# Ants resort to heuristics when facing relational-learning tasks they cannot solve

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## Abstract

We humans sort the world around us into conceptual groups, such as ‘the same’ or ‘different’, which facilitates many cognitive tasks. Applying such abstract concepts can improve problem-solving success and is therefore worth the cognitive investment. In this study, we investigated whether ants (*Lasius niger*) can learn the relational rule of ‘the same’ or ‘different’ by training them in an odour match-to-sample test over 48 visits. While ants in the ‘different’ treatment improved significantly over time, reaching around 65% correct decisions, ants in the ‘same’ treatment did not. Ants did not seem able to learn such abstract relational concepts, but instead created their own individual strategy to try to solve the problem: some ants decided to ‘always go left’, others preferred a ‘go to the more salient cue’ heuristic which systematically biased their decisions. These heuristics even occasionally lowered the success rate in the experiment below chance, indicating that following *any* rule may be more desirable then making truly random decisions. As the fact that ants resort to heuristics when facing hard-to-solve decisions was discovered post-hoc, we strongly encourage other researchers to ask whether heuristic development in the face of challenging tasks is a widespread phenomenon in insects.

**Key words**

Heuristics; rule learning; concept learning; ants; cognition;

## Introduction

As humans, we group objects that belong together into categories (classes of items) using learned concepts (mental representations of classes) (Lazareva and Wasserman 2008). While perceptual concepts allow the categorisation of objects by their similar appearance or function (e.g. trees or toys), relational concepts, by contrast, are more abstract and use non-physical features such as the relationship between objects (e.g. ‘same’ or ‘different’) (Lazareva and Wasserman 2008; Zentall et al. 2002; 2008; 2014). Once an animal has learned an abstract concept such as ‘the same’, it can be transferred and used on other stimuli irrespective of their physical nature, i.e. of the employed sensory modality (Avarguès-Weber and Giurfa 2013). The formation of abstract concepts has traditionally been considered a higher-order ability (Katz et al. 2002) and accordingly most concept learning research focussed on vertebrates such as monkeys (Basile et al. 2015; Wasserman et al. 2001; Wright and Katz 2007), birds (Gibson et al. 2006; Martinho and Kacelnik 2016; Pepperberg 1987; Wright et al. 2017) or rats (Peña et al. 2006; Wasserman et al. 2012).

But abstract association learning is not limited to vertebrates. Honeybees have also repeatedly been shown to successfully learn and apply abstract concepts, such as same/different (Giurfa et al. 2001), above/below (Avarguès-Weber et al. 2011; 2012) or numerosity (Howard et al. 2018). In the first demonstration of concept learning, Giurfa et al. (2001) demonstrated that honeybees are not only able to learn a ‘the same’ or ‘different’ task, but also transfer the learned concept from colour to pattern stimuli (or *vice versa*), and even from one modality (colour) to another (odour).

However, how honeybees solve those complex tasks and whether solving them requires equally complex cognition is still debated. Several honeybee brain models suggest that apparent ‘higher-order’ learning could be based on very simple brain circuits (Cope et al. 2018; Peng and Chittka 2017; Roper et al. 2017; Vasas and Chittka 2019). Solving those tasks could be facilitated by behavioural strategies such as sequential scanning of stimuli (Vasas and Chittka 2019), and behavioural studies have argued that honeybees’ success in same/different tasks could be mediated by appetitive or aversive modulation of their innate tendency to revisit similar flowers (Collett 2005, but see Brown and Sayde 2013) or by sensory accommodation, i.e. reduced response to repeated stimuli (Cope et al. 2018), without the need to form a concept.

A recent experiment that closely examined the strategies deployed by bees while learning an above/below concept found that they can use sequential inspection of the presented items to succeed in the task, without the need for a spatial concept (Guiraud et al. 2018). However, this might only be true for close-up inspection of the objects by the bees, which is not possible for decisions made from afar in a Y-maze (Giurfa et al. 2001).

Irrespective of the underlying mechanisms, studies have shown that the usage of concepts can vary between individuals: Successful training requires many visits (60 in Giurfa et al. 2001) and not all bees can go on to apply the concept to novel stimuli (60-80% successful transfer in Avarguès-Weber et al. 2011; 2012; Giurfa et al. 2001; 50-70% in Guiraud et al. 2018, 60-70% in Brown and Sayde 2013 in bumblebees), suggesting that some bees either failed to complete the task or had to rely on other strategies to solve it. This is in accordance with the finding that animal species which were initially unable to learn concepts succeeded after the number of training pairs was increased to a point were associative learning became inefficient (Wright and Katz 2006). That might indicate that animals employ concept learning only after other strategies fail.

Cognitive mechanisms have not evolved to accurately reflect the real world, but to provide decisions which maximise fitness gains (Haselton et al. 2015). Sometimes, quick heuristics (rules of thumb) can surpass more sophisticated strategies by rapidly finding acceptable solutions to a problem at the cost of accuracy (Gigerenzer and Gaissmaier 2015; Haselton et al. 2015; Mhatre and Robert 2018). In other words, if false-positives (actions which lead to an error) only induce minor costs or if the foraging context is highly variable, animals might resort to heuristics instead of learning the precise solution (Arkes 1991; Haselton et al. 2015). Heuristics could pre-equip animals to solve complex problems, e.g. nest size estimation by scouting ants using the frequency of their own trail crossings (Buffon’s needle; Mallon and Franks 2000), best-of-N rule in nest-searching honeybee swarms (Seeley and Buhrman 2001) or prey interception in dragonflies (Lin and Leonardo 2017).

While research on concept learning (Avarguès-Weber et al. 2011; 2012; Brown and Sayde 2013; Giurfa et al. 2001; Guiraud et al. 2018; Howard et al. 2018) and other abilities of honeybees such as metacognition (Perry and Barron 2013) are now being supplemented by studies modelling potential neural mechanisms (MaBouDi et al. 2017; Peng and Chittka 2017; Seilheimer et al. 2014; Vasas and Chittka 2019), studies on complex cognition in insects other than honeybees remain very scarce (Brown and Sayde 2013; Tibbetts et al. 2019). Yet, the prerequisites assumed to be crucial for concept learning are met by other Hymenoptera, such as ants (Avarguès-Weber and Giurfa 2013). *Lasius niger* ants are adept learners and can quickly form associative memories for odours (Oberhauser et al. 2019) which they use to remember food locations (Czaczkes et al. 2014) and can memorise information about a value to compare it to sensory input (Wendt et al. 2019).

