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A Transferrable Change in Preferences of Floral Patterns by Bumblebees through Reward Reversal

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This study examines behavioral transfer across perceptually similar stimuli in bumblebees (*Bombus impatiens*) and addresses whether foraging judgments about a floral stimulus can change in a way that contradicts direct previous experience with that stimulus. Bees from eight colonies underwent discrimination training of stimuli placed in a radial maze. Bees were trained to discriminate between two corresponding object and photograph pairs of artificial flowers, where one object and its corresponding photo were rewarding, while another object and its corresponding photo were unrewarding. Following discrimination training, one stimulus from each pair (either the object or the photo) was removed. The predictive reward values of the remaining stimuli were either switched for one group or stayed the same for another. Subsequent testing on the removed stimuli revealed foraging preferences to shift based on experience with the other stimulus in the group. For instance, bees treated a previously unrewarding object as rewarding after learning that the corresponding photograph had become rewarding. Foraging decisions depend not only on previous experience with stimuli, but also category membership.

In a natural environment, foragers can encounter several different floral species within a single trip. Because even a slowly flying bumblebee can be exposed to several inflorescences a second (Chittka, Thomson, & Waser, 1999), strategies for managing information for rewarding stimuli seem necessary to reduce amount of detail to which it must attend. By generalizing perceptually similar stimuli within a floral species, the forager can obtain rewards more quickly than if it had to learn the characteristics of each individual flower one by one.

Bees are flower constant (Chittka et al., 1999; Raine & Chittka, 2007; Rossi, Santos, Salvarrey, Arbulo, & Invernizzi, 2015), in that they restrict foraging to a few available floral species. Moreover, bumblebees are also more selective when there is variation among flower types in multiple traits rather than in just a single trait (Gegear & Laverty, 2005). This suggests a natural bias to forage on perceptually similar stimuli. In nature, members within a floral species are not identical and the forager must be able to compare and generalize stimuli based on shared attributes. Effective foraging must allow foragers to adjust to distortions while still correctly identifying features that characterize rewarding floral species. Thus, behavioral transfer between similar floral stimuli within a species despite differences between individual flowers is necessary for flower constancy to exist.

Previous research has found evidence of generalization between perceptually similar stimuli. For instance, honeybees were found to be capable of grouping visual images of different flower shapes, plant stems and landscapes (Zhang, Srinivasan, Zhu, & Wong, 2004), as well as properties of floral features such as bilateral symmetry (Giurfa, Eichmann, & Menzel, 1996), orientation and layout (Avarguès-Weber, Deisig, & Giurfa, 2011; Horridge & Zhang, 1995) and configuration (Avarguès-Weber, Portelli, Benard, Dyer, & Giurfa, 2010; Stach, Benard, & Giurfa, 2004). Honeybees can even discriminate between representations of Monet

and Picasso paintings, and generalize their learning to new paintings of the same style (Wu, Moreno, Tangen, & Reinhard, 2013). While most of the research centers on honeybees, bumblebees were also found to prefer stimuli of similar colors (Gumbert, 2000). Bumblebees were able to generalize foraging behaviors to other stimuli sharing a similar color, while ignoring irrelevant features (Dukas & Waser, 1994).

Previously, different-but-similar judgements have been examined in bumblebees using corresponding objects and photographs (Thompson & Plowright, 2014; Xu & Plowright, 2016). Bees were able to generalize between 3D stimuli and their 2D representations based on perceptual similarities, despite also recognizing the two as being different. In the absence of a rewarding object or photograph, its counterpart was accepted as a substitute. This eliminates the possibility of preferences due to a lack of discrimination. The current study takes advantage of the different-but-similar judgments to further investigate the role of behavioral generalization based on perceptual similarities.

Generalization is usually studied by testing subjects on novel stimuli following discrimination training (see Benard, Stach & Giurfa, 2006). In the present study, we took a different approach and instead examined behavior towards learned members of a perceptually similar group through reward reversals. Serial reward reversals had been used previously to examine behavioral flexibility in bees (Strang & Sherry, 2014). By reversing the reward contingencies between stimuli, changes in performance can be measured across reversals. However, rapid reward reversals in quick succession are rarely if ever found within natural floral species. For instance, after natural flowers (e.g., thistles, lilacs, sunflowers) are past their blooming period, they are finished for the season. Within the lifetime of bumblebee foragers, there will be no further reward value reversals.

The use of one reversal has been proposed to test inter-stimulus behavioral transfer (Lea, 1984): after animals are trained to discriminate between two clusters of stimuli, the reward values of one stimulus from each cluster are reversed—what was rewarding becomes unrewarding, and vice-versa. Subsequent testing with the remaining stimuli reveals whether the animals respond to them as if they too had changed their reward value. When the reward value of the original stimulus has changed, behavior should also change for the remaining stimuli. The current study adopts this method. By way of an analogy, we describe an example outlined by Herrnstein (1990). Acorns vary, but for a creature that relies on acorns, they probably resemble each other. Leaving aside for the moment the question of how it is that an animal comes to treat acorns in the same way, suppose that acorns were to become bitter. After tasting one or a few bitter acorns, is bitterness associated with acorns in general? Here we ask a similar question regarding the behavior of bumblebees: if an unrewarding flower such as sunflower becomes rewarding, then is another sunflower treated as also having become rewarding? We modelled this situation in the laboratory in its simplest form: two rewarding flowers of one type, two unrewarding flowers of another type, and one reversal of the reward values.

