



Memory and the value of social information in foraging bumble bees

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Abstract

Not all information should be learned and remembered. The value of information is tied to the reliability and certainty of that information, which itself is determined by rates of environmental change, both within and across lifetimes. Theory of adaptive forgetting and remembering posits that memory should reflect the environment, with more valuable information remembered for longer amounts of time. Theory on biological preparedness predicts that rates of reliability through evolutionary time should influence what is learned and remembered. We use these ideas to predict that differential memory use will reflect the underlying value of the information being learned. We test this by comparing the learning and memory of social information versus floral information in foraging bumble bees. Bumble bees are extremely flexible in their use of both types of information and evidence suggests that social information is “special,” reflecting biological preparedness. Our experiment tests how bumble bees learn and remember social and floral information when their reliabilities, and thus value, differ. We find that bees learn both types of information at a similar speed. Bees show a decrement of memory of the trained associations in both treatments, but retain trained socially reliable information for longer, at both 4-hour and 8-hour retention intervals. Both training treatments influence whether bees match or avoid the locations of demonstrators, and this interacts with retention interval. Bees trained under reliable floral cues and unreliable social cues avoid conspecifics after 8-hr and 24-hr retention intervals. Bees thus learn about the reliability or unreliability of social cues and use this to modify their choices across time.

Keywords Social information · Memory · *Bombus* · Social learning · Foraging · Optimal memory

Introduction

Learning is a way in which animals can gain information and reduce their uncertainty about important aspects of their world. It is a fundamental mechanism for adjusting behavior to a changing environment. Behaviorally adjusting to a changing environment poses a general problem for animals, and decision-making when information is incomplete has been a topic of models and experiments for decades (e.g., Dall et al., 2005; Schmidt et al., 2010; Stephens & Krebs, 1986). The informational challenge for nectar foragers is an excellent one to consider when thinking about the benefits of acquiring and using information. Flowers are typically

an ephemeral resource, varying in combination and reward based on phenology and competition in the wild. Rewards can vary within a single flower, as flowers replenish their nectar rewards at different rates, and some flowers even alter the quality of their nectar rewards over time (e.g., Thomson et al., 1989; Willmer, 2011). This rapidly changing foraging world poses a series of challenges for foragers: what and when to sample resources, what information should be learned and then tracked, and how long this information should be remembered for, and which of these cognitive abilities should be subject to modification by evolution (e.g., Dunlap et al., 2019).

Foragers should be able to remember rewarding resources after they have been sampled and learned. However, it is neither advantageous nor often possible to remember everything indefinitely (e.g., Kraemer & Golding, 1997; Schooler & Hertwig, 2005; Storm, 2011). Models, both conceptual and mathematical, suggest that an organism’s memory should reflect their natural history, their environment, and be shaped by evolution (e.g., Anderson & Schooler,

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1991; Balda et al., 1996; McNamara & Houston, 1987). For instance, a well-studied aspect of comparative spatial memory finds general support for the prediction that birds that live in harsher environments and have a larger reliance on stored seed do show longer retention on memories about where they cache those seeds (e.g., Bednekoff et al., 1997; Dunlap et al., 2006; Pravosudov & Roth II., 2013; Sonnenberg et al., 2019). Across studies, information that is encountered or recalled frequently is more likely to be retained (e.g., Anderson & Schooler, 1991; Hardt et al., 2013; Kraemer & Golding, 1997). Memories can also be costly, both in terms of physiological, economic, and retrieval aspects (e.g., Dukas, 1999; Mery & Kawecki, 2005; Plaçais & Preat, 2013.), and this can also impact when animals should forget memories. The effects of interference, for instance, can interact with the energetic costs of acquiring information to influence memory (e.g., Burns et al., 2010; Laughlin & Mendl, 2004; Lewis, 1986). Finally, memory can be affected by the costs of both remembering and forgetting specific types of information. Memories related to potential predation, for instance, should be long lasting (e.g., Ferrari et al., 2010; Hirvonen et al., 1999).

Optimality models from behavioral ecology explicitly tie the value of remembering information to the value of that information itself. These models belong to a larger group of work that tie the rates of change in the environment to the value of learning and memory generally (reviewed in Dunlap et al., 2019). The value of information is tied to its ability to match the future state of the environment, or how well learned information now can be employed in the future (e.g., McNamara & Houston, 1987; Stephens, 1987, 1989). Thus, the value of information is connected to the degree to which it reduces uncertainty about some aspects of the environment for the animal (e.g., Behrens et al., 2007; Dall et al., 2005; Donaldson-Matasci et al., 2010). An environment with a lower rate of change is more predictive for a longer amount of time (Dunlap et al., 2009; Dunlap & Stephens, 2012; McNamara & Houston, 1987), while very fast rates of change may promote strategies other than learning, nullifying the need for memory (e.g., Dunlap & Stephens, 2016; Stephens, 1991). But in general, more recently gathered information is the best predictor of the current state of the environment because it is more likely to match it (McNamara & Houston, 1987). One specific type of change that influences learning and memory is reliability. Typically defined as a conditional probability with which a given cue accurately predicts the presence of a reward, reliability influences what animals should attend to and learn (e.g., Koops, 2004; McLinn & Stephens, 2006), and when learning should evolve (e.g., Dunlap & Stephens, 2009, 2016). Extending the logic of these models of learning to that of memory, Dunlap et al. (2006) showed that a decrease in the reliability of a given cue–reward pairing as well as the economic costs of

choices can decrease the value of information and thus the length of memories. In general, regardless of the specific memory mechanism involved, we can predict that more valuable information should last longer, and information that is costlier to acquire should also last longer. When change increases, memory should become shorter, and as conditions worsen, older memories should be lost.