In this study, we investigated *Lasius niger* ants’ ability to learn the relational rule of ‘the same’ or ‘different’. Ants were trained on a Y-maze and continuously confronted with new odour pairs, and only matching (or non-matching in the ‘different’ treatment) the stem odour to the arm odour led to a reward. Thus, ants could only succeed when using the relationship between the stimuli as guidance, i.e. when they applied a relational rule.

## Material and methods

### (a) Collection and rearing of colonies

Eight stock colonies of the black garden ant *Lasius niger* were collected on the University of Regensburg campus and kept in plastic foraging boxes with a layer of plaster of Paris on the bottom. Each box contained a circular plaster nest (14 cm diameter, 2 cm high). The collected colonies were queenless and consisted of 500-1000 workers. Queenless colonies forage and lay pheromone trails, and are frequently used in foraging and learning experiments (Devigne and Detrain 2002; Dussutour et al. 2005; Grüter et al. 2015). All colonies were kept on a 12:12 day/night cycle and were provided *ad libitum* with water and 1M sucrose solution and supplemental *Drosophila* feeding. The colonies were deprived of food for 4 days prior to each trial. Tested ants were permanently removed from the colony to prevent pseudo-replication.

### (b) Solutions and odours

1M sucrose and 60mM quinine (both Merck KGaA, Darmstadt, Germany) solutions were used as reward and aversive stimulus during the experiment, respectively. Quinine punishment was found to improve visual discrimination learning in honeybees (Avarguès-Weber et al. 2010) and has also been used in learning paradigms in ants (d'Ettorre et al. 2017; Dupuy et al. 2006; Guerrieri and d'Ettorre 2010; Josens et al. 2009). Paper runways were impregnated with one of 12 different essential oils (Mit allen 5 Sinnen, Grünwald, Germany; see table S1 & electronic supplementary material (ESM) 3) by keeping runways in an enclosed box containing 100 µl of the corresponding essential oil on filter paper for > 2 h (see also Oberhauser et al. 2019). To control for potential influences of shared compounds between oils (see below), we compared all the identified compounds of each corresponding oil from the literature. Linalool was found to be present in 6 of the tested odours at a percentage of at least 5% (see ESM1); we therefore considered a potential heuristic under which ants chose whichever scent contained linalool (see below). A list of all oils and their compounds are provided in ESM3.

### (c) Experimental procedure

Ants were allowed onto a Y-maze (following Czaczkes 2018) via a drawbridge. The Y-maze was surrounded by a barrier to prevent landmark orientation (see figure 1 & figure S1). Each visit, we presented the ant with a new combination of odours (new odour pair) by placing scented overlays over the Y-maze stem and arms, which were replaced by new overlays the next visit. One odour was present on one arm, while the other was present on both stem and arm (see figure 1). In order to find a reward (1M sucrose), ants had to non-match (‘different’ treatment) or match (‘same’ treatment) the odour present on the stem with that on the arm, while the incorrect arm led to quinine punishment. This way, the only predictor for the rewarded Y-maze side available to the ants was the relationship between odours, not the odour identity. As soon as an ant crossed a decision line 2cm inwards of either arm, this was scored as its first decision. Touching either the sucrose or quinine droplet was scored as final decision.

To begin an experiment, 3-5 ants were allowed onto the maze. The first ant to reach the reward was marked with acrylic paint and all other ants were returned to the nest. From now on, only the marked ant was allowed onto the setup via the drawbridge to make 48 visits to 48 different odour pairs. While each pair was unique, each odour was presented multiple times over the course of the experiment. To prevent differences in reward association strengths between odours, each odour was presented as rewarded or unrewarded odour in alteration. Thus, each odour was rewarded approximately once in 12 visits, resulting in 4 rewarded visits per odour (see ESM1). As we did not have preference data on all odour pairs, we used a fixed experimental procedure, in which all ants experienced the same odour sequence (see table S1). This allowed us to investigate possible odour pair induced effects (e.g. ants always prefer odour A to B). Moreover, as the procedure was fixed, we could compare the two concepts (same/different) at each visit by taking the inverse performance of one of them (correct choice in the ‘different’ treatment = went to different odour = incorrect choice in the ‘same’ treatment). The sequence of left and right was fixed, with each side being rewarded in half of the visits and half of the ants starting with either side being rewarded.

### (d) Statistical analysis

All statistical models were generalized linear mixed-effect models (GLMM) (Bolker et al. 2009) produced with the glmmTMB function (Brooks et al. 2017) in R version 3.6.1 (R Core Team 2019). Since ants from 8 different colonies were tested, each of which made repeated visits, we included each ant ID nested in colony as random intercept factors in all models. Each model was tested for fit and dispersion using the DHARMa package (Hartig 2019). Post-hoc tests were conducted using estimated marginal means (Lenth 2019). Receiver Operating Characteristics (ROC) curves (Fawcett 2006) were calculated using the package pROC (Robin et al. 2011).

#### Rule learning performance

The performance (correct/incorrect decisions) of ants was analysed separately for the ‘same’ and the ‘different’ treatment. The binomial GLMM predictors were defined *a priori*, following Forstmeier and Schielzeth (2011), as:

*Decision (correct/incorrect) ~ Visit (1:48) \* Side (left/right) + random intercept (Colony/Ant\_ID)*

Furthermore, as the succession of odours was identical in both treatments, an incorrect choice in the ‘same’ treatment corresponds to a correct choice in the ‘different’ treatment. Therefore, we could directly compare performance between the treatments by calculating an inverse performance for the ‘same’ treatment (correct decision scored as incorrect and *vice versa*). For this comparison, we ran a binomial GLMM with performance as dependent variable and treatment (‘different’, ‘same inversed’) as predictor (see ESM1).

#### Streak lengths

To obtain an estimate of individual performance consistency, we calculated the longest streaks (visits in a row) of correct, incorrect, left, and right decisions, and the visit the corresponding streak started at (referred to as streak onset). For both streak length and streak onset, we ran separate GLMMs for correct/incorrect streaks or side streaks as predictors:

*Streak length OR Streak onset ~ Streak type (correct/incorrect OR left/right) \* Treatment (same/different) + random intercept (Colony/Ant\_ID)*

In case a Poisson error distribution was inadequate, a negative binomial distribution was used (see ESM1).

