



Floral Categorization by Bumblebees: The Perceptual and the Functional

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Abstract – This study examines generalization and perceptual similarity judgments in bumblebees (*Bombus impatiens*) and addresses whether category formation of floral stimuli is based upon perceptual floral features alone or foraging experiences from reward associations. Previous experiments have found that bees transfer learning based on category membership, but little is known as to how membership is formed. Two experiments using twelve bumblebee colonies examined a) if bees were able to generalize between flowers with little or no perceptual similarity, and b) if bees were able to change which features of the flowers they generalize under different circumstances. All bees were given discrimination training in a radial arm maze using objects and corresponding photographs. Bees in Experiment 1 were trained to categorize stimuli based upon their reward associations while ignoring their perceptual features. Bees in Experiment 2 were trained to categorize either by floral type or dimensionality (2D vs 3D) of the stimuli. Results of tests using unrewarding stimuli revealed that bees were unable to group items without perceptual similarity cues. When perceptually similar flowers did not share the same reward, bees still generalized between them, regardless of experience. However, the reward values of the flowers were not spontaneously disregarded by the bees. Generalizations differed based on the bee's experiences, although preferences for perceptual similarity remained. Bees grouped flowers based on the relevant features learned through experience rather than just relying on perceptual similarity, but also do not immediately discount similar flowers during foraging, giving a preliminary insight into the role of function in perceptual similarity judgments.

Keywords – Bumblebees, Categorization, Mediated generalization, Perceptual similarity judgement

Foragers in nature are presented with a wide array of stimuli, varying in shape, size, and color. To forage effectively, individuals must be able to manage information for rewarding stimuli to reduce the amount of details attended to. Categorizing objects allows foragers to simplify a complex environment, by grouping distinguishable objects based upon a family resemblance and treating them as equivalent (Troje et al., 1999). Categorization requires two main processes: discrimination between different categories of objects and generalization of responses towards objects within a category. Generalization within a categorization task differs from simple generalization in that the boundaries between categories are clear in categorization tasks, while generalization may involve a gradual increase or decrease of responding towards objects that are similar or dissimilar to one another. Because category boundaries are difficult to examine in a behavioral context, only the generalization process may be inferred in this instance.

Many species of bees are flower constant, where they restrict foraging to one or a few species of flowers within a foraging trip (Chittka et al., 1999; Rossi et al., 2005). Effective foraging strategies would include differentiation between floral species and generalizing their learning from one flower to another of

the same species. The ability to generalize is essential for any categorization task and takes two different forms: simple generalization and mediated generalization (Zentall et al., 2008).

In perceptual categorization, learning is transferred to other stimuli sharing perceptually similar characteristics: there is perceptual generalization. Often these characteristics reflect perceptual features of the objects, such as shape or color. Using simple generalization, bees may select flowers during a foraging trip that physically resemble the rewarding flowers already experienced and ignore other resources. As a result, perceptually similar flowers that are unrewarding will still be considered part of the rewarding category. In typical foraging environments, the flowers that most resemble a rewarding species are most likely conspecifics, and foraging based on simple generalization would increase efficiency where there is a low chance of failure.

Much of the previous research provides evidence for simple generalization in bees, where they demonstrated positive learning transfers from one stimulus to a novel set of stimuli sharing common features with the original (Benard et al., 2006). Honeybees were able to generalize on a simple, one-feature basis on tasks involving symmetry (Giurfa et al., 1996; Plowright et al., 2011), configuration (Avaluès-Weber, Portelli, et al., 2010), and orientation (Avaluès-Weber, Deisig, & Giurfa, 2011). They were also able to generalize and group more complex stimuli with multiple characteristics, such as flower shapes, plant stems, landscapes, and trees (Zhang et al., 2004), and they demonstrated the ability to differentiate between Monet and Picasso paintings, generalizing the learning to novel paintings (Wu et al., 2013). Similarly, bumblebees have also demonstrated successful simple generalization both with single feature tasks, such as color (Dukas & Waser, 1994; Gumbert, 2000; Muth et al., 2015) and with more complex stimuli, such as behavioral transfers of preferences from 3D artificial flowers to their photographs and vice versa (Thompson & Plowright, 2014; Xu & Plowright, 2016).

However, generalizations can be based not only on the features of the flowers, but also on the experience of the forager. For instance, bees that were trained on two rewarding colors generalized their behavior to all novel colors within the spectral range, while bees that were trained on only one color did not (Benard & Giurfa, 2008). Color generalizations have been shown also to apply to specific flower parts. Bees trained on two bicolored patterns were able to generalize based on one of the two colors while ignoring the other (Dukas & Waser, 1994). This suggests that bees may be capable of changing the features they generalize based on their experiences. If bees can generalize specific floral features that are functionally relevant, then this suggests the categories they form may be dependent on the functions each flower serves to the bee, and not just the physical floral characteristics.

This leads to the second possibility of mediated generalization, which is necessary for the formation of functional categories. Under such circumstances, there is generalization on the basis of a common consequence (Delius et al., 2000), such as reward associations, whereas simple generalization requires only the perception of physical attributes - indeed, in the study reported here, function is defined in terms of consequences. Stimuli in this case are grouped together because they share a common function to the animal and these generalizations should be based on learning (Herrnstein, 1990), and thus, possible without perceptual similarities. However, it is often more difficult to distinguish between perceptual and mediated generalization within a natural setting, as objects that share functions also tend to share similar features. Mediated generalization has been found in other species, through sorting food and non-food items by pigeons (*Columba livia*) (Watanabe et al., 1993), Japanese monkeys (*Macaca fuscata*) (Tsutsui et al., 2016), and baboons (*Papio anubis*) (Bovet & Vauclair, 1998). Additionally, in a case study with a German Shepherd (*Canis familiaris*), mediated generalization of novel objects to toys was obtained after playful interaction with them (Feuerbacher & Rosales-Ruiz, 2017). Dolphins also were able to categorize two different auditory tones together while rejecting similar tones (von Fersen & Delius, 2000). Bottlenose dolphins (*Tursiops truncatus*) trained with reversal tasks were able to correctly group two sets of tones with larger similarities between the sets than within the sets. At the same time, Sykes's monkeys (*Cercopithecus albogularis*) classify monkey calls under the same grouping and different from other bird calls, despite their similarity (Brown et al., 1994). These items can bear little to no resemblance to one another but are still categorized based on the function they serve to the animal.

Similarly, objects in a bee's environment would serve distinct functions to the foragers. Apart from food resources, bumblebees can recognize landmarks (Cartwright & Collett, 1983), and nestmates and other conspecifics (Foster, 1992). While most of these objects would be perceptually dissimilar to one another and easy to differentiate, it is not impossible for objects to appear similar but serve different functions to a forager. Through mediated generalization, objects sharing similar roles are categorized together and learning from one object transfers to others within that category. For instance, bees use landmarks to determine locations of foraging grounds (Cheng et al., 1986; Kheradmand et al., 2018) or the colony (Brünnert et al., 1994) and must be able to differentiate landmarks from food sources. Also, flowers can differ in resources such as pollen and nectar and must also be differentiated based on the colony's needs, where more pollen is collected with more brood present (Free, 1967) and low pollen storage levels (Fewell & Winston, 1992).