Across evolutionary time, the reliability of the contingency between cue and reward influences when learning evolves and when prepared learning evolves (Dunlap & Stephens, 2009, 2014). In preparedness, the evolutionary history of how reliably stimuli, reinforcers, and outcomes are linked can result in some cues being learned much more quickly than others (e.g., Seligman, 1970, 1971). Unreliable contingencies, which are completely uninformative, may even result in contrapreparedness, where associations have evolved to be more difficult to learn. In this way, both the current rates of reliability plus the evolutionary history of these rates of reliability affect when learning should occur and what stimuli should be learned more easily. The process of learning is only one way that evolutionary preparedness can influence cognition, and many other aspects of stimuli and context can also intervene. Saliency, or roughly how “important” a stimulus is for a given context, has a long history in work on animal learning (e.g., Mackintosh, 1974; Rescorla & Wagner, 1972), and preparedness is one of many potential mechanisms through which some stimuli evolutionarily acquire special saliency. Once acquired, saliency is predicted to influence memory. For instance, predation events and predator cues are typically associated with long memories. A special case of preparedness, known as selective associations, describes an interaction between a stimulus and reinforcer that results in faster learning of a conditioned response with one conditioned stimulus, but an opposite effect with a different conditioned stimulus. Selective associations have been shown to be more resilient and remembered for longer amounts of time (e.g., LoLordo, 1979). This basic prediction should logically apply across reliably rewarding stimuli that are prepared by evolution to be learned in an enhanced way (Dunlap & Dexheimer, 2022). However, overall evidence for preparedness leading to longer lasting learning, whether it be longer memories or, more typically, greater resistance to extinction, is mixed (e.g., Åhs et al., 2018; Krause et al., 2003; McNally, 2016), and appears to depend on both the context and the experimental system. These mixed results may reflect the bias in the literature on preparedness within in the context of fear conditioning, and a lack of tests on memory length and forgetting, rather than extinction.

One well-studied class of salient information is that which can be learned about or from other animals. Cues from conspecifics have long been showed to be subject to selective associations and adaptive specializations, particularly in

the context of sexual selection, taste aversion, and predation (e.g., Domjan, 2015; Domjan et al., 2004; Krause & Domjan, 2017; Öhman & Mineka, 2001). The presence of conspecifics, for instance in a foraging context, can lead to social information use. Social information is information gained through observation of conspecifics or heterospecifics and learning from conspecifics has been proposed as a case of biological preparedness in learning (Leadbeater & Dawson, 2017). While terminology can vary, in general, social information is contrasted to personal information, which is gained solely through trial-and-error learning of an animal interacting directly with its environment (e.g., Danchin et al., 2004). The use of social information has several benefits, and many of these benefits are also tied to rates of change in the environment. For instance, the use of social information can decrease the cost of acquiring information via the need for sampling, and groups are better able to track more rapid changes than individuals (e.g., Giraldeau & Dubois, 2008; Krebs & Inman, 1992). In general, the value of social information increases with the uncertainty of the forager. This leads to predictions that foragers should rely on social information more when they are naïve or when a changing environment has left them with less accurate information about the state of the world (e.g., Kendal et al., 2004; Rieucau & Giraldeau, 2011). And then, although social information may be relatively cheap to acquire, it can also be less reliable than personal information gained through trial-and-error learning (Danchin et al., 2004; Kendal et al., 2004; Rieucau & Giraldeau, 2009, 2011). Many theoretical papers have weighed social information against personal information. However, direct comparisons are few, and none incorporate memory (Danchin et al., 2004; Kendal et al., 2004; Krebs & Inman, 1992).

In this paper, we focus on bumble bees as our model foragers. Bumble bees show robust and flexible learning about where to forage from conspecifics and using social information reduces the cost of acquiring information by allowing the observer to learn where food is without having to sample each flower. Bumble bees follow the foraging decisions of non-nest mates or even model bees (Chittka & Leadbeater, 2005; Worden & Papaj, 2005). Naïve foragers can show a preference for occupied flowers (e.g., Kawaguchi et al., 2006, 2007), and this preference is a flexible trait that can be positively reinforced through conditioning (Leadbeater & Chittka, 2007, 2009). Model bees appear to be a more salient cue than floral complexity in learning complex flowers (Leadbeater & Chittka, 2007), and associative learning about social cues is also present in the absence of observed preference for conspecific locations (e.g., Dawson et al., 2013). As predicted by the social learning literature broadly, bees do tend to rely on social information when they are naïve or uncertain. For instance, bumble bee foragers may use a “copy-when-uncertain” strategy for using social

information (Smolla et al., 2016). Social information can also interact with both personal information and innate bias, with social information used more by bees when personal information is lacking, when their experience is with flowers with a low-quality reward, and when social information directs them toward their innate bias (Jones, 2015). The use of social information is also quite flexible, likely reflecting that conspecifics are both informers of good resources as well as competitors for those resources (e.g., Baude et al., 2011; Plowright et al., 2013). Dunlap et al. (2016) directly tested for the value of social information, the presence of conspecifics, versus personal information, floral color, by factorially manipulating the reliabilities of each form of information. They found that bumble bees show a preference for social information over personal information about flowers when social information is more reliable or even as equally reliable as personal information. But is this value reflected in terms of memory length? In general, long-term memory for flowers is not well studied in bumble bees. But we have much evidence that features of the environment are reflected in at least short-term memory, and some evidence that this can predict longer term memory. Pull et al. (2021) show that short-term memory predicts foraging efficiency in the field, and that this changes across the summer season, reflecting abundance of floral resources. An earlier study by Saleh and Chittka (2007) induced the use of long-term versus short-term memories in bees learning routes by keeping the spatial arrangement of flowers fixed versus changing between foraging trips. However, we currently do not know how bumble bees weigh social or personal information in their memory.