#### Heuristics

To analyse whether ants might have used specific rules to guide their decisions, we considered and then tested six potential heuristics: ‘go to different odour than stem’, which can also be described as ‘go to more salient cue’ (see discussion), ‘go to odour as stem’, ‘go left’, ‘go right’, ‘go last rewarded’ or ‘go linalool’ (see table 1). A score was calculated for each ant and heuristic, by scoring 1 for each visit the ant’s decision was following the corresponding rule, and 0 if it did not. In ‘go to the more salient cue’, each visit was scored 1 when the ant went to the odour different to the stem. In ‘go left’, we scored 1 for each visit the ant went left and *vice versa* for ‘go right’. In ‘go last’ we scored 1 when an ant went to the Y-maze arm which was rewarded on the previous visit (see table 1). As our ants always found a reward at the end of each trial, this corresponds to a win-stay strategy. Please note that both ‘go to same/different’ and ‘go left/right’ are mutually exclusive – an ant which always choses the different odour or left side cannot also chose ‘same’ and ‘right’.

The additional, sixth, heuristic, ‘go linalool’ was introduced to account for it being a shared compound of 6 of the odours used (see solutions and odours section) and scored 1 if ants chose an odour containing linalool. However, in 22 visits linalool was either present or missing on both arms thus making it impossible to conclude whether ants were using it as a heuristic or choosing randomly in those visits. Accordingly, we also performed an analysis including only visits in which linalool was present on one arm per visit. Similarly, we also investigated whether odour preferences of ants could explain the results (see ESM1).

To identify potential heuristic usage at the individual level, we counted, for each, heuristic all ants which chose in accordance to each heuristic in at least 2/3 (66.6%) of visits (32/48). To also assess the false-positive rate of this arbitrarily-set-threshold procedure, we ran a simulation using the same reward side pattern used in the experiments (see table S1) with random choices. We simulated 40000 ants (four different random generator seeds, 10000 iterations each). The result was added in figure 4 to provide information about how often a heuristic would be assigned by chance alone.

To estimate the predictive power of the heuristics on group level, we produced a model for each heuristic using the formula:

*Performance*(correct/incorrect) ~ *Heuristic*(correct/incorrect) + *random intercept*(Colony/Ant).

For each visit of each ant, the model thus compared the ant’s decision (performance) with the predicted decision of the heuristic. To compare the predictive power of each model, we established Recipient Operant Characteristic (ROC) curves (Fawcett 2006) for each heuristic and a null model containing only the random effect (ant ID and colony). The predictive power of all models was then compared using Area under the Curve (AUC) values of each ROC.

### Data accessibility

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## Results

In total, 55 ants were tested. However, 7 ants performed fewer than 48 visits and one ant was accidentally trained on a different sequence of odour pairs. These ants were excluded from the analysis, resulting in 19 and 18 tested ants in the ‘different’ and ‘same’ concept treatments, respectively. One ant had two visits with a different odour-pair combination. It was left in as its removal did not affect the results in a significant way.

### Rule learning performance

If ants learned the relational rule to go to ‘same’ or ‘different’, we should observe a significant increase in correct choices over time. In the ‘different’ treatment, ants indeed improved significantly over 48 visits (binomial GLMM, χ2 = 5.724, p = 0.0167, see figure 2A). Furthermore, ants’ performance was significantly higher when the reward was presented on the left (χ2 = 5.8525, p = 0.0155). No significant interaction between visit and reward side was found (χ2 = 0.03, p = 0.8537), so performance was not better, for instance, at early visits and reward on the left. Note that we included ‘reward side’ in the model and present it here due to *L. niger*’s tendency for left biases (Oberhauser et al. 2018; 2019), and we therefore chose to include it in the *a priori* model. A separate test for the ‘go left’ heuristic is presented below.

By contrast, no improvement over visits was found in the ‘same’ treatment (binomial GLMM, χ2 = 0.2546, p = 0.6138, see figure 2B), but a significantly higher proportion of correct visits was made when the reward was on the left (χ2 = 34.4, p < 0.001). Again, no significant interaction between visit and reward side was found (χ2 = 0.03, p = 0.8549). In both treatments, the majority of ants (~92%) did not switch sides between entering one arm (first decision) and touching the droplet (final decision), the rest switched from the correct to the incorrect side (~5%), or *vice versa* (~3%, see figure 2). For simplicity, due to these small differences, we only used the first decision of each ant as measure of performance in subsequent analyses.

When we directly compared the two treatments, we found a significantly better performance in the ‘different’ treatment (binomial GLMM, χ2 = 20.6961, p < 0.001, see figure 2C). However, there was no significant difference between performance in the ‘different’ task and the inverse of performance on the ‘same’ task (χ2 = 0.4255, p = 0.5142, see figure 2C). This implies that ants responded in a similar way towards the encountered stimuli irrespective of the treatment.

### Streaks

Group level analyses do not adequately capture individual behaviour (Pamir et al. 2011) and a poor group performance can mask individuals which managed to learn the task. On an individual level, consistency is a good measure of learning. If ants learned the task, we would expect them to display longer streaks of correct decisions, as they repeatedly choose the correct Y-maze arm. Our analysis revealed a significant interaction between treatment (same/different) and streak type (correct/incorrect) (χ2 = 8.9718, p = 0.0027) which is reflected by significantly longer correct than incorrect streaks in the ‘different’ treatment, but the opposite pattern in the ‘same’ treatment (Estimated marginal mean contrasts, ratio = 1.372, p = 0.0374; ratio = 0.723, p = 0.0382, respectively, see figure 3A). The longest correct streaks were 9 visits long in both treatments, whereas the longest incorrect streaks spanned 10 and 11 visits (‘different’ and ‘same’, respectively).