In contrast with perceptual generalization, mediated generalization has received comparatively little attention in the literature on bee cognition, although work on concept learning and relational learning in bees suggests that it is within their capabilities (Avarguès-Weber & Giurfa, 2013; Giurfa, 2019; Giurfa et al., 2001; Gross et al., 2009; Howard et al., 2018). Nonetheless, generalization based on shared associations rather than perceptual features would be advantageous in natural environments for sorting objects based on function rather than physical characteristics, such as when dealing with floral mimics. Whereas animals that eat one or limited food types would not require a functional category for food, bees would encounter many stimuli that would give the same resources and others that appear similar but give little to no resources. In such instances, being able to place dissimilar items in the same category while separating them from similar items is useful for remembering specific inflorescences (Greggor & Hackett, 2018). Although behavior towards mimics from foragers have yet to be investigated from a categorization standpoint, research has shown bees to successfully discriminate between flowers with perceptual elements. Previously, bumblebees have been shown to learn floral associations when perceptual similarity judgments are unreliable. For instance, bees demonstrated behavioral flexibility using serial reversals (Strang & Sherry, 2014). Bees reacted similarly between two perceptually different stimuli that they otherwise would have treated differently without training. Additionally, bees have been found to learn fine discriminations between colors and patterns given differential rather than absolute training (Avarguès-Weber, de Brito Sanchez, et al., 2010; Giurfa, 2004), where bees trained with both rewarding and unrewarding stimuli performed better than those given exposure to just a rewarding stimulus. As a result, bees are capable of distinguishing subtle differences, and thus treating two otherwise similar stimuli as being different.

Because mimics have developed signals that hinder discrimination, visual discrimination between mimics and rewarding flowers is slower when not accompanied by odor cues (Kunze & Gumbert, 2001; Leonard et al., 2011). Additionally, odor cues are also learned when flowers are unrewarding (Palottini et al., 2018). Given that visual features such as color have previously proven to be salient cues to bees, discriminations between mimics requires ignoring salient visual similarities to some degree by the forager. Recent work has highlighted the interplay of saliency and reward value on attentional capture by bumblebees in visual search for targets among unrewarding distractors (Nityananda & Chittka, 2021). Bees also previously demonstrated the ability to discriminate minute features in limited capacities. Honeybees were found to accurately discriminate fine features of flowers, such as color, when given differential training in the past (Dyer & Murphy, 2009), but still visited the known unrewarding flowers in the absence of a rewarding counterpart, further expanding the findings that the presence of unrewarding stimuli could influence learning transfers onto novel stimuli (e.g., Ronacher, 1992). Additionally, bees given differential training recognized more parts of the stimuli compared to those exposed to only absolute training (Giurfa et al., 1999). Similarity has been found to interfere with category formation in other instances as well and some bees preferred generalizing on the basis of floral features rather than the relationships between flowers (Wiegmann et al., 2000). Through training, bees were able to discriminate between perceptually similar stimuli that may have been generalized by the bees under other circumstances. Similarly, the use of mediated generalization between perceptually different flowers could aid in discriminating rewarding flowers from mimics in a natural setting. By determining which features are needed to form the category, bees can benefit from more accurate foraging to meet colony demands. Because previously bees have been

found to make fine discriminations under the right conditions, this same level of differentiation can be used to sort perceptually similar floral stimuli into different groupings despite their similarities. In short, contemporary research on floral mimicry focuses on the role of pollinator perception, learning and decision-making (e.g., Garcia et al., 2020) in plant-pollinator interactions. This paper contributes to the “cognitive ecology of pollination” (Chittka & Thomson, 2001) by adding categorization to the list of cognitive processes under investigation.

Because research on the subject appeared mixed, the following two experiments evaluate the degree to which perceptual similarities are used in the foraging process. Experiment 1 examined whether bees group flowers based on physical features even when the groupings contradict their foraging experience. This determines if bees can transfer learning based upon perceptual similarity despite the stimuli being known to serve different functions to them. Following this, Experiment 2 examined whether bees change which floral features to generalize based upon their experiences and the functions of the flowers.

Experiment 1

It is still uncertain if bumblebees are capable of mediated generalization, or if they rely on perceptual features solely during foraging trips. Most categorization tasks involve generalization to novel stimuli. However, because mediated generalization is based on the function of the flower, and thus relies on the forager’s previous experience, generalization to novel stimuli here may not be sufficient. Previously, bees were found to generalize behavior to perceptually similar objects (Xu & Plowright, 2017). In that study, bees were trained to group photographs and objects based on corresponding picture-object pairs for yellow flowers and blue flowers, where one pair was rewarding and the other unrewarding. When one member of the group has its reward values changed, bees transferred their learning about one member to all members of the group. For instance, when 3D yellow flowers and photographs were rewarding, and the photograph suddenly became unrewarding, bees also avoided the 3D flower and treated it as having become unrewarding despite only experiencing it was rewarding. This behavioral transfer occurs even when bees have experienced the objects as unrewarding previously, suggesting that perceptual similarity provides a stronger cue than learned consequences.

However, it is difficult to say to what extent the experience of a common reward between the flowers influences the bees’ foraging behaviors. Bees may always treat flowers with similar perceptual features as similar without having any learned experiences with them. Here, we used the same methodology as in Xu and Plowright (2017), with one difference: the stimuli were grouped with no perceptual similarity during training, to determine if different groupings would have an effect on the bees’ similarity judgements. The situation models that of encountering floral mimics where only one of two perceptually similar flowers are rewarding. The results will give more insight into how bees treat instances in nature where stimuli are perceptually similar but functionally different.

Bees were trained with two perceptually dissimilar stimuli that were rewarding, while perceptually similar stimuli were separated with different reward values. One flower from each group was then removed and the remaining flowers had their reward associations switched. Bees were then tested to learning transfers on the removed flowers. Through this, we examined how bees treated perceptually similar stimuli that have different reward consequences, and how learning can transfer when those reward consequences change. The rationale is given in an analogy by Herrnstein (1990), as follows. For a creature that deals with acorns, suppose that acorns became bitter. The animal with a representation of the class of acorns, rather than specific exemplars, will have bitterness propagate over other class members that were not yet tasted. In nature, bees would encounter flowers that have similar features but offer different resources or levels of resources. If bees are able to group together flowers without any perceptual similarities, then learning transfers will occur based upon the initial reward values of the flowers, as found previously, where if one of two flowers change reward values (a rewarding flower was depleted, or an unrewarding flower was refilled), the other would also be treated by the foragers as having changed value as well. In other words, in our previous study, the workers behaved as if they had concluded that if one member of a floral group had become either profitable or unprofitable, then so had the other, or at the very least, bees should treat

perceptually similar flowers as having different functions and rely instead on rote memory. However, if bees require some perceptual similarities between flowers to categorize them, then generalization will occur based on the level of similarity between the stimuli.

Method

Subjects

Forty-two bumblebees (*Bombus impatiens*) were used from four colonies and supplied by Koppert Biological Systems Canada with 9 to 11 bees tested in each colony. The colonies were fed *ad libitum* a paste of fresh-frozen pollen mixed with honey solution. Different colonies were housed in separate boxes indoors at a set temperature of 18 to 20°C. The colony was placed on top of foam carpet backing to minimize disruption of behaviour due to vibration. High frequency (> 40kHz) light ballasts (Sylvania Quicktronic T8 QHE4x32T8/112 with fluorescent bulbs Sylvania model FO32/841/XP/SS/EC03) were placed above the colony and turned on during the day and off at night. Individual workers were labelled with colored numbered tags glued onto their thoraces. The colony was given access to explore the maze and drink freely from the feeders two days prior to the start of training. The bees had not been let out of their boxes prior to the experiment. Only bees from the same colony foraged together.