Method

Subjects

Seventy six bumblebees (*Bombus impatiens*) from eight colonies, supplied by Koppert Biological Systems Canada, were used for this study. The colonies were fed pollen ad libitum and trained with 2:1 sugar to water solution by volume in a radial arm maze. Individual bees were labelled with numbered tags on the thorax. The bees had no pre-experimental experience outside the colony.

Materials

The commercial colonies were each housed in a plastic box within a cardboard box (28 cm long × 25 cm wide ×20 cm high) and connected to a wooden walkway (40 cm long) covered with square glass plates. A tubular screen tunnel connects the walkway to an opening in the center of the floor of the radial arm maze. The maze consists of 12 corridors (14 cm long x 15 cm high), with an entrance that opens into a central area (17 cm diameter), shown in Figure 1. Eight of 12 corridors were in use, with the remaining blocked off with Plexiglass® dividers. The same eight corridors were used each time. The grey walls and clear cover of the maze were also of the same material (53 cm diameter).
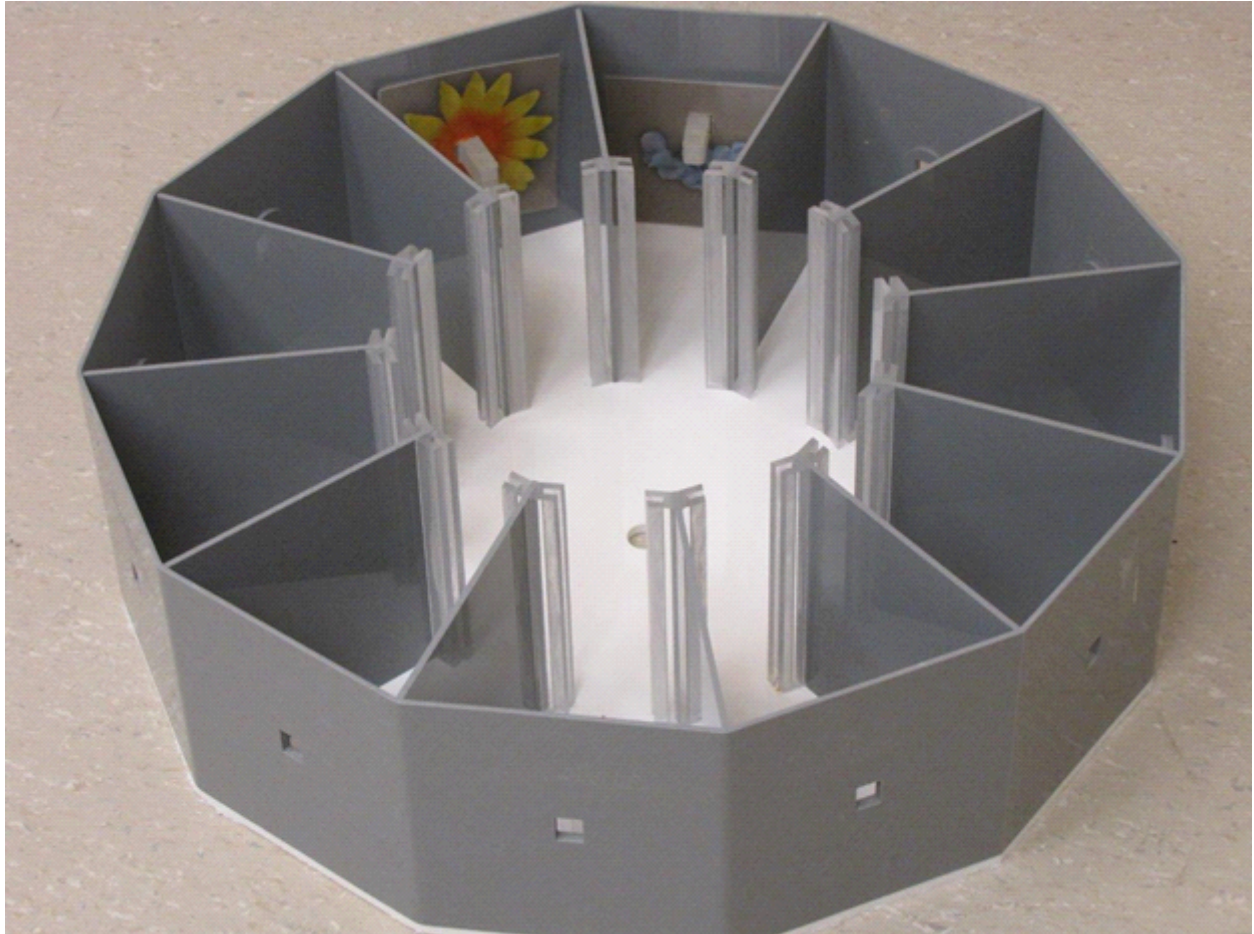