Furthermore, we found that some ants displayed strong side biases. The length of left side streaks was significantly longer than right streaks (χ2 = 5.0779, p = 0.0242), and estimated marginal mean contrasts revealed that this was within ants in the ‘same’ treatment (ratio = 0.635, p = 0.0219), but not within the ‘different’ treatment (ratio = 0.851, p = 0.3788). The longest left streak in the different treatment was 17 visits, while one ant in the ‘same’ treatment went left 27 times in a row (56% of visits, an event that is expected to happen by chance at a rate of less than 1 per twelve thousand billion). Longest right streaks were 19 and 9 visits long (‘different’ and ‘same’, respectively).

The onset of correct streaks during training started consistently later than incorrect streaks (χ2 = 8.4317, p = 0.0037, see figure 3B), but the effect was significant in the ‘different’ treatment only (contrasts: ‘different’: ratio = 2.107, p = 0.0034; ‘same’: ratio = 1.093, p = 0.2782). The onsets of left and right streaks did not differ significantly (χ2 = 0.0001, p = 0.9941).

### Heuristics

To analyse which potential heuristics were used by individual ants (see table 1), we assigned each ant to a heuristic if it chose the arm the heuristic would suggest in at least 2/3 (66.6%) of its visits. This proportion corresponds to p < 0.05 in 48 visits when chance of being correct is 50%. Using this method, we found that 58% (11/19) of ants in the ‘different’ treatment deployed a heuristic according to our criterion, as did 56% (10/18) of ants in the ‘same’ treatment (two ants could have been using two heuristics, see table 1 and figure 4). Our simulation result demonstrated that the chance of meeting the criterion by choosing randomly was only 5.5% (2198 of 40000 simulations).

The most prominent heuristic in both treatments was to go to the odour different from the stem (‘go different’). Further analyses including a potential ‘go linalool’ heuristic on the 26 visits did not find any indication of a ‘go linalool’ heuristic. Also, a close look at odour preferences by ant revealed a preference for sandalwood, which, however, could not explain the observed results (see ESM1).

An explicit threshold (here 66.6%) increases clarity but does not provide information on how faithfully an ant follows a given heuristic. Thus, we provide an additional figure with scores for all heuristics per ant in the supplement (see figure S2A & B).

To estimate how well performance of ants can be classified using heuristics on group level, we compared Area under the Curve values (AUC) of each ROC model based on heuristic to a null model (only including colony and ant). The AUC values differed only slightly (±0.02) from the null model with an AUC of 0.651 (see ESM1). The null model was thus highly explanatory and demonstrated that performance is best described by the individual ant, with no dominant heuristic at the group level.

## Discussion

Our experiment revealed that ants were able to significantly improve their performance in a non-matching-to-sample (NMTS) task, where they had to choose a Y-maze arm odour which was different from a sample odour presented on the stem to find a reward. However, ants failed to improve in a match-to-sample (MTS) task, as we hypothesised they would. Our analyses suggest that ants did not use a relational rule of same/different to guide their decisions, and may not be able to do so. Rather, they seemed to base their decisions on heuristics such as ‘go left’ or ‘go to the most salient cue’ (see below).

Although significant, the increase in performance in the ‘different’ treatment was modest, with 65% correct decisions (74/114) in the last bin compared to 60% (68/114) in the first bin (see figure 2A). While we do expect a high proportion of ants failing to learn complex tasks due to individual variation in learning abilities (Chittka et al. 2012), the high initial performance of 60% correct decisions and the fact that the ants’ performance did not resemble an asymptotic learning curve suggests that the majority of ants did not rely on learning. Rather, the high initial performance indicates that some ants used unlearned heuristics to systematically guide their decisions. Moreover, the fact that the inverse overall performance of ants in the ‘same’ treatment resembled that of the ‘different’ treatment (figure 2C) also suggests that ants were not learning and using a relational rule of ‘different’ but rather other cues common to both treatments. It is worth noting that the low performance in the second bin (figure 2A) in the ‘different’ treatment suggests initial learning attempts, as ants predominantly chose the odours presented at the stem which were acting as targets and thus rewarded in the first six visits.

However, considering averaged performance might mask individuals which did manage to learn to go to ‘same’ or to ‘different’. To estimate individual performance consistency, we analysed the length of observed streaks, i.e. visits in a row which were correct or incorrect. If learning occurred, we would expect longer correct streaks with an onset in the latter part of the visits. Conversely, incorrect streaks should be short and their onset randomly distributed. Indeed, ants in the ‘different’ treatment had significantly longer correct than incorrect streaks, which started significantly later than incorrect streaks (see figure 3). This suggests that ants did modify their behaviour over the course of the treatment. Conversely, ants had significantly longer incorrect streaks in the ‘same’ treatment, again indicating that ants acted similarly in both treatments. These findings suggest that ants did not learn a relational rule, as we originally hypothesised they would.

Instead, we believe that these response similarities are due to ants’ attempts to follow heuristics unrelated to the treatments. The frequency at which ants decided to ‘go different’ is particularly noteworthy, as its successful application seems to suggest that ants did use a relational rule of ‘different’. However, our setup lacked a ‘neutral’ area devoid of the sample odour (no *delayed* MTS), as the scented stem paper overlay extended until the decision area. Therefore, while walking over the stem overlay, the ant was continuously exposed to the same odour right until the decision point. This could have caused sensory adaptation – the gradual adaptation of receptors to continuous stimulation – which leads to reduced sensation. At the decision point, a new odour would then be perceived as more salient, which, in turn, could be the target of associative learning. Thus, the tested ants might have associated the more salient cue as rewarding. This also well explains the similarity of the inverse performance of the ‘same’ treatment with that of ‘different’ (see figure 2C) and that ants improved their performance over visits in the ‘different’ treatment. In other words, the ants might have not used the heuristic ‘go different’ but rather ‘go to the most salient cue’.

At a first glance, the sensory adaptation hypothesis does not seem to explain why ants would also use this rule in the ‘same’ treatment. However, in our experiment, once the ant had made a wrong decision, it was allowed to correct itself by walking to the other arm. It thus again experienced a change in odours. In other words, using ‘go to the more salient odour’ leads to reward in both treatments, but in the ‘same’ treatment requires two choices to follow the different odour. Such persistence of erroneous behaviour was also reported in a study by Macquart et al. (2008), where ants took longer to learn a new rule once a misleading rule was in place. Zhang (2000) also reported that two bees persisted to use a rule to ‘always go to one side’ which took longer but also allowed them to navigate the maze.

