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Training Honey Bees (*Apis mellifera*) to Push a Cap: Shaping, Observational Learning, and Memory

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The cap pushing response (CPR) is a free-flying technique where honey bees are trained to fly to a target where they push a cap to reveal a hidden food source. In this paper, we report the results of three studies. First, we provide information on three techniques used to shape the CPR. Second, we provide preliminary data suggesting that honey bees can learn the CPR through observing a previously shaped bee. Finally, we provide preliminary data on the ability of a honey bee to recall the CPR response. In addition to the three studies, we also continue to advocate for the use of Observation Orientated Modeling (OOM) for comparative investigations.

Keywords: cap pushing response, honey bee, learning, observations

The cap pushing response (CPR) is a technique in which honey bees (*Apis mellifera*) are trained to return to a target where they push a cap to reveal a hidden food source (Abramson, et al., 2016). The CPR has been used in a series of experiments on discrimination, punishment, and toxicology (Abramson et al., 2016; Chicas-Mosier et al., 2019; Rodriguez et al., 2023). Our previous research with the CPR suggests that this new technique can open the door to a host of complex free-flying problems as the CPR is readily integrated into the traditional odor, color, and/or position experiments common with honey bees (Abramson, 1990).

The purpose of this study is four-fold. First, we wanted to provide data on how to shape the CPR. One aspect of the CPR that may hinder wide acceptance is that some researchers may find the shaping process difficult and therefore quit trying to shape the bee to push the cap. Subsequently, the researcher may believe that the technique is difficult to use or simply ineffective. To assist researchers, we provide those interested in using the technique with three methods of shaping the CPR.

Second, in addition to providing information on how to shape the CPR, we also provide data on the ability of honey bees to emit the CPR by utilizing observing learning. This is the first study we know of where a honey bee learned by observation. Previous research suggests that bumblebees can learn by observation, and we had interest in knowing whether observational learning is also present in honey bees (Avarguès-Weber & Chittka, 2014).

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Third, we wanted to provide preliminary observations on the ability of honey bees to recall the CPR. We do not provide a formal study on memory of the CPR. Rather, we wanted to know whether honey bees will return to the experimental situation after 12-, 24-, and 48-hr post-training and push the cap. For researchers interested in studying bees' memory of the CPR this study provides useful preliminary data.

Fourth, we have discussed the importance of Observation Orientated Modeling (OOM) for comparative psychology in previous publications (Abramson, 2023; Craig et al., 2012, 2014; Dinges et al., 2013; Grice, 2011; Rodriguez et al., 2023) and here we supply additional data on its usefulness. We believe that OOM is an excellent statistical method for comparative psychological investigations. Accordingly, our approach is to compare OOM with traditional statistics using Statistical Package for the Social Sciences (SPSS Version 26, IBM Corporation, Chicago, IL).

General Methods

This research was primarily performed at the Malemi Organic Hotel located in Skala Kallonis, Lesvos, Greece (longitude 39.208896, latitude 26.204095). All three studies follow the same general protocols. Forager honey bees from three colonies (foragers are approximately 20+ days of age) were trained to visit a communal feeder containing 8-10% sucrose solution by weight. When an individual bee landed on the feeder it was picked-up in a small matchbox and brought over to the experimental table. The table was located approximately 4 m from the colonies.

The bee was slowly removed from the matchbox and transferred onto a gray target. The target was a petri dish (59 mm diameter) painted flat gray. The center of the target contained a well that had a diameter of 10 mm in which a 100 mL drop of 50% sucrose solution (by weight) was placed. While the bee was drinking, it was marked with one of several colors of Testors acrylic paint. If the bee did not return, as it often failed to, it could be found on the communal feeder where it was again captured in the matchbox and brought over to the gray target containing 50% solution. This procedure continued with the same bee until it returned twice on its own accord. For detailed instructions on establishing an artificial feeder and training the bee to shuttle from the hive to the laboratory area, see Abramson (1990). On its third consecutive return visit, the bee was shaped to push the cap.

