per se, but to study relational learning.

The results of the two experiments reported here provided additional support for oddity learning in honeybees, the only invertebrate, so far, for which there is any evidence of "relational learning." The results raise questions about how the honeybees are solving these oddity problems, which are essentially the same questions that are raised for the results of oddity experiments with vertebrates (Aust & Steurer, 2013). Although the oddity problem seems to be the simplest of the relational learning problems that have been studied in vertebrate species, it also seems to present the most serious challenge for interpretation. Mainly, the issue is whether the discrimination of oddity is based on perception of size, number of distractors, stimulus configurations, or on a same/different relational concept.

There are other relational problems, such as, matching-to-sample and nonmatching-to-sample, that have been studied extensively in vertebrates. These also present challenges for interpretation (See Premack, 1983). To further test the robustness of relational learning in bees, it might be instructive to study simultaneous same/different discrimination problems of the general type that Premack (1983) argued should produce the strongest evidence of relational learning. A number of species have been successful with such problems: chimpanzees (King, 1973; Robinson, 1955), orangutans (King, 1973), coati (Chausseil, 1991), echidnas (Russell & Burke, 2016), pigeons (Blaisdell & Cook, 2005), and ducklings

Simultaneous Same/Different Discrimination Problem

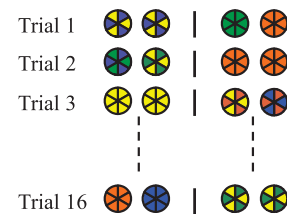


Figure 10. An example of a trial-unique simultaneous same/different problem for honeybees. (The black bar between the two pairs is a divider to distinguish the pairs perceptually.) Note that on half of the trials, the patterns are the same and the solids are different, and on the other half of the trials, the solids are the same and the patterns are different. See the online article for the color version of this figure.

(Martinho & Kacelnik, 2016). There was also an attempt to teach archerfish a same/different problem, but it was not successful (Newport, Wallis, & Siebeck, 2015).

In a prototypical simultaneous same/different problem, two sets of stimuli are presented concurrently; one of the sets contains stimuli that have a "same" relationship, and one of the sets contains stimuli that have a "different" relationship. An example of a same/different experiment that could be conducted with honeybees using the two-color patterns and solid stimuli is shown in Figure 10. The experiment would require two groups of bees, one rewarded for choosing the "same" relationship and one rewarded for choosing the "different" relationship.

The advantage of this kind of design is that it requires the subject to compare the stimuli in each pair before making a choice. If honeybees succeed in solving such a problem, then there are a variety of manipulations possible that could determine what features they are attending to in order to make a choice. For example, the two pairs might share the same colors, blue–yellow patterns versus a blue solid and a yellow solid. In addition, it would be possible to incorporate same and different pairs into an oddity problem. Obviously, there is much work yet to be done to understand relational learning in honeybees. It is only after systematic variation (Bitterman, 1975) in the problems, the stimuli, and the training procedures that it will be possible to determine the extent to which invertebrate and vertebrate relational learning is similar.

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