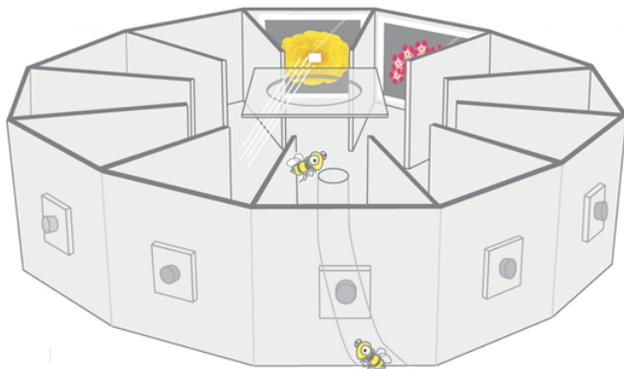
After testing, individual workers were isolated from the colony and freeze-killed. At the end of each experiment, the entire colonies were killed in a deep freeze. Applicable guidelines of the American Psychological Association and the Canadian Council on Animal Care were followed. The procedures in this research were reviewed in 2015 by the Animal Care Committee of the University of Ottawa (Protocol: PY-2115-A1). In subsequent years, when the research was carried out, no protocol was required.

Materials

The colonies were contained in a plastic cubic box, with a 40-cm tube connecting the container to a rectangular wooden walkway, topped with glass plates. A tunnel connected the walkway to an opening in the center of the maze floor. The radial arm maze, constructed of opaque grey Plexiglass consisted of 12 corridors (14 cm long and 15 cm high), which opened into a central area (17 cm diameter) from an entrance (6 cm wide). Only eight of the corridors were in use for the experiment. The remaining four were blocked by opaque Plexiglass® dividers. The maze was covered with a clear Plexiglass® lid (53 cm diameter). A diagram is shown in Figure 1, and a photograph is shown in Xu and Plowright (2017).

Figure 1

Diagram of Maze

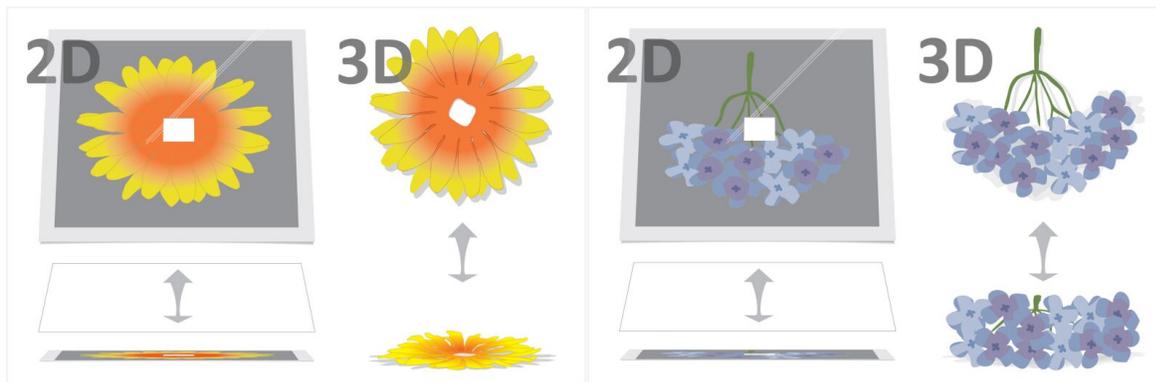


Note. The bee enters the maze through hole in the floor using wire mesh tunnel. Stimuli are mounted on the back walls of the corridors. Figure modified from an original (Plowright et al., 2013) with kind permission from Springer Nature.

One artificial flower, made of synthetic fabric, or photograph (Figure 2) was fixed to each feeder on the back wall of each of the eight corridors in use. The photographs of the flowers (8.5 cm x 10.5 cm) were printed on a grey background. Feeder troughs, protruding through the centers of the floral stimuli, were either filled with sugar solution or left empty (Figure 1). The 2D and 3D portions refer to all parts of the floral stimuli excluding the feeder trough. All stimuli were placed randomly before each training session to eliminate the use of location cues. Four stimuli were used: a single yellow flower (Object X) and a cluster of blue flowers (Object Y) and their corresponding photographs (Photo X and Photo Y). Bumblebees can discriminate between what humans perceive as yellow and blue (e.g., Ings et al., 2009). Figure 3 shows the spectral reflectance curves of the stimuli obtained by Xu and Plowright (2017). Because the corresponding object and photo pairs share perceptual similarities on many aspects (color, shape, etc.), bees may be using different similarity judgements when comparing the two. Despite this, we had previously (Xu & Plowright, 2016) ascertained that these objects and photos were treated as similar-but-different, and as such, they could be thought of as two different instances of the same floral species, even though photos are not encountered in nature.

Figure 2

Object and Photo X and Y



Note. Photo and Object X (on left) and Photo and Object Y (on right). Reprinted from Xu and Plowright (2017).

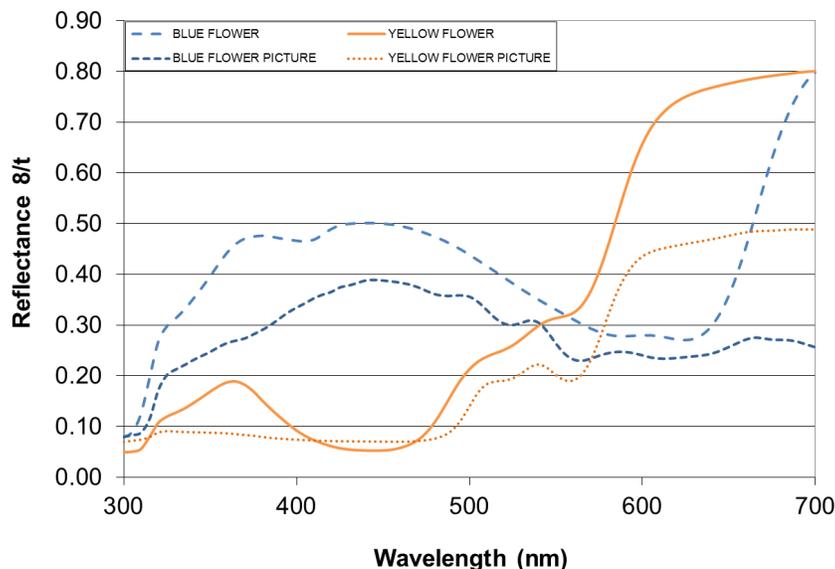
Procedure

Bees were group trained for three to five hours a day with 2:1 sugar to water solution by volume in a radial arm maze, where all bees from the colony were free to enter the maze for training. A choice was recorded when a bee extended its proboscis into the feeder. A new choice was not counted unless the bee first exited the corridor. An individual was selected for testing if it had been observed to forage on two consecutive days and had chosen the rewarding stimuli at least eight times in a row in each of two phases of training described in the Design section. Bees that chose unrewarding feeders were required to restart until the training criterion had been met. The bee also had to have foraged on all rewarding stimuli at least twice. All bees in the same colony were allowed to train in the maze on any training day, but only bees that passed the training criterion would proceed to the testing phase.

Whereas bees were trained in groups, they were tested individually. All the feeders were empty. Choices were recorded when the bee touched the stimulus, the feeder, or the back wall of the maze. As in training, the bee must have exited the corridor before another choice could be made. The first ten choices of each bee were recorded. Experimenters observed the bees in the maze from above for both training and testing and recorded the choices as they were made.

Figure 3

Spectral Reflectance of Stimuli



Note. 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). Reprinted from Xu and Plowright (2017). Figure re-used with kind permission from the National Research Council of Canada.