Figure 1. **Photograph of radial arm maze with stimuli (Photo X and Photo Y) and feeders placed at the back walls.**

Artificial flowers or pictures were attached to the feeders on the walls, with one stimulus per corridor. Feeder troughs were located at the end of the corridor and either filled with sugar solution or left empty. The 2D and 3D portions refer to all parts of the floral stimuli with the exception of the source of nectar, which for our artificial flowers was a three dimensional feeder trough. The stimuli were chosen based on previous findings where bees were capable of both differentiating between a photograph and its object, while also finding an association between them (Xu & Plowright, 2016). During training and testing, bees were able to touch the stimuli while feeding. All stimuli were placed randomly before each training session to eliminate the use of location cues. As shown in Figure 2, four stimuli were used: a single yellow flower (Object X, heretofore referred to as Ob. X) and a cluster of blue flowers (Object Y, heretofore referred to as Ob. Y) and their corresponding photographs (Photo X and Photo Y abbreviated to Ph. X and Ph. Y). Yellow and blue to the human eye are well differentiated by bumblebees (e.g., Ings, Raine, & Chittka, 2009). The artificial flowers were made of synthetic fabric. The photographs (8.5 cm x 10.5 cm) were taken using a Panasonic DMC-FZ20 camera and printed on a grey background with a Canon MP560 ink jet printer.
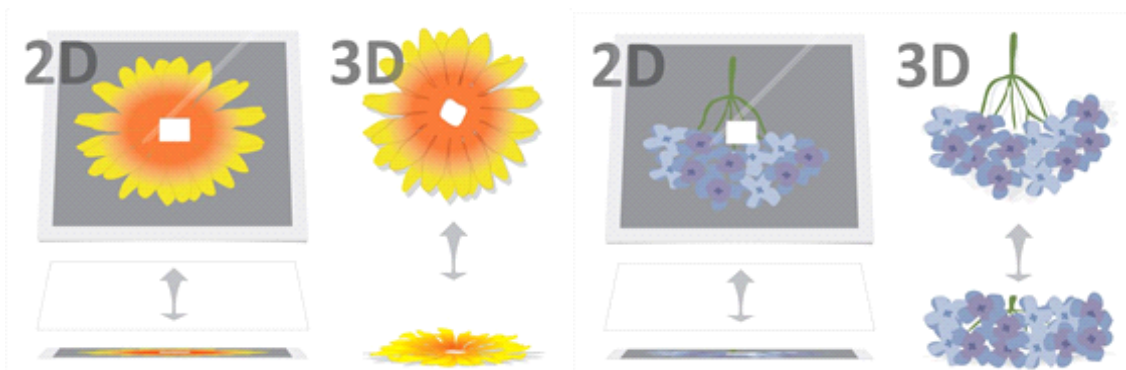
Figure 2. **Images of Photo and Object X (on left) and Photo and Object Y (on right).**

Spectral reflectance curves of the objects and their photos are shown in Figure 3. To obtain these curves, the total diffuse spectral reflectance factors, $\rho(\lambda)$, were measured on a Perkin-Elmer Lambda-19 UV/VIS/NIR spectrophotometer equipped with a diffuse reflectance integrating sphere accessory RSA-PE-19 in accordance with quality system procedure PAR-119 version 1.02. The measurements were performed at ambient temperature $(23 \pm 1)°C$ and for a relative humidity of $(15 \pm 1)\%$. The data were recorded from 300 nm to 700 nm with a fixed spectral bandpass of 5 nm. The measurement geometry was 8° incidence, hemispherical collection (8°:t), with the specular component included. For the diffuse reflectance factor measurements, representative test samples of the objects and photos were prepared or identified. For the two flower picture samples, the test area included all colours and the samples were backed with a black backing. For the fabric flower specimens, eight layers of fabric were sandwiched together alternating dark and light coloured areas to give an opaque specimen. The irradiated area of each test sample was approximately 8 mm x 18 mm. Independent measurements (a minimum of three) were taken on each test sample, and averaged.

High frequency (> 40 kHz) light ballasts (Sylvania Quicktronic T8 QHE4x32T8/112 with fluorescent bulbs Sylvania model FO32/841/XP/SS/EC03) were positioned directly above the maze. The color temperature of the fluorescent bulbs is 4100 K. The bulbs, used in households and offices, have negligible UV emissions.