When the bee pushed the cap on its own to reveal the hidden food source for two consecutive visits, the target was then changed on the third consecutive visit. Rather than the gray training target, the target now was a 3D printed white disk (88 mm diameter). To ensure that the bees were pushing the cap without the benefit of using pheromones, we used the standard protocol for cleaning targets (Scheiner et al., 2013). During the period in which the bee was returning to the hive, the targets were washed and dried thoroughly as a control for pheromones. Moreover, consistent with Couvillon and Bitterman (1980) the cleaned target(s) were selected from a common pool of targets.

Study 1: Three Methods of Shaping the Cap Pushing Response in Honey Bees

The most time-consuming part of any CPR experiment is training the bee to push the cap. For researchers without CPR experience, training a bee to push the cap can be frustrating and can lead to abandoning the procedure. Here, we present three different methods of teaching a bee the CPR. The three methods are: 1) resistance training, 2) using a cap containing slits, and 3) a "self-shaping" technique.

1) Resistance training: In the first method, resistance training was used to shape the CPR. When the honey bee started to feed from the well, the cap was lightly pushed against the bee (weight = 0.47 g, 12 mm diameter, 10 mm height). Eventually, the bee would push back. This "back and forth" could continue for several minutes over several visits. For this method to proceed smoothly, the shaper must closely observe the behavior of the bee around the cap. Once the bee learned to push the cap and find the location of the food well, the cap was placed entirely over the food well. When the bee pushed the cap that was fully covering the food well on its own, it was defined as "trained." A short video clip illustrates an example of the resistance training method (Link to video: https://youtu.be/rLKsekZjhuA).

2) Slotted target: In the second method, a bee was first exposed to a cap that contained slits (weight = 0.31 g, 12 mm diameter, 10 mm height, width between slits = 1 mm). This cap allowed the bee to see the well and extend its proboscis through a slit to reach the sucrose solution. The bee would eventually push the cap to get further into the well on subsequent visits. After two or three successive visits, the training cap containing slits was replaced with the solid cap. The bee learned to generalize between the standard solid cap and the cap, which had slits to get to the food well. The resistance and slotted target methods took about 20 min to train and self-shaping took between 10-15 min.

3) Self-Shaping: In a third method we called “self-shaping,” the bee trains itself to push the cap. After pre-training the bee to visit the target and consume sucrose from the food well, a small bead (weight = 0.25 g, diameter = 5 mm) was placed in the well. The bee gained access to the well by using its proboscis to lift the bead. After a few trials, the bead is replaced with the cap. Through generalization, the bee readily pushes the cap to reveal the hidden food source. Figure 1 presents images illustrating the three methods.

Figure 1
Three Methods of Shaping the Cap Pushing Response

Resistance Method

The honey bee is trained to visit the well.

The cap is lightly pushed against the bee.

Introduction of the cap partially covering the well.

CPR training is completed

Slotted Method

The open slit target is introduced after the bee visits the well.

The target will eventually be pushed by the honey bee.

The open slit target is switched with the cap.

CPR training is completed

Self-Shaping Method

The bead is placed on the well containing sucrose water

The bee lifts the bead with its proboscis.

Auto Shaping is complete.

Results and Discussion

Although all three methods can be utilized, comparisons of the methods revealed a difference between the time and efficiency of acquiring the CPR. The resistance and slotted target methods showed no difference in time and efficiency with both completed in approximately 20 min. In the resistance training method, the cap is placed on the platform and is slowly moved to cover the entirety of the well. This method takes time for the bees to learn how to push the cap and the location of the well, approximately 30 min to complete.

In the slotted target method, the bee is able to reach the sucrose filled well through the slots. This behavior naturally produces a pushing behavior when the bee tries to reach the well with its proboscis. Having the bee push the cap fully and not just partially to reach its proboscis through the slit is the challenge with this method.

Overall, the self-shaping method was the most efficient. In this method, there was no manipulation involved when training the bee. As a result, the bee was able to accomplish the CPR with no previous experience with the cap. In comparison, the bee in the slotted target method pushed the cap faster than in the resistance training method, but it required an additional training procedure. Therefore, we recommend researchers adopt either resistance training or self-shaping (see Figure 1) to shape the CPR. For students, the resistance training method has the virtue of teaching students the importance of observation, patience, and the consistent use of reinforcement.