Design

Bees underwent an initial discrimination training (Phase I) with all four stimuli for two weeks. Photo X and Object Y were rewarded (+) while their corresponding object and photograph counterparts (Photo Y and Object X) were not (-). Once 10 bees had successfully completed the training, a second training phase (Phase II) began (i.e., there was no testing after Phase I). Here, 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). For the experimental group, the remaining stimulus (i.e., the one that was not removed) would switch reward values – the stimulus that was previously rewarding would become unrewarding at this point forward 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 (see Figure 4 for a sample of the design). The procedure was repeated four times in counterbalanced conditions, where two colonies received Phase II training on objects but not photos, and the other two were trained on the photos but not objects, to make a total of four conditions (see Table 1).

Table 1

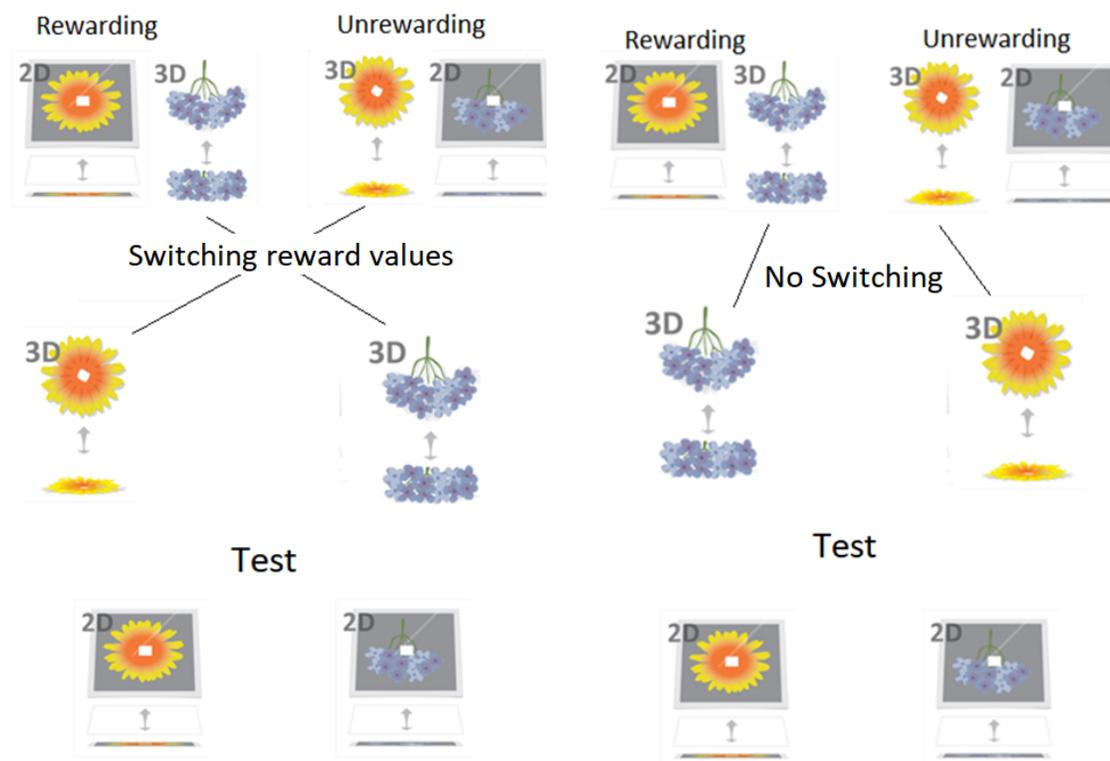
Design for Experiment 1

Phase I Training with Object Y+ Photo X+ / Object X- Photo Y-				
	Condition 1 (n = 10)	Condition 2 (n = 10)	Condition 3 (n = 11)	Condition 4 (n = 9)
Phase II Training	Object X+ / Object Y- (Switch)	Object Y+ / Object X- (Non-switch)	Photo X- / Photo Y+ (Switch)	Photo X+ / Photo Y- (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.

Figure 4

Example of Experiment 1 Design



Note. The images of the 2D and 3D objects are reprinted from Xu and Plowright (2017).

Statistical Analyses

The data were binomial with replication within individuals (each having 10 choices). Accordingly, a replicated Goodness of Fit test (Sokal & Rohlf, 2012) was used. The total G value can be partitioned into individual contributions, which ranged from 0 to 13.86, with 1 df, per bee. The G_P value (P for Pooled) determined if the group proportions differed from a theoretical chance value of 50:50, while the G_H value (H for Heterogeneity) tested for individual differences. Under the null hypothesis, the G test statistic is distributed approximately as a χ^2 distribution.

Results

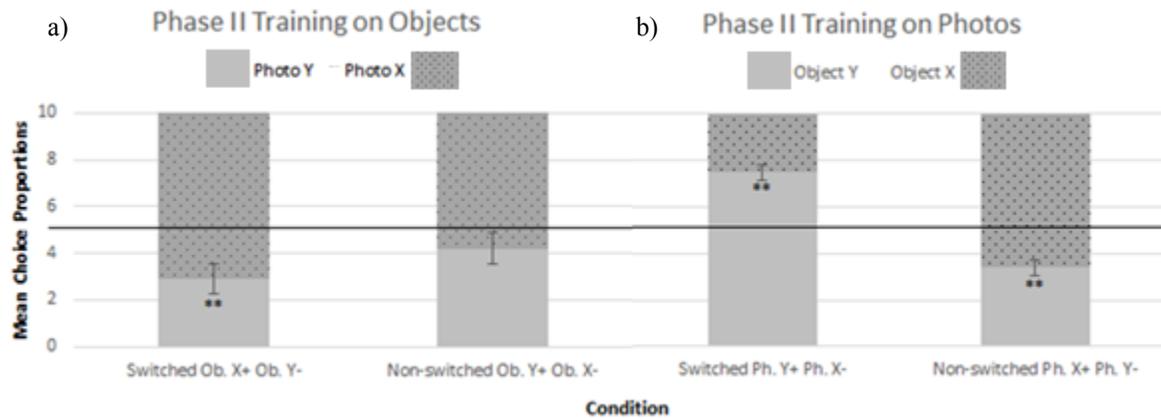
Switching the Reward Values of Objects

Figure 5a shows the effects of reinforcement reversals using the objects. When reward values of Object X and Object Y were switched, so that the previously unrewarded Object X in Phase I was now rewarding and Object Y became unrewarding, bees preferred Photo X over Photo Y ($G_P = 18.2$, $df = 1$, $p < .001$), with significant individual differences ($G_H = 20.53$, $df = 9$, $p = .01$). Bees varied between favoring Photo X and having no significant preferences. No bees showed a preference for Photo Y over Photo X that significantly deviated from the group. Bees did not transfer learning from Object X to Photo Y or Object Y to Photo X. On the other hand, when the objects' reward values remained the same, bees showed no significant

preference for the photos ($G_P = 2.18$, $df = 1$, $p = .39$), with no significant individual differences ($G_H = 9.18$, $df = 9$, $p = .42$).

Figure 5

Experiment 1 Results



Note. Mean frequencies (out of 10 choices) of each stimulus during the testing phase, with standard error bars. Choices are between Photo X and Y in a) and Object X and Y in b), after the corresponding stimuli have had the reward values that were experienced during initial training either switched or not (as illustrated Figure 3). Object Y and Photo X were initially rewarding while Object X and Photo Y were unrewarding for Phase I training. The horizontal line indicates chance. $**p < .001$

Switching the Reward Value of Photos

Figure 5b shows the effects of reinforcement reversals using the photos for bees. When reward values of Photo X and Photo Y were switched, so that the previously unrewarded Photo Y in Phase I is now rewarded and Photo X becomes unrewarding, bees preferred Object Y over Object X ($G_P = 29.88$, $df = 1$, $p < .001$), with no significant individual differences ($G_H = 6.5$, $df = 10$, $p = .77$). Despite having experienced both Object Y and Photo X as rewarding in Phase I, bees failed to act as if the change in reward in Photo X had also occurred in Object Y. On the other hand, when the photos' reward values remained the same, bees preferred Object X over Object Y ($G_P = 12.001$, $df = 1$, $p < .001$), with significant individual differences ($G_H = 37.14$, $df = 10$, $p < .01$). Half the bees showed a strong Object X preference, while the other half had no significant preferences for either.

