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Perspectives

Social learning and culture in bees: Simple mechanisms, complex outcomes

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Bees have been excellent model systems to study social learning – the ability of animals to change their behaviour based on observations of other individuals. Researchers have investigated several aspects of social learning in bees, including how it can lead to cultural traditions. A recent study also argues that bees have the capacity to socially learn behaviours that they could not innovate on their own. To understand these findings better, I review what we know about the mechanisms underlying social learning in bees and use these findings to compare social learning and culture in bees and humans. The findings suggest that the seemingly complex social behaviours of bees could arise from simple mechanisms underlying learning in general. I highlight the importance of investigating cognitive mechanisms and how they might differ across animals.

Keywords. Associative learning; bees; cognitive mechanisms; comparative cognition; cumulative culture; local enhancement; social learning; stimulus enhancement

Over several decades, scientists have made remarkable discoveries about the cognitive capabilities of bees. Bees have been trained to recognize complex patterns (Giurfa *et al.* 1999), to choose stimuli that match another stimulus (Giurfa *et al.* 2001), and to choose between targets that differ in spatial configuration (Avargues-Weber *et al.* 2012) or number (Bortot *et al.* 2019). These findings argue that bees can count, learn concepts, and have a sophisticated capacity for learning. Bees have therefore become excellent models for learning and comparative cognition. A recent paper (Bridges *et al.* 2024) adds further research to this picture, arguing that bees have the capacity for cumulative culture – a key feature of human societies. This would be an impressive feat for bees, given that they have far smaller brains than humans. Some of the coverage of this finding certainly makes a strong case – describing the results as showing that bees show behaviour previously thought to be uniquely human (Fox 2024). Previous research has already demonstrated the hallmarks of cultural traditions in other animals (e.g., whales (Garland *et al.* 2021) and fruitflies (Danchin *et al.* 2018)). The specific case made by the current paper is that bees can socially learn a task that they cannot learn alone – arguably the first step for the advantages that culture gives an organism.

To better interpret what these results mean, we could first consider a key idea in comparative cognition – attending to the mechanisms underlying cognitive behaviour (Chittka *et al.* 2012). The same behaviour or abilities in two animals – say humans and bees – could be achieved by different cognitive processes and understanding the similarities and differences makes for a fascinating field of study. To fully understand the latest research findings, we should see if the mechanisms of social learning and culture in bees resemble those in humans.

Social learning in bees makes for a great case study of comparative cognition. At its simplest, social learning could be defined as the ability to modify behaviour based on observing other individuals. Honeybees and bumblebees, like humans and several other animals, are highly social. Honeybees famously can also communicate the locations and quality of flowers to other bees using their dance communication system. More recently, researchers have shown that bees move towards specific flowers and flower types if they observe other bees on them (Leadbeater and Chittka 2005; Worden and Papaj 2005; Baude *et al.* 2008). This form of social learning has been seen in both controlled experiments in the lab as well as in experiments with wild bees (Kawaguchi *et al.* 2007). This perhaps seems to resemble how humans might observe other humans to learn new knowledge or skills; but how do bees do it?

Thankfully, researchers have investigated these mechanisms in detail (Leadbeater and Dawson 2017). The clearest mechanism identified so far has been associative learning, which involves receiving a reward and associating this reward with some external stimulus. You could also learn a neutral cue that predicts a reward – think of the famous story of Pavlov's dog learning to associate a bell with the prospect of food. Bees are excellent at associating stimulus cues with rewards, including colours, spatial location, and patterns. Bees can similarly associate other bees with rewards if they forage together using either visual or olfactory cues (Leadbeater and Chittka 2009, 2007; Saleh *et al.* 2006). This then leads to them approaching flowers with bees on them since they have learnt that a bee is a good cue to a floral reward. This association can be further built upon. In a laboratory experiment (Dawson *et al.* 2013), bees were allowed to associate the presence of a bee with a reward. They were then allowed to observe foraging bees who visited flowers of a specific colour. The observer bees were later more likely to approach flowers of the same colour as the foraging bees. This is a phenomenon often called stimulus enhancement – where social cues increase responses to a particular stimulus. It can work the other way too. In the same study, if bees were trained to associate an aversive quinine solution with the presence of another bee, they subsequently avoided the flower colour which had bees on it. Naive bees that had not had the opportunity to forage with other bees and associate their presence with reward did not choose flowers based on the presence of other bees. This shows that the association of reward (or aversive stimulus) with other bees is key to subsequently using the presence of bees as a cue to choose (or avoid) a flower colour. Thus, bees were associating the first learnt stimulus (a bee) with a second unconditioned stimulus (the flower colour) – a mechanism called second-order conditioning. Social learning through this mechanism is thus perhaps not particularly social – it results from the mechanisms underlying learning in general (Heyes 2012; Leadbeater 2015).