Shaping the CPR can be performed the day before an experiment is run. This saves time and allows for a sample of bees to already be trained thereby improving training efficiency. Training the CPR a day before the experiment provides “de facto” evidence that the memory of the CPR is at least 12-24 hr. The issue here is that the experimenter may be interrupted with “intruder bees” as they will visit the experimental table where they have been trained and look for the cap to push. In such situations, capture any intruders, we used a small wooden matchbox (Abramson, 1990), and saved them until they were needed.

Study 2: Observation Learning of the Cap Pushing Response in Honey Bees

We now turn our attention to whether a honey bee can learn the CPR by watching another bee complete the task. Observational learning has been found in invertebrates such as bumble bees (Loukola et al., 2017), cockroaches (Avarguès-Weber & Chittka, 2014; Lihoreau & Rivault, 2011), and octopuses (Fiorito & Scotto, 1992). The rationale behind our study is to determine if honey bees can learn the CPR from watching a previously trained honey bee.

We trained several bees to land on a 3D printed target where they consumed a sucrose solution but were never trained to push the cap. We wanted to take advantage of the fact that several bees could approach the platform simultaneously. Thus, we created a natural situation where the trained bee would return to push the cap while other bees would be near the platform.

In the course of studying observational learning, we tried several procedures, such as building various housing mechanisms to force the untrained bee to learn the trained bee’s CPR behavior. In another method, we attached a deceased bee to a stick and used the stick to mimic a trained bee. Unfortunately, none of these procedures worked. We then tried a combination of two methods where a deceased bee was attached to the end of a stick along with a free-flying bee previously trained to push the cap. However, again none of the procedures worked. These attempts finally led us to the idea of allowing the bees to fly around the trained bees rather than capturing them. Bees that were previously trained to push the cap were then observed by those that did not and eventually, the naïve bees would, much to our astonishment, not only push the cap but drink from the well even though they have not been trained to do either. This current study is the first study we are aware of that demonstrates that a honey bee can learn through observation.

Alem et al. (2016) found that bumble bees can learn a string-pulling task to receive food reinforcement, and that this behavior can be diffused throughout a colony’s workers though observation. However, while the authors suggest this is a non-natural object manipulation task, the core string-pulling behavior is within the bee’s natural nest material gathering repertoire (Cumber, 1949). This is not surprising and can be accounted for with non-cognitive principles (Abramson, 2013).

Rather than postulate some hypothetical, almost magical cognitive process to account for observational learning in honey bees, we prefer a behaviorist account (Abramson, 2013). It is important to note that honey bees and bumblebees have a history manipulating objects. For instance, bees display a specific sequence of behaviors when collecting nesting materials (Cumber, 1949; Plath, 1934). The worker bees, primarily responsible for gathering nesting materials, search for suitable materials in their environment. Upon finding a suitable material, they manipulate it with their legs and mandibles, shaping and compressing it to form a transportable bundle (Cumber, 1949). The worker then carries the bundle back to the nest, often using their legs and mouthparts to hold it in place during flight (Plath, 1934). Their ability to manipulate objects is already in the bee’s repertoire of behavior. It would be foolish to deny that such behavior would not generalize to pushing a cap.