Design

Bees underwent an initial discrimination training (Phase I) with all four stimuli for two weeks. One picture-object pair was rewarded (+) while the other was not (–). After the initial training was complete, one stimulus from each pair (either the photograph or the object) was removed. Trained bees then underwent either an experimental or control condition for an additional five days (Phase II). Phase II began once at least 10 bees had completed Phase I successfully. For the experimental group, the remaining stimulus would switch reward values — the stimulus that was previously rewarding would become unrewarding and vice versa. In a separate control colony, the reward values of those stimuli would remain the same. For both colonies, the bees were then tested on the removed stimulus. The procedure was repeated four times in counterbalanced conditions with a total of eight colonies (see Table 1).
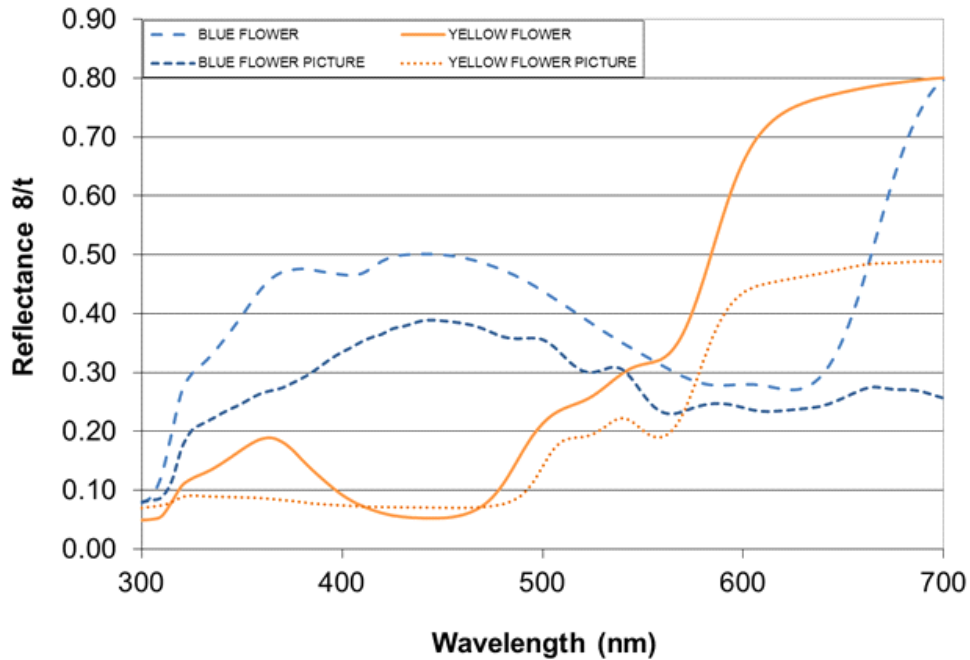
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Figure 3. **Total spectral diffuse reflectance factors (8°:t) for Yellow Flower and Yellow Flower Picture (Object and Photo X) and for Blue Flower and Blue Flower Picture (Object and Photo Y)**

Table 1

Design for Training and Testing Procedures Over Eight Colonies

	Phase I Training with Ob. X+ Ph. X+ / Ob. Y– Ph. Y–			
	Colony 1 *n* = 10	**Colony 2** *n* = 10	**Colony 3** *n* = 10	**Colony 4** *n* = 9
Phase II training	Ob. X– / Ob. Y+ (Switch)	Ob. X+ / Ob. Y– (Non-switch)	Ph. X– / Ph. Y+ (Switch)	Ph. X+ / Ph. Y– (Non-switch)
Test:	Photo X vs Photo Y		Object X vs Object Y	

	Phase I Training with Ob. Y+ Ph. Y+ / Ob. X– Ph. X–			
	Colony 5 *n* = 9	**Colony 6** *n* = 8	**Colony 7** *n* = 10	**Colony 8** *n* = 10
Phase II training	Ob. Y– / Ob. X+ (Switch)	Ob. Y+ / Ob. X– (Non-switch)	Ph. Y– / Ph. X+ (Switch)	Ph. Y+ / Ph. X– (Non-switch)
Test	Photo X vs Photo Y		Object X vs Object Y	

Note. The number of bees that were tested is given for each colony.

Procedure

Upon leaving their colony, bees were trained in groups for three to five hours a day and choices were recorded for each bee individually for 15 days. A choice was made when a bee extended its proboscis into the feeders, and a new choice was recorded only after bees exited the current corridor. For consistency with previous research, an individual was selected for testing if it had foraged for two consecutive days and made at least eight consecutive choices on rewarding stimuli in both Phases I and II. Bees that chose unrewarding feeders must restart the training criterion. The bee also had to have foraged on both the rewarding photo and object at least twice.

Upon reaching training criterion for two training phases, bees were tested individually with empty feeders. Choices were recorded when the bee touches the stimulus, feeder, or back wall of the maze. The bee must have exited the corridor before another choice could be made. The first 10 choices of each bee were recorded.

Statistical Analyses

A first set of analyses compared the choice frequencies, out of 10, of each colony to a theoretical proportion. Because the data were binomial with replication within subjects (each having 10 choices), a replicated Goodness of Fit test (Sokal & Rohlf, 2012) was used to compare choice proportions to a theoretical chance value of 0.5. The G_P value determined if the group proportions differed from the theoretical chance value (50:50), while the G_H value tested for individual differences. G values were compared to the χ^2 value to test for significance.

A second set of analyses was used to compare the switched and non-switched groups. Because the data were binomial, a logistic model was fitted to the choice frequencies using SPSS 22. We compared groups receiving the same Phase I training but different Phase II training, as well as groups receiving the same Phase II training but different Phase I training.