Associative learning can also lead to bees being attracted to locations where they observe other bees. This process is called local enhancement. Within an array of flowers of a certain colour, for example, bees prefer to land on those with demonstrator bees, suggesting that the location rather than the colour takes precedence during social learning – or perhaps they just like flying towards other bees (Leadbeater and Chittka 2007). They also land on areas occupied by other bees even without flowers. In one study, bees observed other bees pulling a string to access rewards (Alem *et al.* 2016). They were subsequently more likely to attempt to access the reward from the same location as the demonstrator bees. Social cues thus lead to local enhancement in bees.

Given these mechanisms, especially the importance of associative learning, we might ask how social bee social learning really is. Is the presence of another bee important or will any other cue do? It turns out the presence of a bee (or a bee-like model) does make a difference. Bees in one study were more likely to learn to visit flowers occupied by bees compared with those occupied by a plastic disc (Dawson and Chittka 2012). It is interesting to note that here, too, bees did visit flowers with the non-social cue with a greater frequency than that expected by chance, but the effect of a social cue was stronger. How about bees that do not have an opportunity to learn an association between social cues and a reward? Naive bees that have not foraged with other bees or encountered rewards also prefer flowers or inflorescences occupied by other bees (Worden and Papaj 2005; Kawaguchi *et al.* 2007; Dawson and Chittka 2012). These bees could not have learnt to associate rewards with the presence of a bee since they had not foraged before – the attraction to other bees occurs even without learning. Here again, the attraction to bees is stronger than the attraction to non-social cues like a wooden cuboid, if the bees are of the same species (Dawson and Chittka 2012), but the non-social cue still attracts more visits than expected by chance. One study (Worden and Papaj 2005) allowed naive bumblebees to observe demonstrator bees foraging from either green or orange flowers. The observer bees were then more likely to land on flowers of the same colour – but only if the demonstrator bees had been on green flowers. This means that naive bees can not only be attracted to occupied flowers (local enhancement) but to specific flower types where they see bees (stimulus enhancement). However, in the same study, naive bees that observed demonstrator bees on orange flowers were not more likely to land on orange flowers compared with control bees. Another study argued that bees that observed demonstrator bees pulling strings for rewards were also attracted to the string as a stimulus (Alem *et al.* 2016). However, if the string was displaced to another location this was no longer true. That suggests that it might be the location rather than the stimulus that was socially learnt in that case.

A couple of experiments have shown that bees are also less likely to learn from demonstrations that do not involve other bees. For example, if a human demonstrated how to pull a string to access a reward, bees did not learn the technique, but they did when they observed other bees (Alem *et al.* 2016). Similarly, in another study bees learnt to push a ball for a reward by observing other bees. If the ball was moved by a magnet without demonstrator bees, observer bees did not learn the task as well (Loukola *et al.* 2017). Clearly bees are attracted to other bees, and this boosts their learning. This has been suggested to stem from a fine-tuning of sensory thresholds towards conspecifics (Leadbeater 2015). What all these results perhaps show best is that bees have sensory systems designed to notice and attend to other bees. The process of learning and associating these cues with a reward, however, are likely be the same as any other learning process. Biased input mechanisms can lead to responses specific to social stimuli even if the learning mechanisms are not different from other associative mechanisms (Heyes 2012).