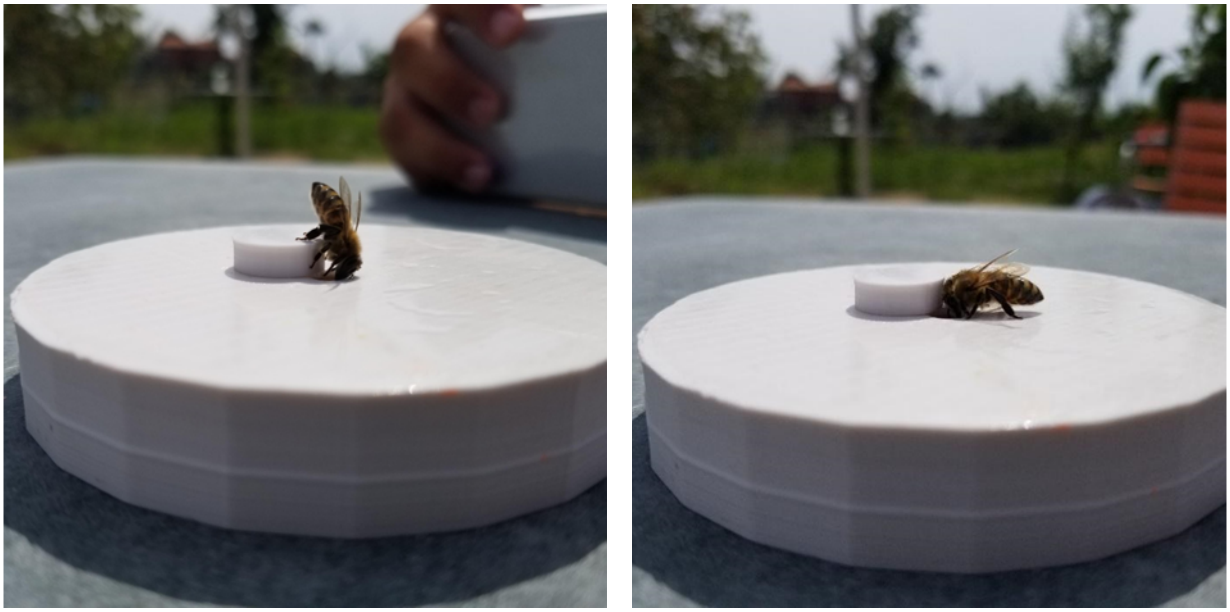
Moreover, in addition to already possessing the necessary manipulative behavior based on previous experience, honey bees are known to follow successful foragers to land on flowers perhaps through a process of second-order conditioning. Therefore, the behaviors necessary to push the cap—following foragers to a target, and manipulating objects—are already in the behavioral repertoire of honey bees.

Such an account can readily explain the observational learning of bumble bees. For example, a bumble bee can acquire flower color preference by observing conspecifics through a screen. Bees that have previously associated conspecifics with food match their color preferences. Additionally, bumblebees that associate conspecifics with unpleasant tastes avoid flower colors where other bees have been observed (Dawson et al., 2013). Bumble bee observers then learned to visit the same type of artificial flowers as model bees. However, only bees that had previous experience associating another bee with food learned this preference through observation (Avargues-Weber & Chittka, 2014).

In our experiment, sixteen experimental (i.e., observers) bees pushed the cap by watching a bee who had already been taught to do so (see Figure 2). To determine what we observed was indeed based on observation we employed 16 control bees. Unlike the observer bees, the control bees were pre-trained to consume sucrose from the food well but were not trained to push the cap nor had the opportunity to watch a previously trained bee push the cap. Control bees were also given a 30-min time limit to push the cap on their own accord. If a bee did not emit the CPR within 30-min it was captured and no longer used in the experiment; if the control bee did push the cap, it was recorded as doing so.

The rationale behind the selection of the 30-min limit was that in extinction experiments with honey bees, where a sucrose reward is now replaced with water, the bees typically receive a 20-min time limit. Honey bees will stop landing on such a target in about 10-min. As the 20-min period progresses bees return only infrequently, if at all. We wanted to give the control bees every opportunity to push the cap on their own accord, so we increased the standard time by an additional 10-min. Data for this study is available upon request.

Figure 2
Example of a Bee Learning the Cap Pushing Response Through Observation



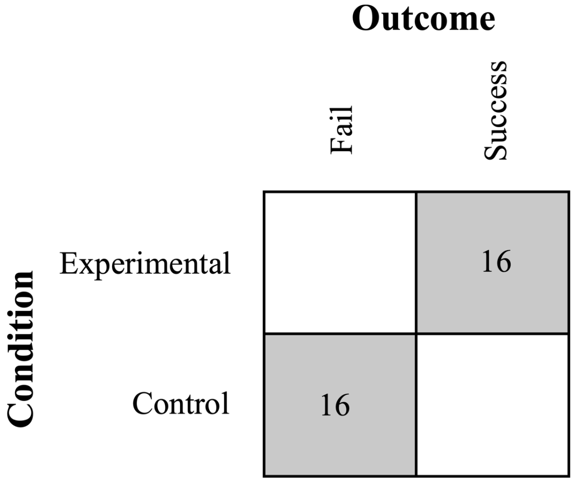
Note. Bee #1 is a CPR-trained bee, and Bee #2 is a bee without any previous CPR training.