A further test of the preparedness of social information is to ask how long this information is used by animals across time. In this manuscript, we test the hypotheses that the presence of conspecifics affects the learning rate and memory length of bumblebees. More valuable information should be remembered for longer periods of time. If social information indeed holds special value through increased salience, information learned socially should be remembered for longer periods of time. Similarly, as in previous experiments and theory, the reliability of the information learned should also affect memory length. In this paper we use memory as a test of the value of information. By comparing social and non-social cues while manipulating the value of information through patterns of reliability, we can test for how social information affects memory length. We use an experimental approach to manipulate the reliability of social cues in the form of the presence or absence of conspecifics, and the reliability of floral cues, the color of the flower. Once bees have experienced and learned under a given reliability environment, we then test the memory of this learning for subsets of bees across three retention intervals: 4, 8, and 24 hours. Specifically, we predict that reliability will affect

which cue is learned, with bees learning the most reliable cue in their treatment. We also predict that recall of the type of information learned (social or floral) will interact with the passage of time: if social information is more evolutionarily prepared, then it will be associated with better performance across the retention intervals. Finally, based on the published work on competition in bees, we predict that the tendency to match the locations of bees will interact with both the learning treatment and the experience gained from unrewarding visits in the test phase.

Methods

Bee husbandry The experimental subjects were captive *Bombus impatiens* purchased from Koppert Biological Systems (Howell, Michigan, USA). Ten separate colonies were used throughout the course of the experiment, with a range between one and 10 subjects per colony. Each colony was housed in a 20.5-cm × 22.5-cm × 10-cm tall wooden box with a Plexiglas lid. A thin layer of pine cat litter lined the bottom of the hive box to absorb moisture from the colony. We fed the colony a 20% sucrose solution (by volume) as a maintenance diet. Ground fresh pollen was delivered to the colony daily by depositing approximately one tablespoon directly onto the hive. We kept the colonies at a 14-hour photoperiod (14L:10D), consistent with the middle of summer in their natural range. Foraging bees were marked with numbered honeybee queen marking tags, fixed with superglue to the dorsal side of the subject's thorax, between the wings. A total of 41 bees were tested.

Experimental design The experiment was designed as a 2 × 3 factorial with two levels of cue reliability and three different retention intervals. The cues were the color of the artificial flowers (human-orange or human-yellow) and the presence or absence of a conspecific. To manipulate the reliabilities of the cues, we followed the methodology of Dunlap et al. (2016). In our experiment two conditions were possible: floral information was completely reliable and social information was completely unreliable or floral information was completely unreliable and social information completely reliable. Reliability here is defined as the conditional probability that a given cue is associated with a sucrose solution reward. So, for instance, if social cues are 100% reliable, every flower which held a conspecific was rewarding, while every flower without a conspecific was unrewarding. Likewise, a 50% unreliable floral cue would mean that half the flowers of a given color, say orange, are rewarding, while half are not, with the same pattern of rewardingness for the yellow flowers. The retention of information gained after experience with these two different reliabilities was then tested after retention intervals of 4, 8, or

24 hours. All subjects were randomly assigned into one of the six treatments, with a randomization within experimental blocks such that each block contained one subject in each treatment. This serves to make treatments somewhat equal over the colonies being tested and helps control for other temporal effects like seasonal changes in humidity. We tested between six and eight individual bees in each treatment, for a total of 41 bees.

Experimental setup All artificial flowers used for pre-training, training, and testing were constructed from craft foam cut into 45-mm discs and glued to floral picks. The bottom ~.2 ml of a microcentrifuge tube was inserted into each artificial flower as a reservoir and sat flush with the top surface of the artificial flower. These flowers would then be firmly placed into a hard foam floor, painted dark green in a foraging arena (70 × 60 × 40 cm) attached to the colony with 1-inch plastic tubing. During testing and training the arena contained 12 artificial flowers spaced equidistant from each other (Fig. 1). For each treatment, the placement of cues was identical. Half the flowers were human-orange and the other half were human-yellow. And then half of each color of flowers each had a desiccated forager from a different colony pinned to them. These pinned bumble bees, all of approximately comparable size, serve as social information and are hereafter referred to as “demonstrators.” The equidistant artificial flower array thus contained four different artificial flowers: orange without demonstrators, orange with demonstrators, yellow without demonstrators, and yellow with demonstrators. There were three flowers of each artificial flower type in the array. These flowers were then arranged semirandomly and rewarded per the reliability treatment—that is, either one artificial flower color is rewarded with sucrose, and the other color is unrewarded (contains plain water) for personal information being reliable, or only artificial flowers with demonstrators are rewarded with sucrose, and artificial flowers without demonstrators contain plain water for social information being reliable. Semirandom order was achieved by first arranging the artificial flowers according to a random number generator, then manually breaking up any groups of four or more similar artificial flowers as needed.