Results

Switching the Reward Values of Objects

Object & Photo X+ / Object & Photo Y− . Figure 4a outlines the results of reinforcement reversals using the objects for bees trained with an initially rewarding Ob. X and Ph. X. When reward values of Ob. X and Ob. Y were switched, bees preferred Ph. Y over Ph. X, $G_P = 18.20$, $df = 1$, $p < 0.001$, with no significant individual differences, $G_H = 7.44$, $df = 9$, $p = 0.59$. Even though Ph. X was last experienced as rewarding, that photo was now avoided. On the other hand, when the objects' reward values remained the same, bees preferred Ob. X over Ob. Y, $G_P = 69.32$, $p < 0.001$, with no significant individual differences, $G_H = 9.74$, $df = 9$, $p = 0.37$.

Object & Photo Y+ / Object & Photo X− . Figure 4b illustrates the results of reinforcement reversals using the objects for bees initially trained with Ob. Y and Ph. Y as rewarding. When the reward values of Ob. Y and Ob. X were switched, bees preferred Ph. X over Ph. Y, $G_P = 7.62$, $df = 1$, $p = 0.006$, with no significant individual differences, $G_H = 8.64$, $df = 8$, $p = 0.37$. The opposite was true when the reward values of the objects remain the same, where bees preferred Ph. Y over Ph. X, $G_P = 13.85$, $df = 1$, $p < 0.001$, with no significant individual differences, $G_H = 10.47$, $df = 7$, $p = 0.02$.
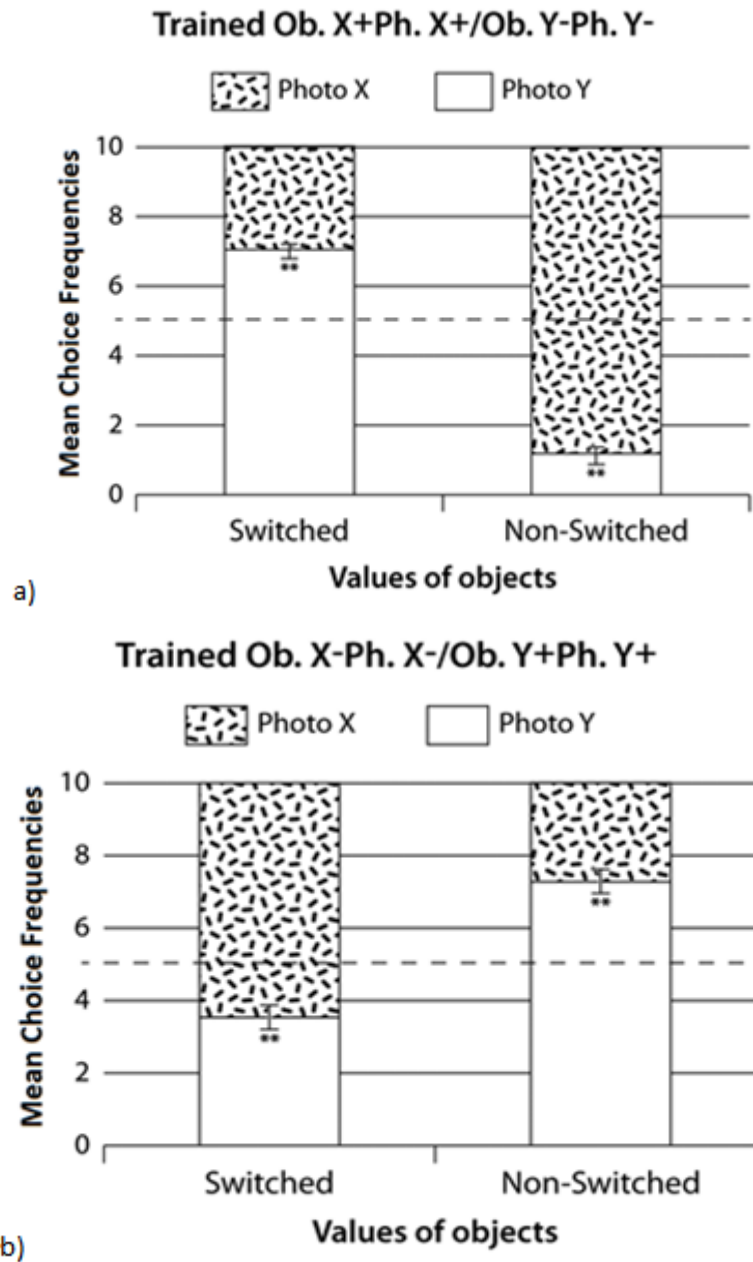
Figure 4. **Mean frequencies, with standard error bars, of choices of photos after the corresponding objects have had the reward values that were experienced during initial training either switched or not**. (a) Object and Photo X were initially rewarding while Object and Photo Y were unrewarding (b) the reverse contingency.   The broken horizontal line indicates chance. ** the choice frequency deviates significantly from chance, $p < 0.001$.