Results and Discussion

The data for all 32 bees in this study were analyzed using the *Crossed-Orderings Pattern Analysis* within OOM (Grice, 2011) according to an *a priori* pattern. The expected *a priori* pattern of behaviors was defined such that bees in the observational learning condition were expected to succeed in learning the CPR behavior, whereas bees in the control condition (not observing) were expected to fail in learning the CPR behavior (see Figure 3). Results revealed that all 32 bees across groups (16 control and 16 observational) fit the expected pattern, PCC = 100%, *c-value* < .001. Moreover, the accompanying randomization test revealed these results to be extremely unlikely due to chance. As predicted, bees can learn the CPR through observation.

We also utilized Statistical Package for the Social Sciences (SPSS) to see if there was a difference between the aggregate and individual level statistics, shown through OOM. A Chi-Square Test of Independence was preformed to examine the performance of the observational and control groups. The results revealed that there was a significant association between the group observing a bee pushing the cap and the group that did not observe, $X^2(1) = 32$, $p < .001$. These results align with the OOM results, the experimental group learned the CPR though observation.

Figure 3
Observational Learning Patterns



Condition	Outcome: Fail	Outcome: Success
Experimental		16
Control	16	

Note. Expected pattern (grey cells) and observed numbers of bees in their corresponding conditions.

This study examined whether a honey bee can learn the CPR by watching another bee perform it. It is important to note that extraneous variables such as odor and sugar water must be meticulously controlled (Dawson, 2013; Leadbeater & Chittka, 2007; Norman, 2015). When refilling the hidden food source after each visit, we thoroughly cleaned both the cap that covered the hidden sucrose reward and the platform to remove any trace residue of the sucrose reward or pheromones. Critical to the success of observational learning, all bees on the platform were removed by bumping them with a stick so that the meticulous cleaning method could be followed without any interference. These steps were completed to ensure that learning was due to observation and not due to an odor signal left behind by a previous bee.

Study 3: Recall of the Cap Pushing Response in Honey Bees

One of the more interesting questions regarding the CPR is how long the bees can remember the response. The purpose of this study is to determine whether honey bees remember the CPR. As we can shape the CPR a day before the bee is actually needed, we know anecdotally that the memory of the CPR lasts at least 12- 24-hr.

Typically, after honey bees are used in experiments, they are sacrificed to keep the honey bee sample naïve. In this study, we did not do this. These bees were used from a previous cap-pushing experiment conducted the day before. Bees received 12 cap-pushing trials followed by a 10 min extinction session. To test honey bee recall, researchers set-up the experimental table at 12-, 24-, and 48-hr and waited 30-min to see how many bees would return. Prior to use, the targets and cap were washed and cleaned based on the standard methods used in the previous studies.

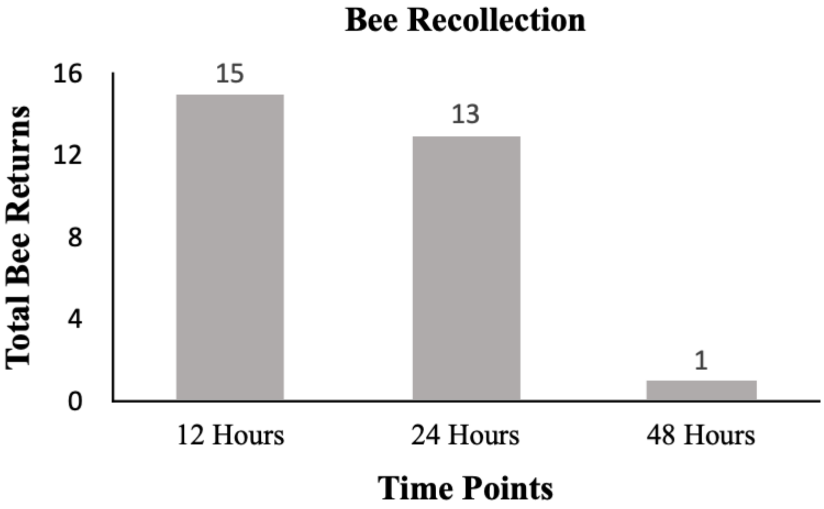
We identified individual bees using their colored markings. It is important to note, that our operational definition of memory was not simply returning to the table and landing on the target, but returning to the table, landing on the target and pushing the cap. We gathered data on memory over a two-week period in June and observed 29 bees.

