Ants combine object affordance with latent learning to make efficient foraging decisions

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The affordance of an object refers to its functional properties. For example, a bowl has the affordance of holding water, but a sieve does not. Here, we report that ants learn the affordance of a novel object without this attribute being rewarded, and use the memory of this affordance to avoid predicted, but never experienced, crowding. Ants were trained to feeders, which could support either only one ant or many. Two feeders were encountered, each of identical design but differently scented. After training, on the outward journey, half the ants encounter nestmates, which had fed on food matching one of the training feeders. Encountering returning nestmates reduced preference for the feeder matching the scent of the encountered nestmates, but only for ants trained on a limited-access feeder; ants trained on an unlimited feeder were unaffected. In other words, only if ants know that the food access is limited, and receive information that this feeder is heavily visited, do they reduce their preference for this feeder. To achieve this, the ants had to combine memories of the feeders' affordance with the presence of nestmates. Then they had to use semantic knowledge that restricted food access combined with nestmate presence predicts a likelihood of crowding, or a rule such as "if the food is restricted and there are nestmates on the path, go to another food source." Regardless of the mechanism, these results demonstrate that ants latently learn the affordance of their surroundings, an unexpected cognitive ability for an invertebrate.

object affordance | cognition | inference | future-oriented behavior | latent learning

Humans use various types of information, drawing both from personal experiences, i.e., episodic memory ("the only memory system that allows people to consciously re-experience past experiences" (1)), and from semantic memory. An important attribute that humans learn is the affordance of an object or environment. Affordance is a rather nebulous term, that can be broadly defined as what an environment or object offers or can be used for (2). A cup, a bottle, and a bowl, for example, all have the affordance of holding liquids, while a sieve, although similar to a bowl, does not. An objects' affordance is not entirely dependent on the properties of the object itself, but also on the subject using it (3–5). A shoebox has the affordance of a hiding place for a mouse, but not for an elephant. Some theories propose that we might not *infer* object affordance, but rather directly *perceive* the object affordance, without having to infer it from its size, shape and color. Nanay (6) states that while people claim that: "we do not really *see* an object as edible, we see it as having certain shape, size and color and we only infer on the basis of these properties that it is." He argues "that we do indeed *see* objects as edible, and do not just believe that they are."

Do animals realize the affordances of the objects surrounding them? How animals perceive their world and what information animals use to make decisions is often hotly debated, especially for invertebrates. Recognizing and remembering the affordances of their environment would be extremely beneficial for animals, especially when forming episodic memories. Whether or not animals have the cognitive capacity to form episodic memories is hotly debated, and something our results will later touch on. Classically, the demonstration of episodic memories involved showing that animals can remember the "what, where and when" of a situation—an important "what" often being the affordance of an item. For example, subjects are asked to remember what is given to them as a reward, where it was given, and when (1, 7). In a seminal paper, Clayton and Dickinson (7) showed that jays could recall what food they hid during a caching task, how long ago, and where. Jays looked for preferred perishable worms when released soon after caching, but reverted to looking for the non-preferred but non-perishable peanuts if a couple of days had passed. Many studies have found similar abilities in apes (e.g., refs. 8 and 9), birds (e.g., refs. 7 and 10), and rodents (e.g., ref. 11). Evidence that other animals can solve similar "*what* happened, *where* did it happened, *when* did it happen" questions has been found in dogs (12), cats (13), zebrafish (14), cuttlefish (15), and honeybees (16). This has been termed "episodic-like" memories to emphasize that, while

they fulfill the evidence criteria set out for episodic memory, we cannot truly know the subjective experience of the animals. Moreover, those studies required extensive training, rendering the interpretation of the results difficult (17).