Discussion

Bees chose the counterpart object or picture of the rewarding flower in Phase II regardless of the associations learned in Phase I. As with previous research (Xu & Plowright, 2016), learning from one flower can be transferred to another without the forager having the same experience on the second flower. Unlike the previous study, bees were trained specifically to discriminate between two similar flowers, but still grouped flowers based on perceptual similarities. As a result, bees do not transfer learning between stimuli groups if the perceptual similarities between members of two different groups of flowers are too large. Nor did the bees rely on rote memorization to distinguish between rewarding and unrewarding flowers despite training to discriminate between them. Instead, bees generalized between perceptually similar stimuli and contradictory experiences on perceptually similar flowers would not significantly impact their ability to generalize between them.

The methodology is similar to that in previous research (Xu & Plowright, 2017), and involves labor intensive and time-consuming training. Finer discriminations often involve a speed trade-off and take

longer to learn (Dyer & Chittka, 2004). Perhaps with more training, the bees would eventually group the different objects and photos as belonging to the same category. Whereas bees do visit more flowers in nature, they are unlikely to have prolonged repetitive exposure to a limited assortment of flowers, and such a method would be impractical and unlikely to occur in natural settings. When unrewarding flowers are rare, foragers have little incentive to discriminate between mimics and rewarding flowers (Lichtenberg et al., 2020). Here, the unrewarding flower is always present and in the same quantity as the rewarding counterpart – a situation unlikely to occur in natural settings. Additionally, previous research shows that bees are capable of discriminating between counterpart objects and photos (Thompson & Plowright, 2014), and could do so without any prior experience or training on the two (Xu & Plowright, 2016), and thus bees should have little issue discriminating between the two.

Moreover, bees in this experiment not only had to transfer learning in the absence of perceptual similarity but were also tested to do so in spite of it, making the task more difficult than tasks used in previous research (e.g., Dyer & Chittka, 2004). The results are in line with previous research (Dyer & Murphy, 2009), where bees visited the stimulus that was perceptually similar to the rewarding stimulus during training, despite being trained to treat it as unrewarding. However, in the current study, bees also rejected a known rewarding stimulus in favor of a perceptually similar one. These lab studies have ecological significance. Field studies show that non-rewarding plants benefit from their proximity to similar rewarding plants: having been drawn to “magnet plants,” pollinators will also visit the perceptually similar non-rewarding plants in the area (Johnson et al., 2003). Perceptual similarity may be too salient for the bees to ignore. By removing the added difficulty of perceptual similarities between groups, bees may have an easier time grouping flowers with little perceptual similarity. Some studies suggest that bees can be trained to attend to and generalize specific portions of patterns (Dukas & Waser, 1994; Fauria et al., 2000). Further research can determine whether bees can generalize by flower function, and the degree in which innate similarity judgments influence their foraging decisions. The next step to examining mediated generalization involves looking into the bees’ abilities to generalize specific floral characteristics based upon reward values rather than simply through similarity, and whether the reward values of the flowers influence how bees perceive similarities between flowers.

Experiment 2

Although objects in a natural environment can serve different functions to a forager, only members of a floral species would normally be observed to change reward values simultaneously. As a result, while two perceptually different flowers may both be originally rewarding, the loss of reward from one flower may not always indicate no reward from another floral species. Nonetheless, this does not indicate that reward associations have no effect on the bees’ ability to generalize between perceptually dissimilar objects. Mediated generalization may still be possible; however, generalizing in the absence of any perceptual similarity may be a difficult task for the bees.

In the following study, we aim to investigate whether bees rely entirely on perceptual generalization during foraging, or if they can be trained to ignore the more salient perceptual similarities for features that are more functionally relevant. The experiment uses the same four stimuli as in Experiment 1, but grouped by the experimenter in two different ways. Along with grouping flowers by ‘X’s and ‘Y’s as was done previously, we also grouped objects and photos of those objects separately (e.g., objects as rewarding and photos as unrewarding). Object X and Photo X, for instance, either belong to the same group or to different groups. Bees were tested on the counterparts of a rewarding object and a novel object.

The goal was to examine whether bees would be able to determine group relationship based on different features of a flower (i.e., the relation between an object and photograph pair vs the relation between 3D and 2D stimuli), and whether having more similarities between groups interfere with how bees categorize flowers that would otherwise belong together. The addition of novel stimuli allows us to examine learning transfers while keeping the learned consequences of the testing stimuli as both unrewarding. The use of novel stimuli allows for investigations of learning transfers onto new objects, where memory alone is insufficient.

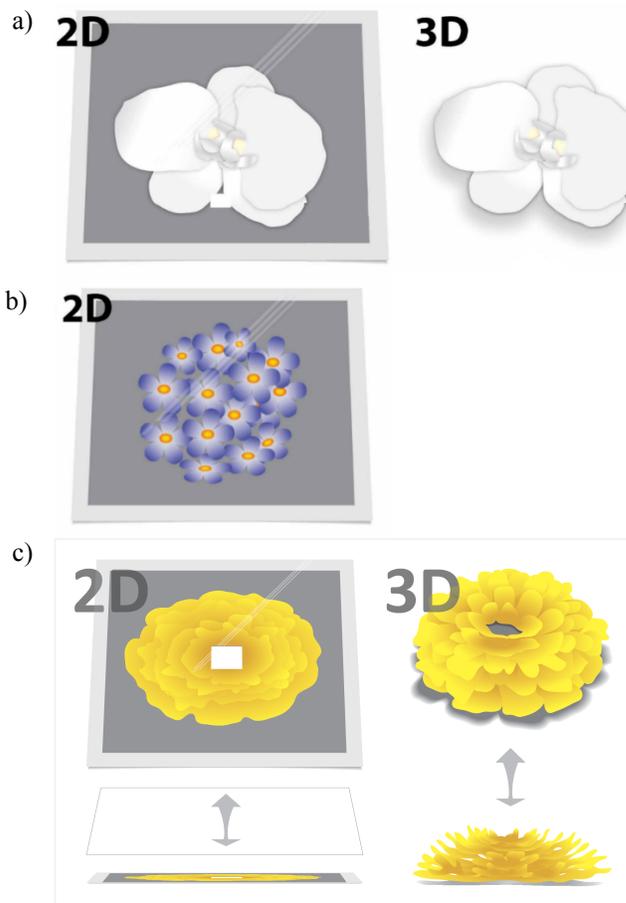
In the absence of learning transfers onto novel objects, previous research showed that subjects may be using memory to sort various items. For instance, pigeons were found to successfully sort hundreds of shapes and photographic slides into random arbitrary categories and remember the stimuli when tested a year later (Vaughan & Greene, 1984). Other birds, such as nutcrackers, are also able to remember hundreds of locations for food caching purposes (Kamil & Balda, 1985). However, a category concept of certain objects also implies that the animal should be able to classify new instances of that object that it has not seen before. Learning transfer tests allow for further investigation as to whether subjects are sorting stimuli beyond rote memorization.