Experimental procedure

Pretraining The purpose of the pre-training phase was to train the bees to forage from the artificial flowers and to identify motivated foragers. During the pretraining phase, human-blue or human-white artificial flowers were filled with 0.4 mL of a 50% sucrose solution and placed in the foraging arena. These flowers were refilled throughout the day. Blue and white artificial flowers were used in this phase

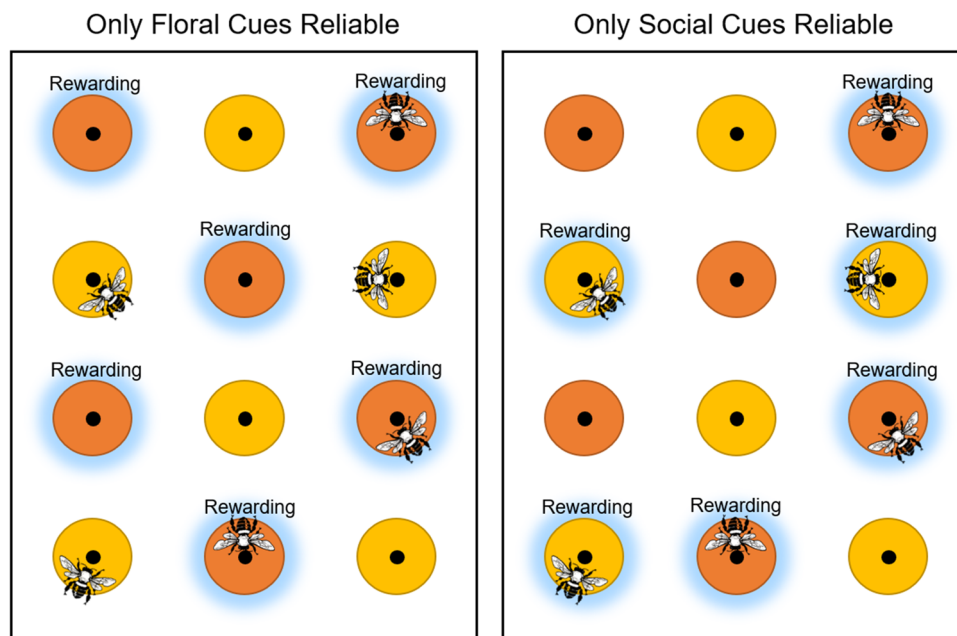


Fig. 1 Diagram of two foraging scenarios for training as viewed from above (not to scale). Twelve flowers are available, half of which are orange and half of which are yellow. Dried conspecific demonstrators are placed on half of each color of flower. Each bee was presented with a random arrangement of these four flower types. The contingency of reward, however, changed according to treatment. When floral color cues are reliable (array on the left), each orange flower, for instance, would contain a sucrose reward while each yellow flower

contains no reward. This is depicted in the figure as a halo around the rewarding flowers, which are also labeled. A forager learning in this scenario should attend to color and ignore the presence of conspecifics, which are only 50% rewarding. For a bee in a social cue reliable treatment (array on the right), each flower containing a bee would contain a reward, and each flower without a bee contains no reward. Here, bees should attend to the presence of conspecifics and ignore flower color cues. (Color figure online)

to allow the foraging bees to learn how to use the artificial flowers while preventing them from learning about the color of artificial flowers they would be experiencing in the training and testing phases. Experimental subjects were determined by identifying foragers that repeatedly visited the blue or white artificial flowers in the foraging arena and returned to the colony to deposit sucrose.

Training Experimental subjects were each trained on one of the two reliability treatments by being allowed to individually forage freely in the foraging arena. During this phase, either one artificial flower color was rewarded (personal information) or only flowers with demonstrators were rewarded (social information). Rewarded flowers contained 10 μ l of 50% sucrose solution, while unrewarded flowers contained 10 μ l of plain water. We allowed the subject to make as many foraging trips as necessary to reach an 80% correct success criterion, defined as making 16 of the most recent 20 landings on rewarding artificial flowers. Landings were counted as a choice only if the subject attempted to forage from the flower (described in more detail below). Each rewarding flower was refilled after a foraging visit to ensure that the treatment reliabilities remained intact throughout the choices. Following attainment of the learning criterion,

we allowed the subjects to return to their colony until their assigned retention interval had passed.

Testing Each bee was tested after a single retention interval. During this testing, the subject was allowed back into the foraging arena where they were presented with a floral array identical that from their training, with both social and floral cues present. However, this was a completely unrewarding foraging array. We recorded the first 10 choices of the bee, after which each subject was freeze killed. We look at the first five choices to measure memory retention, and the full 10 choices to look at the effect of additional experience on choice in the testing phase.

Video and data analysis

Behavioral observations Foraging choices were recorded during each subject's training and testing period, and we used these data to calculate the learning measures of trials to criterion and the accuracy choices in each trial. For our analyses, we consider a trial to be a single floral choice. We also video recorded both training and testing sessions to confirm these data, as well as to collect data on the times

entering and leaving the arena, and the landing and leaving times for each floral choice. During both training and testing a foraging attempt was defined as a bee landing on an artificial flower and inserting its head into the nectar well in the flower. Alternatively, if observed, a proboscis extension response into the nectar well in the artificial flower counted as a foraging attempt. Events where the bee landed but did not extend its proboscis or insert its head into the well were not recorded; these events were extremely rare. We also recorded the type of flower visited for each choice, as well as whether that choice was correct in terms of being rewarded.

Statistical analysis We completed two analyses on the training portion of the data. First, we used *t* tests to determine the simple effect of treatment on learning speed in terms of trials to criterion. We then asked whether there is any difference in the accuracy of choices between the social and floral reliable treatments at each of four phases of their learning trials. To do this we analyzed percent correct choices during the learning phase by breaking each bee's trials to criterion into quartiles and performed an analysis of variance (ANOVA) between quartile and treatment. This allowed us to see if there is any difference in the accuracy of choices during each quartile of the learning phase.