A few studies investigated the "what, where, and when" question in invertebrates: one in honeybees (16), the other two in cuttlefish (15, 18). However, extensive training was required for the animals to complete the task, and it was thus impossible to differentiate direct affordance or episodic-like memory from associative learning. Intriguingly, a recent study on the black garden ant, *Lasius niger*, found that ants were able to integrate multiple contextual cues across modalities, and even seemed to do this given only one training exposure, consistent with episodic-like memories (19). Also relevant is the impressive case of bumblebees displaying an understanding of the affordance of openings in a wall by knowing whether they can pass through them (20). These findings, together with the fact that insects are well known to be able to learn associations and form long-term memories of past experiences (21–29), and the availability of many protocols are available to study this, suggests insects as promising candidates to address the question of object affordance in animals. Especially intriguing suggestions of affordance use in insects arise from ant tool use studies. Ants successfully select the most absorbent tool to collect liquid food rewards, suggesting an efficient utilization of object affordance (30). Whether this behavior stems from learning or from an innate understanding of the tool's properties remains to be established.

In this paper, we focus on ants to address questions such as: Do they have the concept of object affordance? Can they remember information that was not clearly useful at the time they acquired it? Can they learn affordances and locations with only one training exposure? And, can they combine different type of information to take the best decisions? We investigated whether ants could use the memory of a feeder experienced during a single visit (latent learning) and link its affordance to information that the feeder is being used by other ants in a following visit. In nature, the ant *Lasius niger* collects nectar from flowers (31) as well as honeydew from aphids (32). Both

resources are slow to replenish after being collected, and therefore revisiting a heavily attended food source would be suboptimal. On the other hand, if a forager discovers an unexploited but large and productive food source, it would be best if many foragers attend this resource before the arrival of competitors. An efficient strategy could be to avoid nestmate presence *only when* the food source is limited in its access or quantity. In this context, using information on feeder affordance and nestmate presence would benefit the ants, allowing them to forage efficiently and avoid queuing.

To investigate whether ants can display such flexibility, we designed an ecologically relevant foraging task using a Y-maze (Fig. 1). *L. niger* ants were allowed one visit to each branch of the maze. Each branch was scented with lemon or rose, and food with a matching flavor was available at its end. Half of the ants were trained to restricted-access feeders, the other ants to feeders that allowed many ants to feed simultaneously (Fig. 1). Importantly, the trained ants fed *ad libitum* on both types of feeders, and they were trained with either two restricted or two unrestricted feeders. They never experienced crowding or delays in any feeder type. Therefore, they should not be able to form simple associations between a scent and food availability. After those two training visits, the ants were allowed on the maze a third time. Before reaching the Y-maze bifurcation, half of the ants encountered nestmates fed food flavored to match the first-encountered feeder on the way to the bifurcation (implying potential overuse of the corresponding feeder), the other half did not. Ants rapidly gain information about the food other ants have collected from such encounters (33). We recorded the trained ant's path choice. Important here is that ants have a strong preference for the first food cues encountered (34), and we exploited this preference by searching for deviations from it.

Thus, our protocol allows the ants to show flexible behaviors according to context. Moreover, it uses a single trial (the ants visit each arm a single time during training and are tested a single time), as well as an "unexpected task" (the ants did not expect to meet nestmates or that they would have to choose a side of a Y-maze
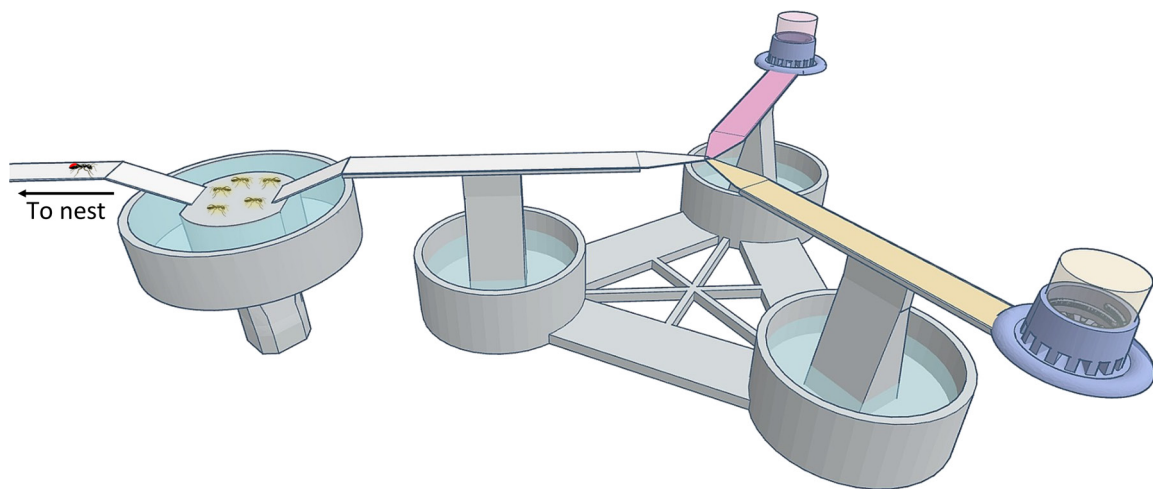