Between group comparisons. There was a significant difference in choice proportions between whether or not the objects had their reward values switched, $\chi^2 = 104.5$, $df = 1$, $p < 0.001$, with the switched groups preferring the photograph of the rewarding object in Phase II over the photograph that was previously rewarding in Phase I. Additionally, there was a significant interaction, showing that the effects of switching were more pronounced in the bees trained with a rewarding X, $\chi^2 = 7.38$, $df = 1$, $p = 0.007$.

Another comparison examining the effects of Phase II training in relation to Phase I training showed that there was a significant difference between results for the non-switched and switched groups for colonies receiving the same Ob. X+/Ob. Y– training in Phase II, $\chi^2 = 15.47$, $df = 1$, $p < 0.001$. Bees trained initially with Ob. X+ and Ph. X+ demonstrated a stronger preference for Ph. X when Ob. X was rewarding in Phase II than bees trained initially with Ob. Y+ and Ph. Y+. No significant differences were found between the remaining two colonies receiving Ob. Y+/Ob. X– during Phase II, $\chi^2 = 0.21$, $df = 1$, $p = 0.65$.

Switching the Reward Values of Photos

Object & Photo X+ / Object & Photo Y– . The effects of reinforcement reversals on photographs are shown in Figure 5a for bees trained on an initially rewarding Ob. X and Ph. X. When the reward values of both photos were switched, the choice proportions of Ob. Y and Ob. X did not differ from chance, $G_P = 1.44$, $df = 1$, $p = 0.23$, though the non-significant bias was in the expected direction of favouring Ob. Y. No significant individual differences were found, $G_H = 3.46$, $df = 9$, $p = 0.94$. A different pattern emerges, however, when the reward values of the photos remain the same, where bees had a strong preference for Ob. X over Ob. Y, $G_P = 46.97$, $df = 1$, $p < 0.001$, again with no significant individual differences, $G_H = 6.02$, $df = 8$, $p = 0.64$.

Object & Photo Y+ / Object & Photo X– . Figure 5b shows the results for reinforcement reversals using photographs for bees trained initially with a rewarding Ob. Y and Ph. Y. A stronger difference was noted, where the switching of the photos' reward values showed bees to prefer Ob. X over Ob. Y, $G_P = 21.98$, $df = 1$, $p < 0.001$, with significant individual differences, $G_H = 24.96$, $df = 9$, $p = 0.003$. All bees had choice proportions at or above chance level on Ob. X with the exception of one bee, which avoided the object, choosing it three times out of ten. In comparison, when the reward values of the photos remained unchanged, bees preferred Ob. Y over Ob. X, $G_P = 41.38$, $df = 1$, $p < 0.001$, with no significant individual differences, $G_H = 5.51$, $df = 9$, $p = 0.79$.

Between group comparisons. As before, there was a significant difference between the switched groups and non-switched groups for object preference, $\chi^2 = 84.08$, $df = 1$, $p < 0.001$. The switched groups preferred the object corresponding to the photo that had been rewarding in Phase II, and not the object that was rewarding in Phase I. No significant effect of the Phase I training was obtained, $\chi^2 = 2.95$, $df = 1$, $p = 0.08$, and there was no significant interaction with switching/non-switching, $\chi^2 = 0.95$, $df = 1$, $p = 0.33$.