Building on these results, researchers next began to explore how complex social learning in bees can get. The simple associative mechanisms we discussed above can nonetheless lead to a good deal of flexibility in how social information is used. For example, bees that experience predation on one type of flower choose to use social cues when faced with this flower type, but not with another (Dawson and Chittka 2014). They also are more likely to use social cues when the task they face is more difficult, when they have experience of low rather than high rewarding flowers, or when resources were more variable (Jones *et al.* 2015; Smolla *et al.* 2016; Baracchi *et al.* 2018). Social information appears to be particularly useful if the floral resources are patchy (Baude *et al.* 2008) and in less complex floral environments (Baude *et al.* 2011). Such behaviour demonstrates flexibility in the use of social information but can also typically be explained through associative mechanisms. For example, when resources are variable, associative learning is known to increase (Heyes 2012) and this would explain the increase in the use of social cues.

Another strand of research began to ask if social learning had longer lasting effects within a colony. Bees in one study were trained on an artificial task – pulling strings to access a reward (Alem *et al.* 2016). These bees were then used as demonstrators to other bees that went on to learn the task themselves. The new bees themselves became demonstrators and other bees learnt to complete the task after observing them. The novel skill of string-pulling thus spread through the colony, suggesting that social learning could lead to an ability spreading within bee societies in a similar fashion to human, primate, or bird societies. Subsequent research went one step further to ask if social learning could result in cultural traditions in bees (Bridges *et al.* 2023). In this study, demonstrator bees were trained to solve a ‘puzzle box’ for reward using one of two techniques. They could either push a red tab counterclockwise or a blue tab clockwise to expose the reward lying underneath a lid. Demonstrator bees were then introduced into colonies having learnt one of the two techniques. These colonies ended up learning the technique of the demonstrator and not the other technique, showing that social learning can bias learning of one technique over another. In addition, when multiple demonstrators who had each learnt a different technique were introduced into colonies, observer bees mostly learnt one of the two techniques. It is, however, worth noting that bees in a colony without demonstrators also learnt to solve the puzzle box problem and in this colony also, only one of the two techniques spread. While these two studies seem to make a case for complex cognitive mechanisms in bees, they actually demonstrate the opposite. Both studies demonstrate that the driving mechanism underlying the behaviour is mostly local enhancement via associative learning, alongside a role for bees’ attraction to conspecifics. The remarkable finding is that seemingly complex behaviour can emerge from simple rules.

This brings us back to the latest study of culture in bees. Bridges *et al.* (2024) set out to test for the capacity for cumulative culture in bees. Cumulative culture is often touted to be the driving force behind the rapid advancement of human societies and finding similar capabilities in bees would be truly impressive. By the definition in Bridges *et al.* (2024), cumulative culture would need an innovation by an individual that is socially learnt, followed by subsequent improvements on this behaviour by other individuals. To generate an innovation – or a behavioural modification – the authors used a two-step puzzle box. Bees were first trained to approach a rewarding yellow dot in this box from above. Subsequently a transparent lid was placed on the box. The bees were trained through a series of steps to use two physical movements in sequence to expose the yellow dot and access the reward. The first movement involved pushing a blue lever away from the dot and the second required the bees to push a red tab to move an opening in the lid above the dot where the reward was placed. Bees that learned this complex task then served as demonstrators for other observer bees who were finally tested to see if they could perform the task without their demonstrators. Five out of fifteen observer bees managed to do this on their own and two of them went on to consistently perform the task by themselves. In comparison, bees that did not have demonstrators never managed to solve the task even after days. The authors therefore conclude that bees are socially able to learn tasks that they could not learn individually.

There are several ways to consider the results. The first is to compare the findings directly with the definition of cumulative culture put forward by the authors. There is no evidence here for any innovation. Any techniques learnt were after careful training of an individual by the researchers. Observer bees also did not improve on the technique they learnt. The results therefore do not support cumulative culture in bees. What about the claim that bees learn better socially? We already know that bees do learn rewards better with social cues, which can be explained by their sensory tuning to other bees. Here, too, it is likely that the presence of the demonstrator bee led to stronger engagement with the puzzle box. However, it is worth highlighting that observer bees that stayed with the demonstrator bees presumably did get access to the reward. There is a good case to be made, therefore, that it was associative learning that led to observer bees learning a sequence of actions. This would demonstrate the effectiveness of associative learning in bees since they would have to associate a prior sequence of actions with reward. But it also means that the presence of the demonstrator bee would be less important beyond simply attracting interest to a region in space or objects (blue lever, red tab). Interestingly, the successful learners all learnt a particular technique that the authors calling ‘squeezing’ which effectively combined the two movements into one continuous action pattern. It looks likely that the bees were first attracted to the region by other bees and then learnt this rewarding action pattern.