Fig. 1. Experimental setup. Note that all elements of the setup are shown in this illustration, but in reality, the encounter platform was not present during training, and the feeders not present during testing. A focal ant was given access to a Y-maze, with access to only one of the arms. A feeder, either unrestricted (pictured) or restricted (identical to that pictured, but with only one feeding hole), was placed at the end of the arm. The feeder offered flavored 0.75M sucrose solution. The arm of the maze leading to it was covered in paper scented to match the feeder flavor (lemon or rose, represented here by pink or yellow). The focal ant fed, was marked, then returned to the nest to unload her crop. On the second visit, the focal ant was given access to only the other Y-maze arm, differently scented, also offering matching flavored sucrose. Before the third visit, the feeders were removed, and an encounter arena was put in place. In half of the trials, 5 nestmate ants, fed with sucrose solution matching the first-encountered sucrose flavor, were placed in the arena. In the other half of the trials, focal ants did not encounter nestmates. On her third outward trip, the focal ant was given access to the encounter arena, where she interacted with nestmates for 1 min, before being allowed to proceed to the Y maze. On this third visit, no feeders were present, but access was given to both maze arms, which were scented as in the training visits. The focal ant proceeded down one of the arms, and this decision was recorded.
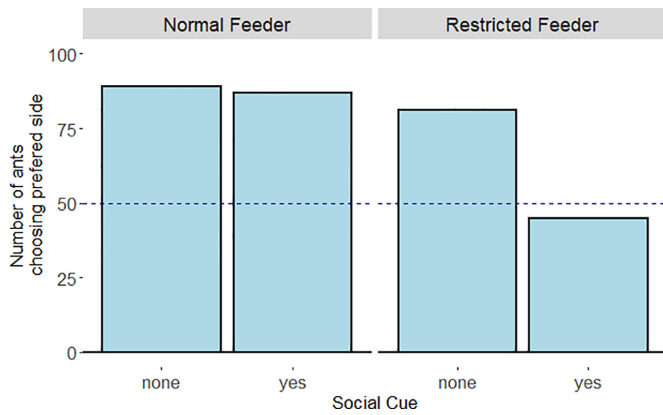
Fig. 2. Number of ants that selected the first side they were trained on, as a function of social cue (i.e., did they meet nestmates before selecting the Y-maze branch) and feeder type (allowing one or many ants to feed at a time). N = 100 for each group.

during test). To solve the task, foragers need to recall social information as well as the affordance, location, and odor of the feeder, to anticipate potential outcomes, which have never been experienced (i.e., will the food be inaccessible or not), and this without the possibility of relying on extensive training.