We then completed two analyses on the testing portion of the data, testing memory accuracy as well as potential shifts towards or away from pinned bees. In the first test, we focus on the accuracy of their memory within their first five choices. We calculated the percentage correct of the first five landings in the memory test and then used an analysis of variance (ANOVA) to test how the factors of reliability (social or floral) and retention interval (4, 8, or 24 hours) affect performance. We used the first five choices rather than the first 10 because previous work in our lab has shown that bees switch their choices quite quickly when foraging in an unrewarding array; we wanted to see the effect of the learning from the training trials and not experience gained within the testing trials. We looked at this experience effect in our second analysis of the test trials. In the literature, there are two hypotheses that predict how bumble bees might be influenced by their prior learning resulting in non-reward. In the first case, this new uncertainty might cause bees to rely on social information. In the second case, the lack of reward may indicate competition from other bees, and thus subjects may use social information as cues where not to forage. We assessed the influence of conspecifics across test trials. we calculated the proportion of choices matching the locations of demonstrators for the first five trials and the last five trials of the memory test, and then analyzed this in a repeated measures ANOVA with factors of reliability treatment and RI, with the repeated measures from each subject. Finally, for all analyses we performed statistical power calculated for main results where *p* values exceeded the 0.05 threshold.

Results

Training

We first looked at the effect of the social cue on learning speed as defined by the number of trials required to reach our criterion of 80% correct choices in the most recent 20 trials (Fig. 2). Here we found no effect of treatment on learning speed ($t_{39} = -0.4962, p = .6225$). Thus, bees were learning about reliable floral color cues with a similar speed as the bees learning about reliable social cues. We then looked at the shape of the learning between these treatments. We divided each bee's training session into quartiles based on number of choices made, and then analyzed these choices in a repeated-measures ANOVA. We found no significant effect of treatment ($F_{1,39} = 1.229, p = .274, \text{power} = 0.19$). As expected for learning, there was a statistically significant effect of quartile ($F_{3,117} = 72.270, p < .00001$). The interaction between quartile and treatment was not statistically significant ($F_{3,117} = 0.805, p = .493, \text{power} = 0.22$). Using contrasts within our ANOVA, we found a statistically significant difference between the first and last quartiles for both treatments (social information reliable: $F_{1,39} = 85.78, p < .00001$; Floral information reliable: $F_{1,39} = 65.135, p < .00001$). These results can be found in Fig. 3.

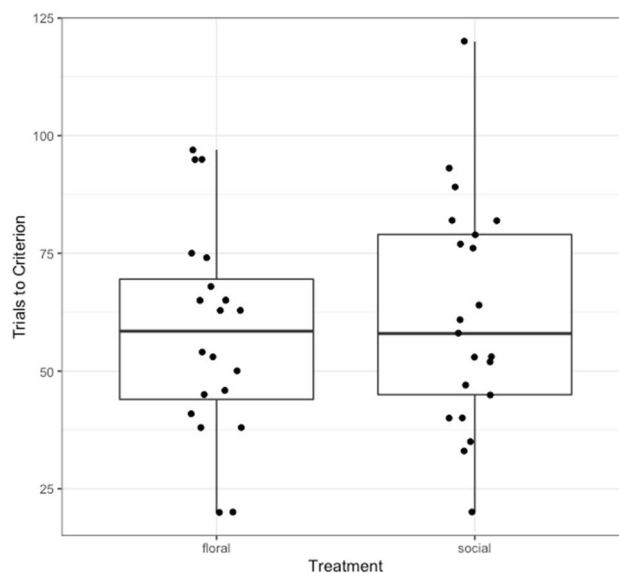


Fig. 2 Individual bee data plotted for the number of trials (floral visits) to reach the learning criterion. There was no statistically significant difference between the treatments for how quickly the focal information is learned. Means and *SD* are 58.25 ± 22.30 and 61.86 ± 24.15 for floral cues reliable ($N = 20$) and social cues reliable ($N = 21$), respectively

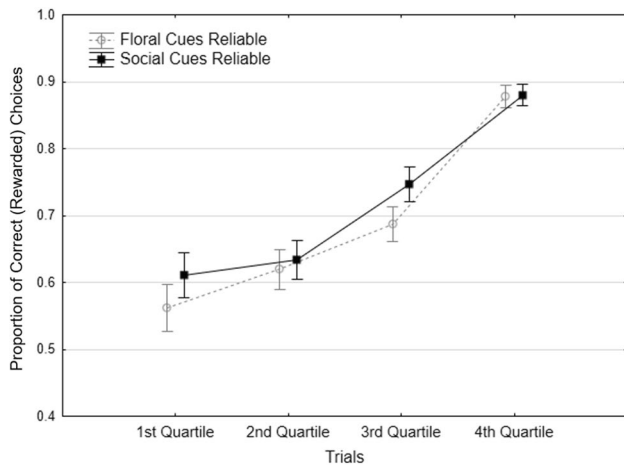


Fig. 3 Proportion correct choices during training, blocked by quartile of trials. Here, correct choices were those which match the reliable cues for a given treatment. We found no significant difference between the treatments across the quartiles of experience, but within both treatments, correct choices increased significantly between the first and last quartiles. Bars depict standard errors

Retention interval testing

Learning appeared quite similar across both treatments, so we turned to how well this information was used following the different retention intervals. In our first analysis, testing accuracy in the first five choices, we found a significant effect of treatment, with social information being retained better than floral color information ($F_{1,35} = 8.458$, $p = .0063$). However, there was not a significant effect of retention interval ($F_{2,35} = 0.984$, $p = .384$, power = 0.21), or of the predicted interaction between treatment and retention interval ($F_{2,35} = 0.825$, $p = .447$, power = 0.18). Using contrasts, we compared the treatments within in retention interval. We found a significant difference between reliability treatments at the 4-hour retention interval ($F_{1,35} = 6.997$, $p = .0121$), but not at the 8-hour ($F_{1,35} = 1.054$, $p = .312$) or 24-hour ($F_{1,35} = 1.749$, $p = .195$) retention intervals. These results can be found in Fig. 4.