The number of demonstrator bees that learnt the task in this study was also low. The fact that at least a couple of bees did efficiently learn the task demonstrates a proof of principle – that bees can learn the complex task. However, it also shows that social learning in this task did not typically lead to success and is therefore unlikely to be an important route to learning complex tasks. The role of social cues is clarified by another finding from the study. When examining how observer bees followed demonstrator bees, there was no difference in following behaviour between successful and unsuccessful observer bees. Thus, it does not seem likely that even the successful bees learnt specifically because they were imitating what the demonstrator bees were doing. Finally, it is perhaps unsurprising that bees without demonstrators did not learn the task. Previous research has already shown that bees cannot learn complex two-step tasks without being trained step-wise to solve each task (Mirwan and Kevan 2014). That would be the case here too. In fact, even the demonstrator bees failed to do so unless they were given specific training on each task separately.

What do all these results tell us about the similarities between bee and human social learning? Humans learn by closely imitating other humans (Heyes 1994; Boyd *et al.* 2011). We also teach each other techniques and share knowledge. All of this can occur in the absence of any monetary or food reward. Of course, the ability to solve a task and the presence of another person or their approval can themselves be reinforcing (Heyes 2012). On the strength of all the work on bee social learning, including the current paper, there is no evidence that bee social learning has these features. The closest resemblance lies in the fact that bees seem to be attracted to the presence of other bees. To go beyond this, we would need experiments to show that bees learn tasks without a sugar reward but purely because of another bee’s presence. It would also be impressive if bees could learn to solve a complex task purely by observing other bees without any prior experience of foraging. Evidence that other bees show teaching-like behaviour would also be good, a case that has been made in ants (Franks and Richardson 2006). It would be important to show that bee learning is improved when bees followed other ‘teaching’ bees, compared to bees that didn’t follow them. Demonstrating these features in wild bees would be ideal – arguing that not only are bees capable of this type of social learning but that it is important for them in nature. There are thus plenty of experiments that remain to be explored.

However, we could instead look at the importance of what has been demonstrated already. By focussing on proof of sophisticated human-like abilities in bees, we are often missing the truly interesting story: learning mechanisms can be simple, and even these simple mechanisms can solve difficult problems and lead to complex outcomes. This is increasingly the picture being painted about 'complex' bee cognition by some relatively unheralded, yet fascinating studies (Cope *et al.* 2018; MaBouDi *et al.* 2020). Rather than focussing on outcomes, we should be investigating mechanisms. And rather than staying fixated on similarities, we need to be paying attention to differences across animals (Howard and Barron 2024).

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References

Alem S, Perry CJ, Zhu X, *et al.* 2016 Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLoS Biol.* **14** e1002564

Avargues-Weber A, Dyer AG, Combe M, *et al.* 2012 Simultaneous mastering of two abstract concepts by the miniature brain of bees. *Proc. Natl. Acad. Sci. USA* **109** 7481–7486

Baracchi D, Vasas V, Jamshed Iqbal S, *et al.* 2018 Foraging bumblebees use social cues more when the task is difficult. *Behav. Ecol.* **29** 186–192

Baude M, Dajoz I and Danchin É 2008 Inadvertent social information in foraging bumblebees: effects of flower distribution and implications for pollination. *Anim. Behav.* **76** 1863–1873

Baude M, Danchin É, Mugabo M, *et al.* 2011 Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. *Proc. R. Soc. B Biol. Sci.* **278** 2806–3281

Bortot M, Agrillo C, Avarguès-Weber A, *et al.* 2019 Honeybees use absolute rather than relative numerosity in number discrimination. *Biol. Lett.* **15** 20190138

Boyd R, Richerson PJ and Henrich J 2011 The cultural niche: Why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci. USA* **108** 10918–10925

Bridges AD, MaBouDi H, Procenko O, *et al.* 2023 Bumblebees acquire alternative puzzle-box solutions via social learning. *PLoS Biol.* **21** e3002019