A significant difference was found between preferences for colonies receiving the same Ph. Y+/Ph. X– training in Phase II, $\chi^2 = 29.62$, $df = 1$, $p < 0.001$. Bees initially trained with Ob. Y+ and Ph. Y+ had a stronger preference for Ob. Y when Ph. Y was rewarding in Phase II than bees trained initially with Ob. X+ and Ph. X+. There were no significant differences between two colonies receiving Ph. X+/Ph. Y– in Phase II training, $\chi^2 = 2.04$, $df = 1$, $p = 0.15$.
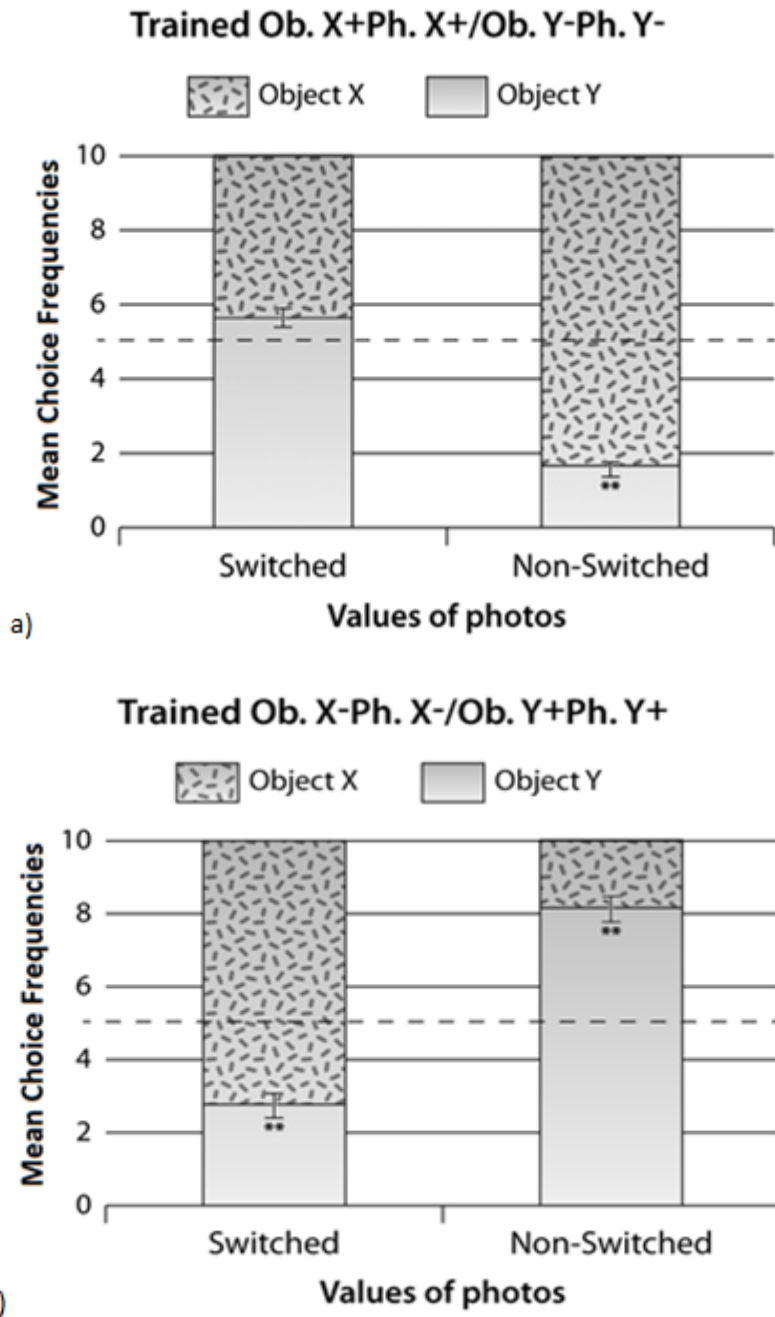
Trained Ob. X+Ph. X+/Ob. Y-Ph. Y-

a)

Trained Ob. X-Ph. X-/Ob. Y+Ph. Y+

b)

Figure 5. **Mean frequencies, with standard error bars, of choices of objects after the corresponding photos have had the reward values that were experienced during initial training either switched or not**. (a) Object and Photo X were initially rewarding while Object and Photo Y were unrewarding (b) the reverse contingency. The broken horizontal line indicates chance. ** the choice frequency deviates significantly from chance, $p < 0.001$.

Discussion

Identifying and grouping flowers that vary in appearance over space and time holds ecological relevance to bees. Although photographs do not appear in their natural environments, the photographs may be viewed as another floral resource within a floral species. When the reward values remained the same in both training sessions, bees consistently chose the stimulus that was previously associated with reward. However, changes in the significance of one stimulus within our groups (X flowers and Y flowers) also changed behaviors toward the other member of that group. When an object in an unrewarding picture-object pair became rewarding, the bees preferred the photo of that rewarding object, despite never having encountered the photo as rewarding. Moreover, bees rejected the photo that they learned as previously rewarding in favour of the photo corresponding to the last rewarding object. The same holds true for photographs: an object previously learned to be unrewarding became more attractive if the photograph of the object became rewarding. By adjusting their behavior immediately to changes in one member of the category, bees can more easily adapt to changing environments without having to relearn anew the value of every flower.

Our methods required labour intensive and time consuming training, training again, and then testing of the same individually labelled bees. Although the amount of exposure varied among individuals in group training depending on when they reached criterion level, no significant individual differences were found in any of the colonies, with the exception of one colony for which the behavior of one bee stood out from that of the rest. Because both experimental and control groups received the same initial training and testing regimen, differences in behavior could be attributed to the switching of reward values.

In cases of differential learning, trained preferences towards rewarding stimuli were accompanied by learned avoidance of non-rewarding stimuli (Giurfa et al., 1999). Following initial training, bees not only learned to prefer stimuli in the rewarding cluster, but also avoided stimuli that were from the unrewarding cluster. The learning transfers observed here from switching the reward values demonstrated that not only were previous preferences to rewarding stimuli disregarded, but also previous learning of avoidance to specific stimuli can be offset by experiencing reward from different stimuli in the same category.

Our results stand in contrast to those obtained in previous research on vertebrates (Delius, Jitsumori, & Siemann, 2000). Despite successful training in pigeons to classify different stimuli into groups, they showed little to no transfer after the reversal training, even with stimuli that were perceptually similar (e.g., Astley & Wasserman, 1998; Fersen & Lea, 1990; Jitsumori, 1993), though with multiple successive reversals, transfer has been obtained (Vaughan, 1988) The current study, however, revealed strong behavioral changes towards stimuli following just one reversal. In spite of the mixed results in vertebrates, bees were capable of successfully transferring learning. Given the difficulties in species comparisons, we can only speculate as to the many possible causes of the difference in performance. One possibility is that the types of objects that are classified differ across studies. With pigeons, categories used have been both unnatural (e.g., cars, chairs) and natural (e.g., trees). In our case, however, not only were the categories natural (i.e., flowers), but they were categories that are crucially important for survival.