A possible interpretation for these results is that when uncertain, bees have been shown to copy the locations of other bees. With this prediction, bees in the social cue reliable treatment may not be remembering better but are simply being scored as correct for matching the locations of bees. However, bees in the treatment where floral color cues are correct would only be scored as 50% correct when using the same strategy of copying the location of conspecifics. Thus, we analyzed these choice data in terms of matching the social cue instead of what had been trained as correct. Specifically, we predicted a shift in how bees matched the locations of conspecifics as their uncertainty increases, both with time and with experience with the unrewarding choices

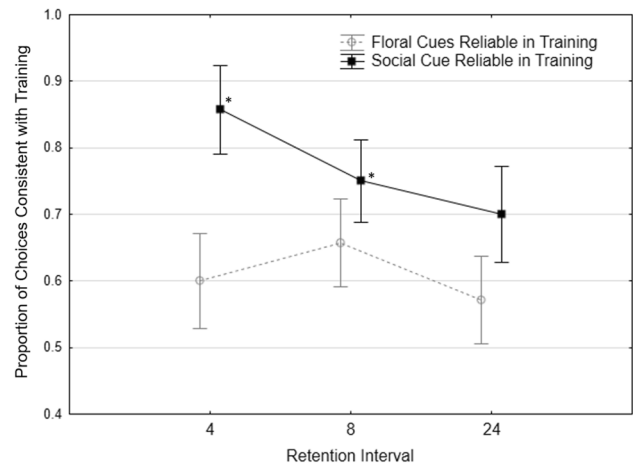


Fig. 4 Memory results in first five choices, where both floral and social cues are available. Effect of treatment is statistically significant, and bees differed in performance between the reliability treatments at the 4-hour RI. Only bees trained under social cue reliable conditions performed significantly above chance, at 4 hr and 8 hr ($t_6 = 9.682$, $p = .00007$, and $t_7 = 3.989$, $p = .00526$, respectively, denoted by asterisks in the figure), but not quite at 24 hr ($t_5 = 2.335$, $p = .0667$). Error bars depict *SEs*

in the test trials, and tested this with a repeated measures, factorial ANOVA. We found a statistically significant effect overall of reliability treatment ($F_{1,35} = 27.670$, $p < .00001$), with bees trained in a social cue reliable treatment overall matching the locations of conspecifics. The effect of RI and the interaction between RI and reliability treatment were not statistically significant, however the statistical power for testing these effects was low (0.1156 and 0.2949, respectively).

As expected for any retention test with multiple unrewarding choices, we found a significant effect of choice block ($F_{1,35} = 4.436$, $p < .0424$). And this effect of choice block interacted with both the reliability treatment and the RI in the choice of matching the locations of demonstrators (Fig. 5; $F_{2,35} = 4.252$, $p < .0222$). We conducted a series of contrasts within the ANOVA to test specific differences between treatments at each RI, for each block of the choices (first five choices, and second five choices). We found that the training experience of differing cue reliabilities induced significant differences in how bees match the locations of other bees at every time point for the first five choices (4hr: $F_{1,35} = 14.159$, $p = .0006$; 8hr: $F_{1,35} = 11.229$, $p = .00195$, and 24hr: $F_{1,35} = 4.887$, $p = .00337$). We saw a similar pattern for the second block of choices, except for the 4-hr RI (4 hr: $F_{1,35} = 0.746$, $p = .3935$; 8 hr: $F_{1,35} = 6.001$, $p = .0194$, and 24 hr: $F_{1,35} = 8.522$, $p = .0061$).

Are bees matching the locations of demonstrators more than expected or are they avoiding the locations of demonstrators greater than expected? We tested the performance to what we would expect by chance, matching the locations of bees with a 0.50 probability. We found that bees trained with