Results

For a Video Overview of the Methods, See *SI Appendix*. We asked whether the probability of ants following their natural preference for the first flavor encountered was affected by the type of feeder type (unrestricted or restricted) and whether or not they had social information from meeting fed nestmates. We relied on a previously reported very strong preference for ants to choose the first odor they were trained to (34). As expected, when the feeders were unrestricted, ants had a very strong preference for the arm they first visited, with 88% choosing this arm. This was the case regardless of whether they also received social information. Ants on the restricted feeders without social information also displayed the same strong preference (81%) (Fig. 2). However, ants trained on the restricted feeders that met fed nestmates showed no preference between the two arms (45% choosing the first odor encountered). Thus, only the interaction between the social information and the feeder type predicted the ants' behavior (binomial linear mixed effect models: Feeder type: $P = 0.1$. Social information presence: $P = 0.7$. Feeder × social information, $P = 0.006$). We ran a control with 20 ants trained on a restricted feeder and meeting ants fed the second-encountered odor. Again, we find that 80% of the ants maintain their preference for the first food.

In an information gathering assay carried out to test whether the ants potentially had information about the quantity of ants a feeder could support, 65% of ants circled the entire feeder, touching on average 54% of the feeding holes. Of note, 88% of the ants circled at least half the feeder. Thus, ants certainly had access to information about whether or not the feeder offered limited feeding access.

Discussion

By inferring that a limited rate feeder with ants returning from it is likely to be overcrowded, without having ever experienced crowding there, ant foragers demonstrate that they have a concept of the feeders' affordance. Neither training on a restricted feeder alone, nor encountering fed nestmates alone, stopped ants from following their innate preferences. However, when both coincided,

a dramatic change in behavior occurred. Critically, ants did not have the opportunity to form associations between the feeder and nestmate presence, and they did not expect to have to make a choice between the two branches, nor to meet nestmates along the way. Moreover, since our two food sources were of the same quality and offered in the same feeder type, we avoided potential differences in motivation for a specific side. Finally, no focus was put on the feeder access during training; ants ate *ad libitum* form each feeder. Ants had therefore no reason to behave differently according to feeder type when they foraged alone, and they did not modify their behavior.

A question that arises from our setup is whether the ants used learned affordance as seen in the use of familiar tools (review in ref. 30) or innate affordance. Ants are fed with the unrestricted feeders in their mother colonies during normal maintenance, so it is a possibility that they have experienced crowding at those feeders. If ants would use an associative rule, they would have avoided the normal feeders, as those are the ones where crowding may have been experienced. However, they do the opposite. Our data therefore suggest the existence of an innate understanding of the affordance of the feeder: that a single small opening equals more likelihood to be crowded than many openings.

Our results also support the theory that object affordance is not always inferred, but may be directly perceived (6). Perhaps the ants *perceive* the feeders as restricted without having to infer it. Recently, bumblebee have been shown to perceive the hole sizes in a flying tunnel, reorienting to pass through according to their body size (20). The bee may likewise have perceived the affordance of the hole as being navigable directly, without inference. The fact that the ants in the current study could perceive the affordance of such a novel object with no analogue in their natural habitat speaks to the flexibility of their affordance perception (or inference).

While the flexibility of this behavior is impressive, other criteria need to be tested. For instance, using different food restriction (for instance a temporal instead of a spatial restriction), and using protocols touching domains other than path selection during a foraging task. This would shed light on whether our findings are restricted to a specific situation (hinting at specifically evolved hard-wired rules), or whether ants can generalize and use object affordances in a variety of contexts. We would like to emphasize the need for additional studies following the recommendations of Suddendorf and Corballis (35), such as using single trials and/or unexpected tasks, novel problems to avoid relevant learning histories, different temporal or spatial contexts, and problems from different domains to avoid specific behavioral predispositions. Such studies are required to disentangle the known *vs* the remembered.