Results and Discussion

Observations of the 29 bees revealed that one bee returned 48-hr later and pushed the cap, and 28 bees returned between 12 and 24-hr later and pushed the cap. In conclusion, the data suggests that at least one bee retained memory of the CPR for 48-hr. Figure 4 shows the total number of bees that came back at 12-, 24-, and 48-hr.

Figure 4

Bee Recollection Responses Across a 48-Hour Period



Note. These data represent the total number of bees that returned to the CPR training platform across three-time points (12-, 24-, & 48-hr)

General Discussion

In Study 1, we highlighted three different shaping methods that can be used to train honey bees to push a cap. All three methods were successful; however, the resistance training and self-shaping methods were more effective than the slotted target method. Shaping is the most time-consuming aspect of the CPR.

Study 2 showed for the first-time observational learning in honey bees. All 16 bees were able to emit the CPR after watching a previously trained bee do so. In contrast, none of the 16 control bees made the CPR even when given 30-min to do so. Especially interesting is that, unlike the control bees, none of the observer bees were previously trained to locate the food well yet after pushing the cap they went to the well. The behavior of going to the food well, even though they had not been trained to do so, may be partially explained by the fact that the distance between the cap and the food well is only 2 mm and the momentum generated by the effort to push the cap led the bee to the well.

We are not surprised that observational learning may be present in honey bees. As Leal and Powell (2012) notes in a study of problem solving in lizards, developing novel responses to unique problem solving situations is a characteristics of organisms with advanced social structures. The possibility of observational learning in honey bees must be independently replicated with some explanation for the effects provided. Until further data is available, we suggest efforts be directed towards a behaviorist rather than a cognitive explanation (Abramson, 2013; Skinner, 1965). It is well known that foraging honey bees have a history of manipulating parts of flowers to gather nectar and in some cases pollen (Gould & Towne, 1988; Thorp, 2000). Moreover, they have a history of foraging on flowers in the company of other honey bees. Such an environmental history of manipulating flowers and foraging with other honey bees may be a good starting point for a behaviorist interpretation. A behavioristic interpretation of observational learning for vertebrates is available (Deguchi, 1984; Masia & Chase, 1997; Skinner, 1965) and well worth considering before any cognitive explanation is accepted uncritically.

Readers may believe that the honey bee waggle dance may be an instance of observational learning. We discount this for two reasons. First, data is available (but seldom cited) that the waggle dance imparts odors of the flowers to be visited rather than imparting such complex information as distance in the waggle. Second, even if one still believes in the dance language, the honey bee must at some point be in direct physical contact with the dancer. As physical contact is required to receive data for the dance, this is not learning through observation (Wells & Wenner, 1973; Wenner & Wells, 1990). In our situation, the observer bee had no physical contact with the bee that was trained to push the cap.

Another experiment showed that a mechanical bee could perform the waggle dance and the follower bees would find the flower (Michelsen et al., 1992). However, it only worked if the odor was applied to the mechanical bee (Michelsen et al., 1992). Responding to an odor is not sufficient to account for our results. We used no odor and even if some uncontrolled odor is present, the bee must push the cap (i.e., make a manipulative response) to gain the reward.

Study 3 was conducted to explore how long bees can recall the CPR. Bees will all return 12-24 hr after training. The data of a single bee suggests that recall may last up to up 48-hr after training. As we have repeatedly stressed, the bee not only must find the table, land on the target, but also push the cap. The data we present in Study 3 is a useful starting point for any researcher interested in studying retention of a manipulative response in honey bees.

The studies described in this paper will be useful for anyone considering using the CPR technique. We provide guidance on how to shape the response, the length of time the CPR can be recalled, and whether observational learning is possible. All together, these findings help add to the CPR literature.

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