Heuristics can provide a rule which may be better than stepwise optimisation through learning in cases of highly complex or uncertain information, and where the costs of errors are low (Gigerenzer and Gaissmaier 2015). Our analyses of ants’ decisions revealed that half of the ants in both treatments chose in a manner consistent with ‘go to different (the more salient odour)’ or ‘go left/right’ in at least 66.6% (32/48) of their visits (figure 4). This was not the case for other potential heuristics such as ‘go to the last rewarded side’ or ‘go to linalool’. It is important to note that our assignment of heuristics is not mutually exclusive. In some visits, ants could have chosen in a manner consistent with more than one heuristic. A ROC analysis further showed that no single heuristic could predict the pooled performance of the ants. This is interesting, as it highlights that heuristics are individual specific, i.e. each ant chooses differently. It is important to emphasise that these interpretations of the results are *post-hoc* in nature and highlight an interesting avenue for required future studies on heuristic use in insects.

Many ants also chose to ‘go left’ during our treatment. Side biases are commonly observed in many animals (Andrade et al. 2001; Bell and Niven 2014; Hunt et al. 2014), and *Lasius niger* are no exception. They were found to display right (Vallortigara and Rogers 2005) and also left biases (Oberhauser et al. 2018). In our study, ants displayed very long streaks to both sides (see figure 3A), but the majority were to the left. The left bias was especially strong in the ‘same’ treatment, with one ant choosing left 27 visits in a row. Such a consistent side bias is intriguing, as the reward side was balanced and led to only 50% success. The lack of improvement and the high prevalence of a left bias in the ‘same’ treatment indicates that a fraction of ants tend to ‘default’ to a side bias when failing to extract a rule from a constantly changing environment. A side bias might lessen the cognitive load of foraging ants, as a sequence does not require the ant to memorise each decision. Indeed, maze studies have been found that ants and bees best memorise repeating sequences such as left-left (Czaczkes et al. 2013; Macquart et al. 2008; Zhang 2000).

Use of heuristics is promoted when error costs are low (Arkes 1991; Haselton et al. 2015). The costs of making a wrong decision might have been too small to promote careful decisions in our setup. If wrong, ants encountered quinine instead of sucrose at the arm’s end. However, after the first encounter with quinine, ants usually approached the droplet very carefully and identified the quinine with their antennae, thereby diminishing its effect as negative reinforcer. Similarly, Josens et al. (2009) also found weak effects of quinine on freely moving ants in a Y-maze. Furthermore, the cost of moving from one arm to the other is likely negligible for the ant in terms of both time and energy.

It is important to note that this experiment was not *a priori* designed to demonstrate heuristic learning in ants – this as a post-hoc insight we gained while running the experiment. We have since replicated the result that, when facing a Y-maze task which we intentionally made unsolvable, ants pick a favoured arm (left or right) and choose for tens of repeated visits (unpublished data). Nonetheless, our results should be taken with caution due to their post-hoc nature, and we strongly encourage other researchers to continue this research direction, validating our findings with *a priori* tests of heuristic use.

In conclusion, no convincing evidence for relational rule learning was found. Rather, we found that ants have a high propensity to resort to heuristics in the face of a complex challenge, sacrificing accuracy for speed and ease of applicability. They even did so when the chosen heuristic led to poorer results than expected by chance. It thus seems that, in some situations, following even an inappropriate heuristic is easier, or in some way preferable, to random choice. Cognitive processes have not evolved to ascertain objective reality, but to provide decisions which maximise fitness gains (Haselton et al. 2015). Heuristics often provide decision rules which can solve a given task quickly and with reasonable error and can range from simple rules such as ‘go left’ to sophisticated sets of rules orchestrating behaviours with highly complex outcomes, such as honeycomb construction by bees (Nazzi 2016). Facing a complex challenge, animals might change heuristics or even modify them by learning (Mhatre and Robert 2018). And indeed, the ants in our study showed striking individual differences, with different ants settling on different heuristics such as ‘go left’, ‘go to the more salient cue’, or ‘go right’. But many would rather use heuristics than simply leaving matters to chance.

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**Authors’ contributions**

FBO and TJC conceived the experiment, FBO and AK collected the data, FBO and MdA analysed the data, FBO wrote the manuscript, all authors revised the draft. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

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**Conflict of interest**

The authors declare that they have no conflict of interest.

**Ethical approval**

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## Figure captions

Figure 1. Setup used for the ‘different’ and ‘same’ treatment. The Y-maze shown on the left depicts the first visit of the ‘different’ treatment (see table on the top right for details). Each visit, ants encountered a new odour pair by walking over scented paper overlays. The sample odour was present on the stem and on one arm. In the ‘different’ treatment, the ant had to go to the arm with the odour different from the sample to find reward (1M sucrose, right on the first visit). In the ‘same’ treatment, the rewarded and punished (quinine) side were swapped (see inset table). The procedure was then continued for the remaining 45 visits with other unique odour pairs, the first three of which are shown here. All scented paper overlays were white, colours are only used for illustration purposes.

Figure 2. Performance of ants over subsequent visits in **(A)** the ‘different’ treatment (n = 19) and **(B)** the ‘same’ treatment (n = 18). **(C)** Performance averaged over all 48 visits. The inverse performance (correct = incorrect and vice versa) of ants in the ‘same’ experiment (‘same inversed’) resembles performance of the ‘different’ treatment. Dashed line represents chance level of 50%. Symbols are means, error bars represent 95% bootstrapped confidence intervals.

Figure 3. **(A)** The longest streaks of correct and incorrect decisions (left) and left and right decisions (right) for each ant and treatment. Three ants with very long streaks (2 left streaks, 27 & 17 visits long; 1 right streak, 19 visits) are not shown. Ants made significantly longer correct streaks in the ‘different’ treatment (p = 0.0374), while the opposite was found in the ‘same’ treatment (p = 0.0382). Left streaks tended to be longer in both treatments, but this difference was significant in the ‘same’ treatment only (p = 0.0219) **(B)** Visits until streak onset for correct and incorrect streaks (left) and left and right streaks (right). Correct streaks started in later visits in both treatments, but this difference was significant in the ‘different’ treatment only (p = 0.0034). No difference was found in the onsets of left and right streaks. Points represent individual ants, horizontal lines in boxes are medians, boxes correspond to first and third quartiles and whiskers extend to the largest value within 1.5 x IQR.