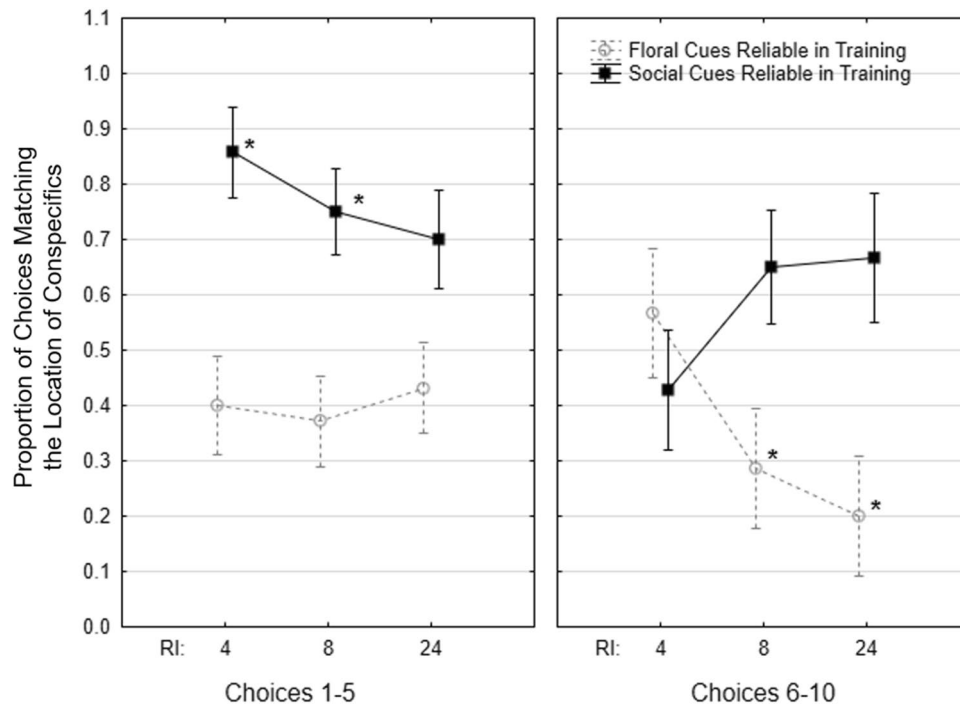


Fig. 5 The degree to which subjects match the locations of demonstrators is affected by the interaction of reliability treatment, RI, and experience within the testing (split into blocks of first 5 versus second 5 choices). Asterisks denote points which statistically significantly

social cues being reliable matched the locations of demonstrators above chance at 4-hr and 8-hr RIs for their first five choices only (4 hr: $t_6 = 9.682$, $p = .00007$; 8 hr: $t_7 = 3.989$, $p = .0053$). Though our formal memory results did not show statistically significant differences at longer RIs, the training experience significantly impacted the choices of some bees at these intervals after their additional experience within the test trials. Bees trained with unreliable social cues avoided the locations of demonstrators for 8 hr and 24 hr, after they have experienced their first five unrewarding choices (8 hr: $t_6 = -2.904$, $p = .027$; 24 hr: $t_6 = -3.074$, $p = .0218$). They are choosing flowers of both colors but choosing primarily flowers without conspecifics.

Discussion

In this paper, we tested the value of information by asking how long two classes of information are learned and then remembered for. Bumble bees have long evolutionary histories with both flowers and conspecifics, using both floral color information and social information to guide their foraging decisions. Previous studies have made compelling claims that social information is “special” and likely reflects a pattern of biologically prepared learning. We tested this by inducing learning about color and about conspecifics

differ from 0.5, the value matching demonstrators by chance. Choices for bees statistically significantly differ between the reliability treatments for all RIs and the two choice blocks, except for the 4hr RI in the right panel

under conditions which manipulated the reliabilities with which these classes of information predicted the presence of reward. We find that bees learn about floral and social cues with comparable speed and pattern. Differences emerge, however when we look at the choices bees are making following 4-hr, 8-hr, and 24-hr retention intervals. We find that when we compare the accuracy of these choices to what bees were trained to, that reliable social information is remembered significantly better than reliable floral information overall, and significantly better than chance at 4-hr and 8-hr retention intervals. Uncertainty, however, could also induce bees to copy the locations of other bees. This uncertainty can occur both through the passage of time as well as with new experiences with making choices that are now unrewarded in a test trial. For these reasons we looked at the choices in the test trials in terms of matching the location of demonstrators. When we consider the first five choices, our results match that of the main retention interval analysis. Bees trained with reliable social information but unreliable floral information perform as before. However, we find that bees trained with reliable floral information but unreliable social information are not increasingly matching the locations of demonstrators. This is what we expect to see if those bees are ignoring the presence of demonstrators. The lack of accuracy in remembering the learned information is not because bees are switching to following bees as retention

intervals increase. Bees in this treatment, however, are learning about the unreliability of bees as well as the reliability of floral cues. When uncertainty is increased through the experience of unrewarding test trials, bees in this treatment significantly avoid the presence of other bees after 8-hr and 24-hr retention intervals. Using this novel method for experimentally testing the value of information, we can conclude that bumble bees attend to the reliabilities of cues and use both reliability and unreliability of social cues to influence their choices with medium- and long-term memory.

We found no statistically significant difference in the trials to criterion between bees that learned from personal information and bees that learned from social information. Several studies have looked at learning speed under social conditions in bumble bees. Leadbeater and Chittka (2007), for instance found in a very comprehensive set of studies that bees began to learn quicker in the presence of experienced conspecifics but the learning process was no quicker when bees foraged alone versus with experienced foragers, suggesting that the time it takes to learn a foraging task is the same in the presence or absence of social cues. Leadbeater and Chittka (2009) found that when conspecifics reliably predict reward, foragers prefer flowers with conspecifics significantly to naïve foragers, to solo foragers, or to foragers that learned that conspecifics do not predict reward. And while social cues can act as social or local enhancement (e.g., Kawaguchi et al., 2006; Leadbeater & Chittka, 2007), the simple associative learning can account for the observational learning of these cues (Dawson et al., 2013). In our experiment, we found no evidence for local enhancement as bees showed no initial preference for the locations of other bees, but rather associative learning. Given these results, and others, researchers have posed the alternative hypothesis that demonstrators might simply be another cue available for floral learning, analogous to a nectar guide or other component of a flower (e.g., Baude et al., 2008; Dawson & Chittka, 2012). However, further work on learning of social cues indicates that although learning processes may be similar for social and non-social cues, the salience of that information is not always similar. Smolla et al. (2016) also experimentally found that non-social cues were learned as readily as social cues but were not attenuated to during testing and that socially salient cues are the most efficient at learning tasks. Other forms of social information are also flexibly used by bees, such as scent marks left by bees upon flowers, which can be both aversively and attractively learned (e.g., Saleh et al., 2007). But information from bees can be used in some surprising ways. For instance, Avarguès-Weber et al. (2018) showed that bumble bees use information from other bees even when it resulted in sub-optimal choices. Finally, Dunlap et al. (2016) factorially manipulated the reliabilities of floral versus social information, and also found no differential effects of the reliabilities of social versus floral cues

on simple measures of learning. They did, however, find differences in how those forms of information were used 30 minutes later. Our findings support previous work suggesting that there is not a fundamental difference in how trial and error learning occurs for social information versus floral information.