Having focused on how bumblebees treat members of our floral groups—what they do—we now interpret these results in terms of a well-known framework for understanding categorization—how they do it. Inherent in this classification scheme (Herrnstein, 1990) is the explicitly comparative approach. Virtually all species, and not just ours, face categorization problems—they confront objects to which they must react appropriately; objects such as stones and nests and worms and grains for which there is natural variability in appearance. The ability to categorize stimuli has turned up most everywhere it has been sought (Herrnstein,

1990). How do animals do it? The underlying processes leading to categorization may differ among species (Chittka & Jensen, 2011).

Five levels of categorization, at increasing levels of abstractness, have been proposed: (1) The first shows the organism behaving in the same way towards members of a cluster because it fails to discriminate among the stimuli. For example, chimps that initiate social behaviour upon viewing their reflections in a mirror indicates a lack of discrimination between their reflection and another animal. (2) The second, categorization by rote, consists of memorizing exemplars as a list. Herrnstein (1990) gives the example of learning the names of the stops on the Boston subway system's "Redline". (3) Beyond rote learning, at the third level, is open-ended categorization. Organisms discriminate between different groups of stimuli while generalizing within them (Keller & Shönfeld, 1950; Benard et al., 2006). By virtue of the perceptual distances between stimuli, organisms have a means of categorizing new objects. For instance, pigeons can be trained to distinguish between photos containing trees or not, and can classify new exemplars (Herrnstein, 1979). (4) The fourth level, that of concepts, involves sorting by function—the use of perceptual similarity is not needed. While the lack of perceptual generalization may appear to be rote memorization, category members are connected by their associated consequences: generalization is "mediated" through a common consequence. Though the term "concept" has been used inconsistently in the literature, "associative concept learning," as defined by Zentall, Wasserman, Lazareva, Thompson, and Rattermann (2008), involves grouping arbitrary stimuli based upon a common outcome. For example, in this issue, Feuerbacher and Rosales-Ruiz (2017) examine the formation of the concept "toy" by a dog through a common response of playing tug-of-war with a variety of different objects. (5) Finally, at the fifth level, the subjects would be capable of categorizing based upon abstract relations (e.g., same/different, inside/outside) among concepts. The conceptual abilities of Alex the Parrot are a case in point (Pepperberg, 1987): Alex learned to identify the number of objects in sets of two to six objects and generalized to new sets.

The results here showed bees to change their behavior despite previous experience based on the similarities between the photos and objects, eliminating the possibility of rote memorization as a foraging strategy. Additionally, because bees could differentiate between the 2D and 3D stimuli (Xu & Plowright, 2016), the behavioral changes with a reward reversal are evidence of the use of categories in foraging. This opens the possibility of the use of open-ended categories based on Herrnstein's descriptions. If so, it remains to be determined what perceptual cues were used. Several aspects of the objects such as texture, size and shape of the original object would differ when degraded to a photo. Color photographs are adapted to human vision and indeed the spectral characteristics of the objects and their photos, while similar, were also different. Although much of previous categorization research varied the stimuli along one trait, such as color (Dukas & Waser, 1994), bees had also grouped stimuli that varied along multiple traits (e.g., Zhang et al., 2004). It seems plausible that bees learned multiple features simultaneously (Ronacher, 1998), and that a set of features may be required for categorization (Avarguès-Weber et al., 2011).

So far, the current results give evidence of simple generalization, where bees generalized their behavior between stimuli having physical similarities. However, we do not discount the possibility of mediated generalization (Shettleworth, 2010): the generalization based on the common associations with an outcome that is at the heart of concept formation (Herrnstein's level 4). Behavioral transfer between the photo and object could be a result of a common consequence between the two, in which they both give the same reward and would be considered equivalent. This equivalence implies only functional equivalence: by virtue of training in which cues become associated with the same consequence, they come to function as substitutes for each other (Hall, 1996) and is not to be confused with formal equivalence, or "equivalence classes", where subjects are

tested for the emergence of the mathematical relations of symmetry, reflexivity, and transitivity (see for example in this issue, Plazas & Cortés, 2017).

Grouping of floral stimuli might still occur even when no perceptual similarities are perceived. After all, non-rewarding flowers that do not physically resemble other rewarding flowers are still all flowers insofar as they are candidate food sources, as opposed to being nestmates or predators. Future research, along the lines of several studies described in this issue (Sturdy et al., 2017; Vonk & Leete, 2017) might extend our work to categorization by function of floral stimuli that bear little perceptual resemblance to each other. Evidence of abstract categorization (Herrnstein's level 5) has been found in previous research, where bees grouped stimuli based upon abstract relations such as sameness/difference (Brown & Sayde, 2013; Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001) and above/below (Avarguès-Weber, Dyer, & Giurfa, 2011). Time will tell whether the abilities of bees in categorization tasks remain more striking than any of their limitations.

Acknowledgments

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