While our results robustly demonstrate that ants can respond to an objects' affordance, how exactly this is used is less clear. Various explanations, ranging from lean to rich, fit the data. The richest reasonable account would be that the ants employ mental time-travel (MTT) to the future, simulating what the experience of arriving at the feeder would be like, given having met many returning ants (or not) along the way. A moderately rich account would involve logical inference, without MTT: The ants may have deduced that a limited rate feeder would be easily crowded if foraging activity is high, without having to subjectively experience this hypothetical crowding. Finally, the leanest explanation would be an innate set of fixed behavioral rules, which code for this behavior. Thus, ants may modify behavior C (reduce preference), but that does not mean that past events A (feeder type) and B (having met ants) are directly linked in a conscious manner to behavior C (36); the ants could use a simple rule "if A and B, apply action C." Such hard-wired behavioral rules are well

documented in animal behavior (37–39). Further evidence is found in birds that cache foods, but lack the flexibility to decrease caching when pilfered (40, 41). Since in nature the ants rely on limited-rate food sources for almost all their carbohydrate intake, it is not unreasonable to postulate such a rule. Nonetheless, even if this were the case, our results still require that the ants categorize the ad-libitum, limited access feeder they encounter as a "limited food sources" required to trigger such a hard-wired rule. Given that the ants have never experienced the current feeder as limited, but still treat it as such, the ants at the very least infer or perceive the affordance of the feeders as limited-rate. While the tradition of Morgans Canon in comparative psychology calls for the leanest explanation to always be preferred, given the weight of evidence accumulating for advanced cognition in animals including insects (e.g., refs. 22, 23, and 42–44), it is unclear whether this is a reasonable position. We remain agnostic as to which level of interpretation is closest to the truth. Regardless, even the leanest reasonable explanation requires the ants to respond to the affordance of a novel object.

However, it is worth noting that this behavior also meets several of the criteria for episodic-like memory and MTT to the future (35). Our results show that ants have a memory of a single event and information that no focus was put on during training, which could indicate episodic-like memory. Ants might also anticipate crowding, which could indicate MTT to the future. By using a single trial and not putting any focus on the feeder type, we avoided a common criticism of MTT research in animals, by preventing extensive learning and associations to occur. These results are especially exciting because MTT behaviors are claimed to be a uniquely human ability by many authors (1, 17, 45–47). Even among humans, MTT is found only in children older than 4 y old (48–51). It is tempting to think that animals more closely related to us and considered "smart" would perform better in MTT tests, and that we would see a continuum from humans to mammals, birds and reptiles, and insects at the bottom of the cognitive abilities ladder. However, rhesus monkeys (52) and rats (53) failed to modify their food intake to avoid future thirst, and chickadees failed at anticipating pilfering at caching spots (40, 41). Insects, having smaller brains, might thus also be expected to perform poorly at tasks requiring MTT to the future (54, 55). However, while insects have long been considered to be robot-like entities (56–58) at the bottom of a hypothetical cognitive abilities ladder, this view has been robustly challenged. Insects have been shown to learn from each other (59, 60), master complex rules and abstract concepts and associations (22, 61–65), and use tools flexibly (30, 44). Our results fit into this body of evidence that insects can rival vertebrates in some cognitive tasks. Importantly, however, we are only making claims about the functional, behavioral definitions of episodic-like memory, and forward MTT as a flexible response to an untrained novel situation, which may occur in the future (45). We make no claims about an episodic-like experience projected into the future.

Our findings might be considered surprising in terms of cognition research, as object affordance, inference, or MTT are usually linked to metarepresentation and consciousness. In an ecological context, however, they are perhaps a lot less surprising, in light of the clear advantages they offer in this ecologically relevant task. Studies like ours encourage us to look for alternative cognitive or neural mechanisms underlying behaviors that might have evolved independently in vertebrates and invertebrates. While further studies are required to confirm similar results in other species, our results challenge our vision of insect cognition, and raise the possibility that invertebrates possess much richer cognitive repertoires than previously thought.

Methods

Biological Material. We used 8 queenless *Lasius niger* colonies collected from the wild, maintained on *ad libitum* 0.5M sucrose solution and chopped cockroaches. The colonies were starved for 4 d before each experiment.