Method

One hundred and twenty bumblebees (*Bombus impatiens*) from eight colonies were used and monitored for 15 days of individual training with 15 bees tested per colony. Materials used are the same as in Experiment 1 with new stimuli added for testing. Flowers used for testing include a white flower (Object Z), a yellow flower different from the Object X (Object X2), and their corresponding photographs (Photo Z, and Photo X2) and an additional photograph of a cluster of blue flowers (Photo Y2) (Figure 6).

Figure 6

Novel Photos and Objects in Experiment 2



Note. Photo and Object Z (a), Photo Y2 (b), and Object and Photo X2 (c). Part (c) reprinted from Xu and Plowright (2016). 3D object X2 reproduced from Thompson and Plowright (2014) with kind permission from Springer Nature.

Bees underwent training to discriminate between the two photos (Photo X and Photo Y) from the two objects (Object X and Object Y). For two colonies, photographs were rewarding (+) and objects were unrewarding (-), and for two other colonies, it was the reverse (Table 2). The same four stimuli were also grouped differently, where bees underwent training to discriminate between instances of X (Object X and Photo X) vs instances of Y (Object Y and Photo Y). For two colonies, Xs were rewarding (+) and Ys were unrewarding (-), and for two other colonies, it was the reverse (Table 2).

Table 2

Design for Experiment 2

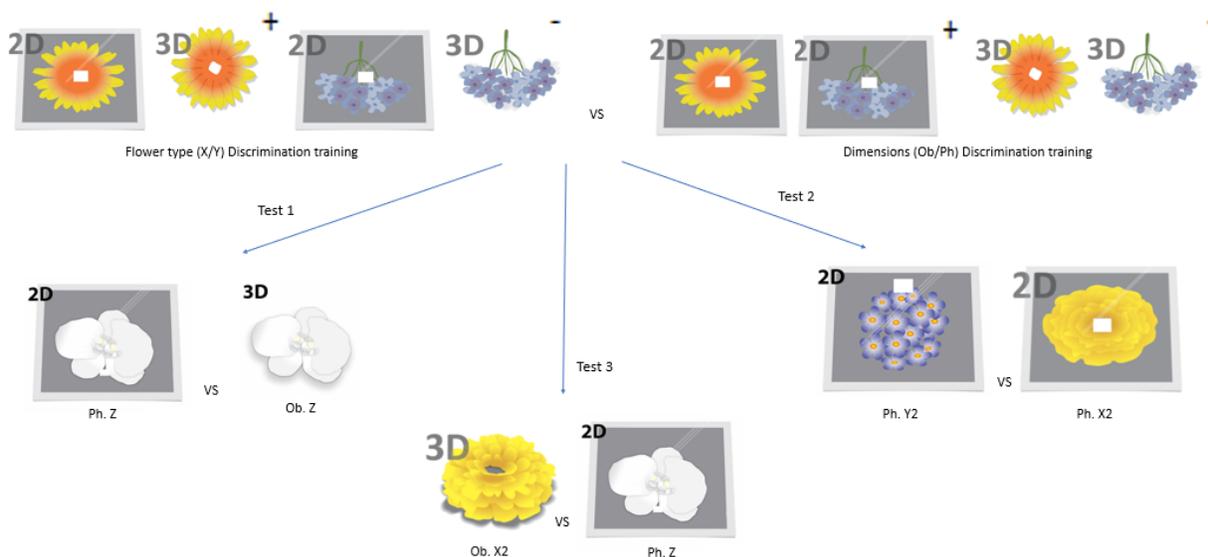
Phase	Colony 1 + 2 (n = 30)	Colony 3 + 4 (n = 30)	Colony 5 + 6 (n = 30)	Colony 7 + 8 (n = 30)
Training	Photos+ / Objects-	X+ / Y-	Objects+ / Photos-	Y+ / X-
Test	1. Dimensionality test: Object Z vs Photo Z 2. Flower type test: Photo X2 vs Photo Y2 3. Similarity judgment test: Object X2 vs Photo Z		1. Dimensionality test: Object Z vs Photo Z 2. Flower type test: Photo X2 vs Photo Y2 3. Similarity judgment test: Photo Y2 vs Object Z	

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

The trained bees were assigned to one of three discrimination tests on unrewarding stimuli (Figure 7) between: 1) a novel photo and object (Object Z and Photo Z), 2) two novel photos resembling the training stimuli (Photo X2 and Photo Y2), and 3) two novel stimuli, with one stimulus perceptually resembling the rewarded training stimuli (Photo Z and Object X2, or Object Z and Photo Y2, depending on the rewarded stimulus during training). A total of 10 bees were used for each test, with five bees from two different colonies.

Figure 7

Example of Experiment 2 Design



Note. This condition shows a comparison of the Ph+/Ob- to X+/Y- group. Permissions: See Figures 4 and 6.

The results from tests 1 and 2 would determine whether bees are able to extrapolate specific features of flowers and generalize them. We hypothesize that bees trained to discriminate between objects and

photos would be able to treat Object Z and Photo Z differently whereas bees trained to discriminate between X and Y would not. The same hypothesis holds true for test 2, where bees trained on X and Y would show a preference for either X2 or Y2, but those trained on objects and photos would not.

The third test examines the influence of perceptual similarity on categorization and how similarity judgment can change with experience. As Experiment 1 demonstrates, the similarities of flowers between groups may influence the bees' abilities to categorize within a group. Here, bees trained to discriminate between objects and photos of those objects are compared to those that are trained to discriminate between X and Y flowers on tests that examine their abilities to categorize new stimuli that were not used during training. Bees trained with objects as rewarding were compared to bees trained with Y as rewarding, and both groups were tested on choices between a novel object (Object Z) or a novel Y photo (Photo Y2). Similarly, bees trained with photos as rewarding were compared to bees trained with X as rewarding, and both groups were tested on choices between a novel photo (Photo Z) or a novel X object (Object X2). Bees that were able to ignore the similarity between X and Y groups would choose the novel flower of the correct dimension while those who could not would fail the test. Bees trained to discriminate between X and Y would need only to generalize based on floral features.

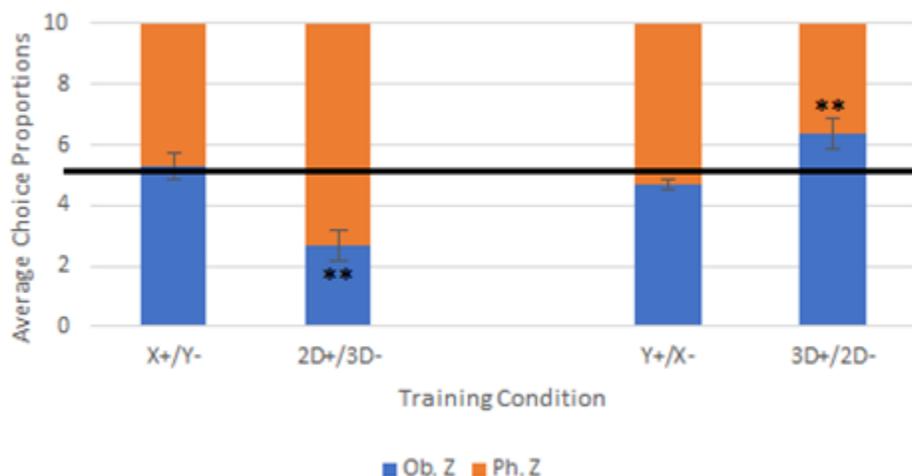
Results

Test 1 Results between Object and Photo Z

As shown in Figure 8, bees trained with objects as rewarding had a significant preference for Object Z over Photo Z ($G_P = 7.95$, $df = 1$, $p = .004$), with no significant individual differences ($G_H = 11.07$, $df = 9$, $p = .27$). Bees trained with rewarding photos had a significant preference for Photo Z over Object Z ($G_P = 21.98$, $df = 1$, $p < .001$), with no significant individual differences ($G_H = 15.32$, $df = 9$, $p = .08$). However, bees trained with either X rewarding or Y rewarding both showed no significant preferences for either Object Z or Photo Z ($G_P = .36$, $df = 1$, $p = .55$; for both groups) with no significant individual differences for either a rewarding X ($G_H = 6.59$, $df = 9$, $p = .68$) or Y ($G_H = 2.49$, $df = 9$, $p = .98$).