Figure 4. Percentage of ants which used a defined strategy for a minimum of 2/3 of their visits in the ‘different’ (n = 19) and ‘same’ treatment (n = 18) and in a simulation using random choices. Over half of the ants acted according to a certain heuristic in the two treatments, while random guessing would only lead to such a behaviour in 5.5% of cases according to the simulation results. Note that the choices of two ants could be assigned to two different heuristics (once ‘go left’ and ‘go different’, once ‘go last’ and ‘go different’, labelled ‘Two’).

## Table caption

|  |
| --- |
| Table 1. Definitions of potential heuristics and how many ants chose corresponding to them for ≥ 66.6% of 48 visits. Please note that two ants in the ‘same’ treatment could be assigned to either ‘go left’ or ‘go last’ in addition to ‘go different’, thus totalling to 20 instead of 18. \* Linalool heuristic was calculated from subset of 22 visits. |

## Supplementary material



Figure S2. Proportion of visits individual ants acted in accordance with a certain heuristic in the ‘different’ treatment (A) and ‘same’ treatment (B). Each panel corresponds to an individual ant. Each ant which had at least one heuristic surpassing the threshold of 2/3 of visits is highlighted with light green. Note that the heuristics ‘go left’ and ‘go different’ can also mean ‘go right’ or ‘go same’ if the value is below 1/3. Each heuristic which is surpassing the threshold is shown with a triangle shape. Additionally, the top of each panel shows the heuristic with the highest accordance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Table S1. Sequence of odours used for both ‘same’ and ‘difference’ treatments. On each visit, ants encountered a different unique odour pair. The sample odour on the stem had to either be matched to the target odour on one arm (‘same’) or non-matched (‘difference’). This table shows the 'difference' treatment, in which reward was placed on the end of the arm with an odour other than the stem (non-match rewarded). In the ‘same’ treatment, the succession of pairs was identical, but reward was on the arm with the same odour as the stem. Half of the ants started with L (left), half with R (right, shown here). | | | | | | | |
| **Visit** | **Sample** | **Target** | **Reward side** | **Visit** | **Sample** | **Target** | **Reward side** |
| **1** | bergamot | sandalwood | R | **25** | bergamot | peppermint | L |
| **2** | cypress | geranium | L | **26** | cypress | melissa | L |
| **3** | basil | ylang-ylang | R | **27** | basil | sandalwood | R |
| **4** | clove | lemon | L | **28** | clove | geranium | L |
| **5** | rosemary | peppermint | R | **29** | rosemary | ylang-ylang | R |
| **6** | lavender | melissa | L | **30** | lavender | lemon | L |
| **7** | geranium | bergamot | R | **31** | melissa | bergamot | R |
| **8** | ylang-ylang | cypress | L | **32** | sandalwood | cypress | R |
| **9** | lemon | basil | L | **33** | geranium | basil | L |
| **10** | peppermint | clove | R | **34** | ylang-ylang | clove | L |
| **11** | melissa | rosemary | R | **35** | lemon | rosemary | R |
| **12** | sandalwood | lavender | L | **36** | peppermint | lavender | L |
| **13** | bergamot | ylang-ylang | R | **37** | bergamot | clove | L |
| **14** | cypress | lemon | L | **38** | cypress | rosemary | R |
| **15** | basil | peppermint | R | **39** | basil | lavender | R |
| **16** | clove | melissa | R | **40** | sandalwood | lemon | L |
| **17** | rosemary | sandalwood | L | **41** | geranium | peppermint | R |
| **18** | lavender | geranium | L | **42** | ylang-ylang | melissa | L |
| **19** | lemon | bergamot | R | **43** | rosemary | bergamot | R |
| **20** | peppermint | cypress | L | **44** | lavender | cypress | L |
| **21** | melissa | basil | R | **45** | clove | basil | L |
| **22** | sandalwood | clove | L | **46** | peppermint | sandalwood | R |
| **23** | geranium | rosemary | R | **47** | melissa | geranium | R |
| **24** | ylang-ylang | lavender | R | **48** | lemon | ylang-ylang | L |

References

Andrade C, Alwarshetty M, Sudha S, Suresh Chandra J (2001) Effect of innate direction bias on T-maze learning in rats: Implications for research. J Neurosci Methods 110:31–35. https://doi.org/10.1016/S0165-0270(01)00415-0

Arkes HR (1991) Costs and benefits of judgment errors: Implications for debiasing. Psychol Bull 110:486–498. https://doi.org/10.1037/0033-2909.110.3.486

Arrighi R, Togoli I, Burr DC (2014) A generalized sense of number. Proc Royal Soc B 281. https://doi.org/10.1098/rspb.2014.1791

Avarguès-Weber A, Giurfa M (2013) Conceptual learning by miniature brains. Proc Royal Soc B 280:1-9. https://doi.org/10.1098/rspb.2013.1907

Avarguès-Weber A, de Brito Sanchez MG, Giurfa M, Dyer AG (2010) Aversive reinforcement improves visual discrimination learning in free-flying honeybees. PLoS One 5:e15370. https://doi.org/10.1371/journal.pone.0015370

Avarguès-Weber A, Dyer AG, Giurfa M (2011) Conceptualization of above and below relationships by an insect. Proc Royal Soc B 278:898–905. https://doi.org/10.1098/rspb.2010.1891

Avarguès-Weber A, Dyer AG, Combe M, Giurfa M (2012) Simultaneous mastering of two abstract concepts by the miniature brain of bees. Proc Natl Acad Sci 109:7481–7486. https://doi.org/10.1073/pnas.1202576109

Basile BM, Moylan EJ, Charles DP, Murray EA (2015) Two-item same/different discrimination in rhesus monkeys (*Macaca mulatta*). Anim Cogn 18:1221–1230. https://doi.org/10.1007/s10071-015-0891-z

Bell ATA, Niven JE (2014) Individual-level, context-dependent handedness in the desert locust. Curr Biol 24:R382-3. https://doi.org/10.1016/j.cub.2014.03.064

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html. The R Journal 9:378–400

Brown MF, Sayde JM (2013) Same/different discrimination by bumblebee colonies. Anim Cogn 16:117–125. https://doi.org/10.1007/s10071-012-0557-z