Bridges AD, Royka A, Wilson T, *et al.* 2024 Bumblebees socially learn behaviour too complex to innovate alone. *Nature* **627** 572–578

Chittka L, Rossiter SJ, Skorupski P, *et al.* 2012 What is comparable in comparative cognition? *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **367** 2677–2685

Cope AJ, Vasilaki E, Minors D, *et al.* 2018 Abstract concept learning in a simple neural network inspired by the insect brain. *PLoS Comput. Biol.* **14** 1–21

Danchin E, Nöbel S, Pocheville A, *et al.* 2018 Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* **362** 1025–1030

Dawson EH, Avarguès-Weber A, Chittka L, *et al.* 2013 Learning by observation emerges from simple associations in an insect model. *Curr. Biol.* **23** 727–730

Dawson EH and Chittka L 2014 Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. *Proc. R. Soc. B Biol. Sci.* **281** 20133174–20133174

Dawson EH and Chittka L 2012 Conspecific and heterospecific information use in bumblebees. *PLoS One* **7** e31444

Fox D 2024 Bumblebees show behaviour previously thought to be unique to humans. *Nature https://doi.org/10.1038/d41586-024-00669-6*

Franks NR and Richardson T 2006 Teaching in tandem-running ants. *Nature* **439** 153–153

Garland EC, Garrigue C and Noad MJ 2021 When does cultural evolution become cumulative culture? A case study of humpback whale song. *Philos. Trans. R. Soc. B* **377** 20200313

Giurfa M, Hammer M, Stach S, *et al.* 1999 Pattern learning by honeybees: Conditioning procedure and recognition strategy. *Anim. Behav.* **57** 315–324

Giurfa M, Zhang S, Jenett A, *et al.* 2001 The concepts of 'sameness' and 'difference' in an insect. *Nature* **410** 930–933

Heyes C 2012 What's social about social learning? *J. Comp. Psychol.* **126** 193–202

Heyes C 1994 Social learning in animals: categories and mechanisms. *Biol. Rev.* **69** 207–231

Howard SR and Barron AB 2024 Understanding the limits to animal cognition. *Curr. Biol.* **34** R294–R300

Jones PL, Ryan MJ and Chittka L 2015 The influence of past experience with flower reward quality on social learning in bumblebees. *Anim. Behav.* **101** 11–18

Kawaguchi LG, Ohashi K and Toquenaga Y 2007 Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. *Proc. R. Soc. B Biol. Sci.* **274** 2661–2667

Leadbeater E 2015 What evolves in the evolution of social learning? *J. Zool.* **295** 4–11

Leadbeater E and Chittka L 2009 Bumble-bees learn the value of social cues through experience. *Biol. Lett.* **5** 310–312

Leadbeater E and Chittka L 2007 The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav. Ecol. Sociobiol.* **61** 1789–1796

Leadbeater E and Chittka L 2005 A new mode of information transfer in foraging bumblebees? *Curr. Biol.* **15** R447–R448

Leadbeater E and Dawson EH 2017 A social insect perspective on the evolution of social learning mechanisms. *Proc. Natl. Acad. Sci. USA* **114** 7838–7845

Loukola OJ, Solvi C, Coscos L, *et al*. 2017 Bumblebees show cognitive flexibility by improving on an observed complex behavior. *Science* **355** 833–836

MaBouDi HD, Galpayage Dona HS, Gatto E, *et al*. 2020 Bumblebees use sequential scanning of countable items in visual patterns to solve numerosity tasks. *Integr. Comp. Biol.* **60** 929–942

Mirwan HB and Kevan PG 2014 Problem solving by worker bumblebees *Bombus impatiens* (Hymenoptera: Apoidea). *Anim. Cogn.* **17** 1053–1061

Corresponding editor: Renee M Borges

Saleh N, Ohashi K, Thomson JD, *et al*. 2006 Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. *Anim. Behav.* **71** 847–854

Smolla M, Alem S, Chittka L, *et al*. 2016 Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. *Biol. Lett.* **12** 20160188

Worden BD and Papaj DR 2005 Flower choice copying in bumblebees. *Biol. Lett.* **1** 504–507