Figure 8

Test 1 (Object Z vs Photo Z) Results from Experiment 2



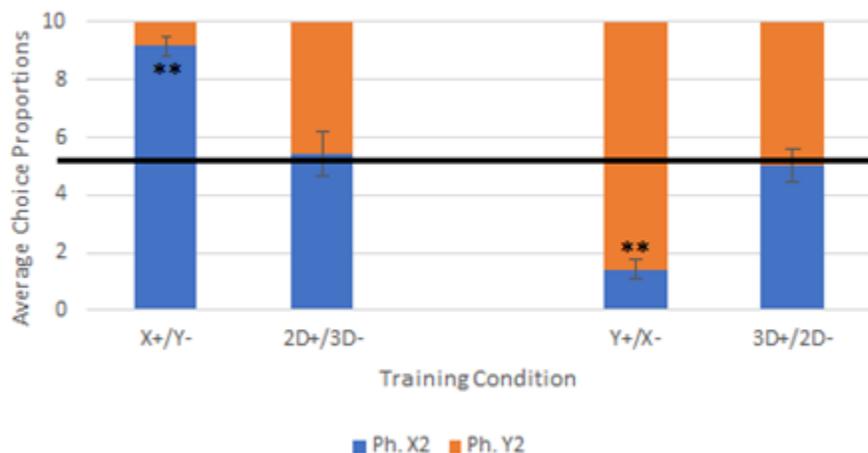
Note. Mean frequencies, with standard error bars, of choices between photo and object Z following discrimination training on either X and Y or Objects and Photos in Experiment 2. The horizontal line indicates chance. ** $p < .001$.

Test 2 Results between Photo X2 and Photo Y2

Bees trained with a rewarding Object and Photo X had a significant preference for Photo X2 over Photo Y2 ($G_P = 82.88$, $df = 1$, $p < .001$), with no significant individual differences ($G_H = 14.01$, $df = 9$, $p = .12$). Similarly, bees trained with a rewarding Object and Photo Y had a significant preference for Photo Y2 over Photo X2 ($G_P = 57.64$, $df = 1$, $p < .001$), with no significant individual differences ($G_H = 9.25$, $df = 9$, $p = .41$). Bees had no significant preferences for either Photo X2 or Photo Y2 when they were trained to prefer either objects ($G_P = .00$, $df = 1$, $p = 1.00$) or photos ($G_P = .64$, $df = 1$, $p = .42$), with no significant individual differences for the group trained with rewarding objects ($G_H = 4.90$, $df = 9$, $p = .84$). However, there was a significant heterogeneity in the group trained on rewarded photos ($G_H = 18.54$, $df = 9$, $p = .03$), where half the bees were at chance level while the other half preferred either X or Y. Upon closer inspection, significant individual differences were found at the colony level in that condition for one of the colonies ($G_H = 12.95$, $df = 4$, $p = .01$), but not the other ($G_H = 3.00$, $df = 4$, $p = .55$), indicating possible innate X and Y preferences in individual bees in the absence of experience (Figure 9). However, this is not the case for photos or objects as they appear to be equally appealing to bees trained on either X or Y in the previous test.

Figure 9

Test 2 (Photo X2 vs Photo Y2) Results from Experiment 2



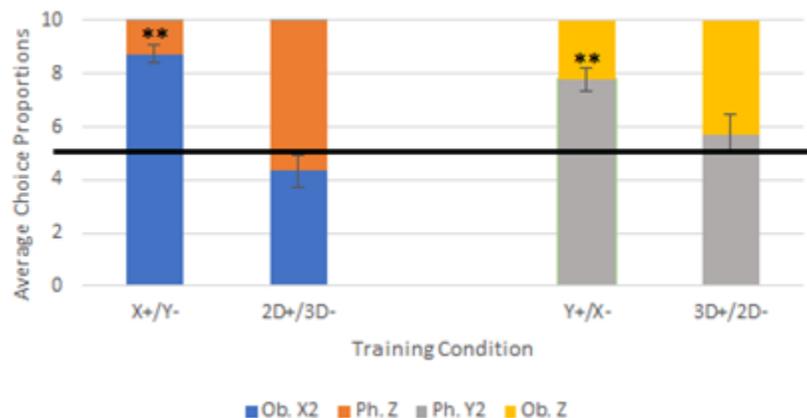
Note. Mean frequencies, with standard error bars, of choices between X2 and Y2 after discrimination training with X vs Y or Photos vs Objects in Experiment 2. The horizontal line indicates chance. ** $p < .001$.

Test 3 Results between Object X2 and Photo Z or Photo Y2 and Object Z

As shown in Figure 10, bees trained with either Photos (+) or Xs (+) were tested on Object X2 and Photo Z in Test 3. Both testing stimuli were new and had never been used in training. Bees trained to prefer X over Y had a significant preference for Object X2 over Photo Z ($G_P = 61.35$, $df = 1$, $p < .001$) with no significant individual differences ($G_H = 12.04$, $df = 9$, $p = .21$). Bees trained to prefer photos over objects had no such preference ($G_P = 1.97$, $df = 1$, $p = .16$) with no significant individual differences ($G_H = 15.80$, $df = 9$, $p = .07$).

Figure 10

Test 3 (Object X2 vs Photo Z; Photo Y2 vs Object Z) Results from Experiment 2



Note. Mean frequencies, with standard error bars, of choices between Object X2 and Photo Z for the first two groups in the figure, or Photo Y2 and Object Z for the last two groups, after training with X vs Y or Photos vs Objects in Experiment 2. X2 and Y2 are depicted on the lower bars, while Object and Photo Z are depicted above. The horizontal line indicates chance. ** $p < .001$.

Bees trained with either Objects (+) or Ys (+) were tested on Photo Y2 and Object Z in Test 3. As before, testing stimuli were new and had never been encountered by the bees during training. Bees trained to prefer Y over X had a significant preference for Photo Y2 over Object Z ($G_P = 33.25$, $df = 1$, $p < .001$), with no significant individual differences ($G_H = 6.28$, $df = 9$, $p = .71$). Bees trained to prefer objects over photos also had no such preference ($G_P = 1.97$, $df = 1$, $p = .16$), with no significant individual differences ($G_H = 1.97$, $df = 9$, $p = .99$).

Discussion

When bees are trained to discriminate between flower types, they always choose the flowers that most resemble the training flower types, ignoring differences in dimensionality (2D and 3D). Bees trained to discriminate based on dimensionality were able to generalize to other flowers of the correct dimensionality, while also showing no overall preference for flower types.

Although they were able to generalize to the corresponding object or photo Z during tests with novel stimuli, bees trained on dimensions (2D vs 3D) were not able to do the same when one of the choices also had a higher resemblance to the training stimuli (Test 3). At the same time, while bees did not spontaneously choose the option of the correct dimension during Test 3, they also did not spontaneously choose the option with the highest perceptual similarity. Bees instead viewed both options as equally appealing. Bees trained on flower type, however, did not, and had strong preferences for the correct flower type presented. Previous experience on the flowers appears to dictate the level of similarity perceived by the foragers. Novel flowers that would not have appeared rewarding now did because of experience on different rewarding flowers.