Chittka L, Rossiter SJ, Skorupski P, Fernando C (2012) What is comparable in comparative cognition? Philos T Roy Soc B 367:2677–2685. https://doi.org/10.1098/rstb.2012.0215

Collett TS (2005) Invertebrate memory: Honeybees with a sense of déjà vu. Curr Biol 15:R419-21. https://doi.org/10.1016/j.cub.2005.05.033

Cope AJ, Vasilaki E, Minors D, Sabo C, Marshall JAR, Barron AB (2018) Abstract concept learning in a simple neural network inspired by the insect brain. PLoS Comput Biol 14:e1006435. https://doi.org/10.1371/journal.pcbi.1006435

Czaczkes TJ, Grüter C, Ellis L, Wood E, Ratnieks FLW (2013) Ant foraging on complex trails: route learning and the role of trail pheromones in *Lasius niger*. J Exp Biol 216:188–197. https://doi.org/10.1242/jeb.076570

Czaczkes TJ, Schlosser L, Heinze J, Witte V (2014) Ants use directionless odour cues to recall odour-associated locations. Behav Ecol Sociobiol 68:981–988. https://doi.org/10.1007/s00265-014-1710-2

Czaczkes TJ (2018) Using T- and Y-mazes in myrmecology and elsewhere: A practical guide. Ins Soc 65:213–224. https://doi.org/10.1007/s00040-018-0621-z

d'Ettorre P, Carere C, Demora L, Le Quinquis P, Signorotti L, Bovet D (2017) Individual differences in exploratory activity relate to cognitive judgement bias in carpenter ants. Behav Processes 134:63–69. https://doi.org/10.1016/j.beproc.2016.09.008

Devigne C, Detrain C (2002) Collective exploration and area marking in the ant *Lasius niger*. Ins Soc 49:357–362. https://doi.org/10.1007/PL00012659

Dupuy F, Sandoz J-C, Giurfa M, Josens R (2006) Individual olfactory learning in *Camponotus* ants. Anim Behav 72:1081–1091. https://doi.org/10.1016/j.anbehav.2006.03.011

Dussutour A, Deneubourg J-L, Fourcassie V (2005) Amplification of individual preferences in a social context: the case of wall-following in ants. Proc Royal Soc B 272:705–714. https://doi.org/10.1098/rspb.2004.2990

Fawcett T (2006) An introduction to ROC analysis. Pattern Recogn Lett 27:861–874. https://doi.org/10.1016/j.patrec.2005.10.010

Forstmeier W, Schielzeth H (2011) Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol 65:47–55. https://doi.org/10.1007/s00265-010-1038-5

Gibson BM, Wasserman EA, Cook RG (2006) Not all same-different discriminations are created equal: Evidence contrary to a unidimensional account of same-different learning. Learn Motiv 37:189–208. https://doi.org/10.1016/j.lmot.2005.06.002

Gigerenzer G, Gaissmaier W (2015) Decision making: Nonrational theories. In: International encyclopedia of the social & behavioral sciences. Elsevier, pp 911–916

Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933. https://doi.org/10.1038/35073582

Grüter C, Maitre D, Blakey A, Cole R, Ratnieks FLW (2015) Collective decision making in a heterogeneous environment: *Lasius niger* colonies preferentially forage at easy to learn locations. Anim Behav 104:189–195. https://doi.org/10.1016/j.anbehav.2015.03.017

Guerrieri FJ, d'Ettorre P (2010) Associative learning in ants: Conditioning of the *maxilla-labium* extension response in *Camponotus aethiops*. J Insect Physiol 56:88–92. https://doi.org/10.1016/j.jinsphys.2009.09.007

Guiraud M, Roper M, Chittka L (2018) High-speed videography reveals how honeybees can turn a spatial concept learning task into a simple discrimination task by stereotyped flight movements and sequential inspection of pattern elements. Front Psychol 9:1–10. https://doi.org/10.3389/fpsyg.2018.01347

Hartig F (2019) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. https://CRAN.R-project.org/package=DHARMa

Haselton MG, Nettle D, Murray DR (2015) The evolution of cognitive bias. In: Buss DM (ed) The handbook of evolutionary psychology, 2nd edition. John Wiley & Sons, Hoboken, New Jersey, pp 968–987

Howard SR, Avarguès-Weber A, Garcia JE, Greentree AD, Dyer AG (2018) Numerical ordering of zero in honey bees. Science 360:1124–1126. https://doi.org/10.1126/science.aar4975

Hunt ER, O'Shea-Wheller T, Albery GF, Bridger TH, Gumn M, Franks NR (2014) Ants show a leftward turning bias when exploring unknown nest sites. Biol Lett 10:1-4. https://doi.org/10.1098/rsbl.2014.0945

Josens R, Eschbach C, Giurfa M (2009) Differential conditioning and long-term olfactory memory in individual *Camponotus fellah* ants. J Exp Biol 212:1904–1911. https://doi.org/10.1242/jeb.030080

Katz JS, Wright AA, Bachevalier J (2002) Mechanisms of same-different abstract-concept learning by rhesus monkeys (*Macaca mulatta*). J Exp Psychol Anim B 28:358–368. https://doi.org/10.1037/0097-7403.28.4.358

Lazareva OF, Wasserman EA (2008) Categories and Concepts in Animals. In: Byrne JH (ed) Learning and memory: A comprehensive reference. Elsevier, Oxford, UK, San Diego, CA, pp 197–226

Lenth R (2019) Emmeans: Estimated marginal means, aka least-squares means. https://CRAN.R-project.org/package=emmeans

Lin H-T, Leonardo A (2017) Heuristic rules underlying dragonfly prey selection and interception. Curr Biol 27:1124–1137. https://doi.org/10.1016/j.cub.2017.03.010

MaBouDi H, Shimazaki H, Giurfa M, Chittka L, Kreiman G (2017) Olfactory learning without the mushroom bodies: Spiking neural network models of the honeybee lateral antennal lobe tract reveal its capacities in odour memory tasks of varied complexities. PLoS Comput Biol 13:e1005551. https://doi.org/10.1371/journal.pcbi.1005551

Macquart D, Latil G, Beugnon G (2008) Sensorimotor sequence learning in the ant *Gigantiops destructor*. Anim Behav 75:1693–1701. https://doi.org/10.1016/j.anbehav.2007.10.023