Overview. Individual ants visited each arm of a Y-maze once (two training visits). Each arm was scented by covering it with a paper overlay matching the flavor of the food offered on that arm (with a different smell on each side). The feeders were either restricted on both visits or unrestricted on both visits. On their third visit, ants either encountered nestmates fed with the food flavor encountered first, or did not encounter nestmates. We subsequently recorded which side and scent the ant chose. All else being equal, ants have a very strong preference for the first odor/flavor encountered (34). Our assay aimed at triggering a deviation from this preference, by implying in one of the combinations (restricted feeder & encountering fed ants) that the preferred feeder will be overexploited.

Detailed Experimental Procedure. A single forager was allowed to climb onto a bridge leading to the maze (Fig. 1). Initially, the ant only had access to one arm of the maze (either left or right, systematically varied). A feeder, offering 0.75M flavored sucrose solution (see below), was located at the end of the arm. The maze arm was covered by a scented paper overlay, matching the flavor of the feeder. The feeder was either unrestricted (14 holes) or restricted (1 hole). The ant located the feeder and, while feeding, was marked with a dot of acrylic paint on the abdomen. When satiated, she was allowed to return freely to the nest to unload the collected food to her nestmates. While unloading, the maze was rearranged, providing access to the second arm. This arm now offered an identical feeder type, but offering a second flavor, and was covered by a matching scented paper overlay. Once unloaded, the focal ant was again allowed to freely climb the bridge, travel down the second arm, feed from the second feeder, and return to the nest again. While unloading, the maze was rearranged again. An encounter arena (30 mm diameter, surrounded by a water moat) was affixed before the Y-maze entrance. Then, 5 nestmate ants were allowed to feed to satiation on sucrose matching the flavor of the first food encountered by the focal ants. This was done because *L. niger* has a very strong tendency (c. 80% of ants) to choose the first odor they are trained on, all else being equal (34), see also Fig. 2. As we expected a reduction in the proportion of ants choosing the first odor trained on, due to our treatments, using this method provided high sensitivity. The focal ant was allowed to freely enter the bridge a third time, and given access to the encounter arena, where she was confined with the fed nestmates for 60 s, before being allowed onward to the Y-maze. The Y-maze now offered access to both arms, each arm covered by a fresh scented paper overlay, scented as they were during training (e.g., lemon on the left, rose on the right). No feeders were present during this test visit. The arm choice of the focal ant was unequivocal, and defined as crossing a line 8 cm from the bifurcation. The raw data are provided in *SI Appendix*, Supplement S1. As a control, 20 ants trained on the restricted feeders met nestmates fed the second food.

Food Flavoring and Path Scents. The feeders were filled with 0.75M sucrose solution containing 1 microliter of rose or lemon food flavor per mL. The maze arms were scented using paper overlays that were changed between each visit to prevent pheromone influence. The papers were scented by being stored in a closed box for at least 24 h with 500 microliters of flavoring. Ants did not show a preference for a side (without social cue, 87% selected the first food when it was on the left side of the maze, vs. 85% when it was on the right) or a smell (88% chose the first food when it was lemon, vs. 82% when trained on rose first), and had the same food quality on both sides, allowing us to discard potential effects of motivation to forage on one side or the other.

Information Gathering Assay. If ants are to respond differently to limited and unlimited feeders, they must know that the feeders are limited or not. Thus, in a separate experiment using different ants, we allowed 20 ants to feed on a restricted or unrestricted feeder, and noted a) whether the ant circled the entire feeder and b) how many of the feeding holes it contacted.

Statistical Analysis and Subject Exclusion. Analysis was carried out in R (66) (4.2.0) via RStudio 2022.07.0+548, using binomial linear mixed effect models in the package *lme4* (67). We used social information and feeder type as fixed effects, and colony and date as random effects. The entire code and output are provided in *SI Appendix*, Supplement S2. Ants that failed to find the food or to

return to the bridge for a new visit after 10 min were discarded (42 ants discarded over all treatments).

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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