Bees trained to discriminate objects and photos did not significantly prefer Object or Photo Z in the presence of X2 or Y2; however, they did significantly choose the correct novel object or photo Z with no other similarities present. Even though they cannot completely ignore the salient floral features, they also do not immediately choose the most salient similarity. Categories, therefore, are flexible, and learning on new flowers are generalized not only based on their physical features, but also on a forager's previous experience and the alternatives available.

These results point to the real possibility of mediated generalization in bumblebees, by making use of perceptual associations, though more research is required on other sets of stimuli. As noted by Sturdy et al. (2017), functional and perceptual categorization are not mutually exclusive. Bumblebees can extrapolate and generalize specific floral details to novel flowers, but this ability becomes unreliable if there are more salient perceptual similarities present as a distractor. However, bees do not spontaneously prefer flowers based only on perceptual similarity either, and in cases where both group membership and perceptual similarities interfere, bees will visit both possibilities with no overall preference for one over the other. Bees appear to categorize based on both the reward values of the category members and the similarities of the flowers available in the area. Future research using the Delayed Matching to Sample Task might further explore these possibilities. In addition, methods comparable to ours could be built up to include a wider selection of stimuli, as in nature, which may further incentivize category formation. Overall, bees rely on perceptual similarity to form categories, but the similarity judgments change based on previous experience and the functional value of flowers to foragers.

General Discussion

Objects in a bee's environment can serve different functions to the bee, such as floral resources or landmarks. Additionally, food resources serve different functions, depending on the amount of pollen or nectar it gives, where pollen serves as a source of protein for feeding larvae while nectar serves as a source of carbohydrates for energy. While individual bees may not specialize for either pollen or nectar foraging (Russell et al., 2017), they are still able to differentially forage for pollen or nectar depending on the needs of the colony (Fewell & Winston, 1992; Plowright et al., 1993; 1999). As such, it stands to reason that the bees' foraging techniques reflect an ability to generalize between the functions of the objects in their environment.

In Experiment 1, bees preferred the photograph or object most perceptually similar to the last rewarding stimulus experienced, regardless of reward associations. Bees chose the counterpart object or picture of the rewarding flower in Phase II regardless of the associations learned in Phase I. As with previous research (Xu & Plowright, 2017), learning from one flower can be transferred to another without the forager having the same experience on the second flower. However, while bees can successfully discriminate between two similar flowers, they were unable to generalize their learning between flowers sharing little perceptual similarity, and categorized the flowers based upon perceptual similarity. Generalizations between perceptually similar flowers are not significantly affected by the bee's experience on each individual flower and perceptual similarities between the groups might cause interference with the ability to generalize between flowers sharing reward associations.

To follow up, Experiment 2 showed that bees were able to extrapolate specific details of flowers and categorize using those features. However, perceptual similarities between groups interfered with the bees' generalizations. Bees chose both the flowers with relevant features similar to the rewarding groups and the flowers that resembled the learned rewarding flowers in other similar though functionally irrelevant characteristics. For instance, bees were able to find the 3D flower when given novel 3D and 2D stimuli, but not when given novel 3D and novel Y stimuli, in which case, bees see both the 3D and the Y flowers as equally attractive. The floral categories formed depend on the floral features as well as the resource selections available.

In line with previous research, where bees were able to discriminate between fine details in stimuli (Dyer & Chittka, 2004), bees here were able to differentiate similar flowers when trained to do so. Additionally, context specific foraging has been previously demonstrated using serial reversals (Strang & Sherry, 2014), where bees transferred learning between perceptually different stimuli through multiple reversal training. In previous research, bees have been trained successfully to avoid perceptually similar stimuli in favor of other less salient cues such as the number of objects (e.g., Gross et al., 2009; Howard et al., 2018). Bees have also demonstrated the ability to reject perceptually similar stimuli in relational categorization tasks (e.g., Howard et al., 2017; 2018), but have yet to do so when trained on a perceptual categorization task with no relational element, although this ability has been found in other animal studies,

such as dolphins (von Fersen & Delius, 2000). Bees still categorized based on perceptual similarity despite their training experience. Whereas bees are able to make fine discriminations, it appears to be context specific and training may, therefore, not be applicable in other situations. The addition of similar features between groups may limit this ability. Flower categorization relies upon innate preferences for similarity and is not solely based upon learning and experience.

Selection in mimicry has favored forager confusion from the original rewarding flower. Inexperienced pollinators were more likely to be deceived by mimics than those with foraging experience (Garcia et al., 2020). However, the photographs and objects used here are distinguishable to the bees even without prior experience (Xu & Plowright, 2016). These results, therefore, cannot be attributed to an inability to discriminate between the stimuli, even in the absence of the counterpart. Instead, the learning transfers demonstrated might indicate an inability to generalize to perceptually different stimuli in the presence of similar stimuli rather than a lack of discrimination between the photographs and objects. Objects in nature that appear similar usually share consequences. Even in cases when the opposite is true, where flowers that appear different give the same rewards, perceptual similarities still play a part in flower selections. For instance, tomato and blueberry flowers may be both rewarding to a bee, but each flower still shares similarities to other conspecifics. Groupings of floral stimuli can occur despite contradictory experience. Additionally, because of natural variability, it is not uncommon for pollinators to visit flowers that would normally be rewarding and receive no reward. Given that competition between foragers can create situations where resources have already been drained, effective foraging may not always favor the avoidance of non-rewarding flowers.

Bees that have learned to differentiate between two flowers in one context can treat them similarly in another context. However, the results do not suggest that bees are incapable of mediated generalization, but rather, bees require some degree of perceptual similarity to make judgments regarding categories. While category boundaries cannot be determined using the behavioral data available, the evidence presented here is consistent with generalization principles that underlie categorization mechanisms.

Whereas previous research gives evidence of perceptual categorization in bees, in this instance, similarity judgments change based on previous experience and the function of the flower. Mediated generalization is a crucial ability for higher levels of category formation, such as the formation of functional categories, where group membership relies on more than perceptual characteristics (Shettleworth, 2010). Despite being unable to completely disregard perceptual similarities during foraging, bees were able to change responding to certain perceptual features of floral stimuli as a result of different reward consequences. Little investigation has been done in functional categorization in bumblebees, but evidence has been found in other species, where subjects were capable of categorizing items with little physical resemblance to one another (e.g., Bovet & Vauclair, 1998; Feuerbacher & Rosales-Ruiz, 2017; Savage-Rumbaugh et al., 1980; von Fersen & Delius, 2000). Moreover, honeybees have been successful at relational categorization (e.g., Avarguès-Weber, Dyer, & Giurfa, 2011; Avarguès-Weber & Giurfa, 2013; Brown & Sayde, 2013; Giurfa et al., 2001), suggesting they are capable of more abstract forms of categorizing. The nature of representation of visual scenes, how it differs across species and how it is modulated by experience are currently active areas of investigation in comparative cognition (Avarguès-Weber et al., 2020).

Our conclusions are in line with the current view that brain size may not always be a reliable indicator of behavioral repertoires or cognitive abilities (Chittka & Niven, 2009). Instead, categorization may be particularly adaptive for species with miniature brains and that the nature of representation is likely to be economical (Srinivasan, 2006), so as to reduce the number of features memorized by the forager. The results also show that bees are unable to ignore perceptual features completely during foraging. As perceptual categorization appears to be common across many species, limitations within their categorization abilities may give further insight into the degree of learned and innate mechanisms involved in category formation. Considerations of the foraging problems that bees encounter in nature, as delineated here, suggest that functional categorization and the neural and cognitive mechanisms that underpin it are promising avenues for further investigation.

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