Mallon EB, Franks NR (2000) Ants estimate area using Buffon's needle. Proc Royal Soc B 267:765–770. https://doi.org/10.1098/rspb.2000.1069

Martinho A, Kacelnik A (2016) Ducklings imprint on the relational concept of "same or different". Science 353:286–288. https://doi.org/10.1126/science.aaf4247

Mhatre N, Robert D (2018) The Drivers of Heuristic Optimization in Insect Object Manufacture and Use. Front Psychol 9:1015. https://doi.org/10.3389/fpsyg.2018.01015

Nazzi F (2016) The hexagonal shape of the honeycomb cells depends on the construction behavior of bees. Sci Rep 6:28341. https://doi.org/10.1038/srep28341

Oberhauser FB, Koch A, Czaczkes TJ (2018) Small differences in learning speed for different food qualities can drive efficient collective foraging in ant colonies. Behav Ecol Sociobiol 72:1–10. https://doi.org/10.1007/s00265-018-2583-6

Oberhauser FB, Schlemm A, Wendt S, Czaczkes TJ (2019) Private information conflict: *Lasius niger* ants prefer olfactory cues to route memory. Anim Cogn. https://doi.org/10.1007/s10071-019-01248-3

Pamir E, Chakroborty NK, Stollhoff N, Gehring KB, Antemann V, Morgenstern L, Felsenberg J, Eisenhardt D, Menzel R, Nawrot MP (2011) Average group behavior does not represent individual behavior in classical conditioning of the honeybee. Learn Mem 18:733–741. https://doi.org/10.1101/lm.2232711

Peña T, Pitts RC, Galizio M (2006) Identity matching-to-sample with olfactory stimuli in rats. J Exp Anal Behav 85:203–221. https://doi.org/10.1901/jeab.2006.111-04

Peng F, Chittka L (2017) A Simple Computational Model of the Bee Mushroom Body Can Explain Seemingly Complex Forms of Olfactory Learning and Memory. Curr Biol 27:224–230. https://doi.org/10.1016/j.cub.2016.10.054

Pepperberg IM (1987) Acquisition of the same/different concept by an African Grey parrot (*Psittacus erithacus*): Learning with respect to categories of color, shape, and material. Anim Learn Behav 15:423–432. https://doi.org/10.3758/BF03205051

Perry CJ, Barron AB (2013) Honey bees selectively avoid difficult choices. Proc Natl Acad Sci 110:19155–19159. https://doi.org/10.1073/pnas.1314571110

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/

Robin X, Turck N, Hainard A, Tiberti N, Lisacek F\a’e, Sanchez J-C, Müller M (2011) pROC: An open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77

Roper M, Fernando C, Chittka L (2017) Insect bio-inspired neural network provides new evidence on how simple feature detectors can enable complex visual generalization and stimulus location invariance in the miniature brain of honeybees. PLoS Comput Biol 13:e1005333. https://doi.org/10.1371/journal.pcbi.1005333

Seeley TD, Buhrman SC (2001) Nest-site selection in honey bees: How well do swarms implement the "best-of- N" decision rule? Behav Ecol Sociobiol 49:416–427. https://doi.org/10.1007/s002650000299

Seilheimer RL, Rosenberg A, Angelaki DE (2014) Models and processes of multisensory cue combination. Curr Opin Neurobiol 25:38–46. https://doi.org/10.1016/j.conb.2013.11.008

Skorupski P, MaBouDi H, Galpayage Dona HS, Chittka L (2017) Counting insects. Philos T Roy Soc B 373. https://doi.org/10.1098/rstb.2016.0513

Tibbetts EA, Agudelo J, Pandit S, Riojas J (2019) Transitive inference in *Polistes* paper wasps. Biol Lett 15:20190015. https://doi.org/10.1098/rsbl.2019.0015

Vallortigara G, Rogers LJ (2005) Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci 28:575-89; discussion 589-633. https://doi.org/10.1017/S0140525X05000105

Vasas V, Chittka L (2019) Insect-inspired sequential inspection strategy enables an artificial network of four neurons to estimate numerosity. iScience 11:85–92. https://doi.org/10.1016/j.isci.2018.12.009

Wasserman EA, Fagot J, Young ME (2001) Same-different conceptualization by baboons (Papio papio): The role of entropy. J Comp Psychol 115:42–52. https://doi.org/10.1037//0735-7036.115.1.42

Wasserman EA, Castro L, Freeman JH (2012) Same-different categorization in rats. Learn Mem 19:142–145. https://doi.org/10.1101/lm.025437.111

Wendt S, Strunk KS, Heinze J, Roider A, Czaczkes TJ (2019) Positive and negative incentive contrasts lead to relative value perception in ants. Elife 8. https://doi.org/10.7554/eLife.45450

Wright AA, Katz JS (2006) Mechanisms of same/different concept learning in primates and avians. Behav Processes 72:234–254. https://doi.org/10.1016/j.beproc.2006.03.009

Wright AA, Katz JS (2007) Generalization hypothesis of abstract-concept learning: Learning strategies and related issues in *Macaca mulatta*, *Cebus apella*, and *Columba livia*. J Comp Psychol 121:387–397. https://doi.org/10.1037/0735-7036.121.4.387

Wright AA, Magnotti JF, Katz JS, Leonard K, Vernouillet A, Kelly DM (2017) Corvids outperform pigeons and primates in learning a basic concept. Psychol Sci 28:437–444. https://doi.org/10.1177/0956797616685871

Zentall TR, Galizio M, Critchfied TS (2002) Categorization, concept learning, and behavior analysis: an introduction. J Exp Anal Behav 78:237–248. https://doi.org/10.1901/jeab.2002.78-237

Zentall TR, Wasserman EA, Lazareva OF, Thompson RKR, Rattermann MJ (2008) Concept learning in animals. CCBR 3. https://doi.org/10.3819/ccbr.2008.30002

Zentall TR, Wasserman EA, Urcuioli PJ (2014) Associative concept learning in animals. J Exp Anal Behav 101:130–151. https://doi.org/10.1002/jeab.55

Zhang S (2000) Maze navigation by honeybees: Learning path regularity. Learn Mem 7:363–374. https://doi.org/10.1101/lm.32900