Importantly for our study, the lack of a difference in the speed of learning these cues sets up a good comparison for memory length of these forms of information. We find that recall of learning about the rewarding social cues is more accurate across time than recall for learning about the floral color cues. However, both forms of information are present in each treatment and bees in the floral cue reliable treatment are also learning about social cues. The experience of bees in this treatment with unreliable social cues results in an avoidance of demonstrators 8 and 24 hours later. Thus, it appears that bees learn about both the reliability and unreliability of social information and use that to modify behavior in later decisions. There is not much directly relevant literature in bees to guide us in comparisons of our results with others. The literature on memory experiments in bumble bees is not large as with work on honey bees, and most studies test olfactory conditioning at relatively short retention intervals (minutes to hours; e.g., Giurfa & Sandoz, 2012; Smid & Vet, 2016). Studies of learning about social information in non-human animals also typically focus on acquisition rather than retention, with test trials occurring within the range of short-term memory. Memories about flowers and foraging can most certainly exceed this timeline. For instance, memory retention of foraging skills in bumblebees is imperfect overnight but does not diminish significantly over several days (Keasar et al., 1996). And this sensorimotor behavior as well as color associations can be retained for weeks, if not longer (Chittka, 1998; Muth et al., 2016). Even beyond work in bees, empirical studies that compare the effects of uncertainty and its changes in the value of information upon memory remain rare. Testing short-term memory, Pull et al. (2021) showed that bees changed their investment in memory, as tested in a win-shift radial maze task, and that this change tracked changes in floral abundance in the field. Dunlap and Stephens (2012) modeled the value of memory in a changing environment and found in an empirical study that blue jays did change the weighting of memories based upon manipulated rates of change. Ferrari et al. (2010; Ferrari et al., 2012) also manipulated certainty for information about predation for larval frogs, and overlaid this with their subjects' evolutionary history with cues from predators. They find that with increasing uncertainty about predator-associated cues, prey decrease the length of their memories. Theoretical work on memory reflecting rates of uncertainty in the environment appears to be generally supported in the few systems in which it has been tested, but more work is very much needed.

As with any study of memory length, we are faced with the potential effects of the learning-performance distinction as we are relying upon the choices of the animal and not, for instance, directly measuring some evidence of a memory trace in the brain. This is particularly true for a paradigm in which stimuli are rewarding at different rates. It is likely, for instance, that both potential reward values of a resource are remembered. Dunlap and Stephens (2012) showed that the choice between two options interacted both with the rate of change as well as the passage of time, with blue jays changing their decisions over the course of days. In bumble bees, Chittka (1998) showed long-term memory under reversal training, indicating that bees were suppressing irrelevant information with enough training trials. Weighting of information likely what is happening with social information and time. For instance, while flowers within a species may have natural variability throughout the day, a major source of missing rewards for bees is the effects of competition from other nectar foragers. Our experimental design differs from typical studies in that instead of a simple discrimination task with cues being either completely reliably rewarding, or completely reliably unrewarding, we made cues unreliable. Thus, the discrimination is between a cue which is always associated with a reward, and a cue which is half of the time associated with a reward. This approximates in some ways the effects of competition. Baude et al. (2011) experimentally manipulated the density of conspecifics and the complexity of the floral community and found flexibility in the way social information benefits foragers. Foragers tend to use conspecifics as sources of information for where to forage when they are naïve and conspecifics are at low densities. Plowright et al. (2013) found that the tendency of naïve bees to match the floral locations of other bees depended on both the frequency of other foragers and the relative sizes of the available flowers. And Dawson and Chittka (2012) demonstrated that the matching behavior was not limited to conspecifics, but to other nectar foragers, generally, supporting this idea of the importance of informers who can also be competitors. Thus, bees modulate their matching behavior even when naïve based upon the ecological and social conditions they encounter upon first foraging, and they modulate their behavior in a way that is not seen for any of the floral cues yet examined.

The evolution of ecologically relevant memory is perhaps best studied in the context of adaptive specialization, for instance in the spatial memories of birds and mammals for cache sites. Less well-studied is ecologically relevant memory in the context of biological preparedness. While both frameworks predict the effects of evolution upon cognitive traits, adaptive specializations predict enhanced ability as a consequence of a long-term history of cognitive demand in a specific cognitive realm. Concepts of optimal forgetting as well as the evolution of biological preparedness

are connected by the underlying prediction that the value of information is determined by rates of reliability in the environment. More reliable contingencies between cue and reward should be remembered for longer and over evolutionary time, should come to become biologically prepared for learning and in some cases memory. It has become quite clear that social information holds special importance for foraging bumble bees. The joining behavior in bees is a flexible trait that can be reinforced through conditioning and adapted to local circumstances. Bumble bees appear to flexibly use social information, implying that this information indeed holds special salience and is evolutionarily prepared. To this literature, we add the novel aspect that the use of social information interacts with the passage of time. We argue that our results add to the burgeoning evidence that social information is biologically prepared in bumble bees. In summary, we present a novel method for testing the value of information, using memory as a proxy for value. Our results provide new information about the value of social information in a variable environment and the importance of context in foraging decision-making.

Data availability

The data sets analyzed during the current study are available in the online supplementary information for this manuscript.

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