Advanced cognition in ants

Tomer J. Czaczkes

Abstract

Interest in the advanced cognitive abilities of insects has grown rapidly over the past decades. However, most studies have taken place on a handful of model organisms: fruit flies, honey bees, and bumblebees. Ants are in many ways ideal models for the study of cognition, offering a wide range of ecologies, often coupled with ease of training and maintenance. This review aims to collate the often disparate research on advanced cognition in ants. I focus specifically on "advanced" cognition, which is defined as requiring mental abstraction, internal self-reference, or control. Ants have been demonstrated to show impressive cognitive control abilities, suppressing a dominant response (e.g., feeding) in order to carry out a secondary goal (e.g., searching for a feeding tool). Tool use is well documented in ants, including tool manufacture and situation-dependent tool selection and use. Some evidence of abstract algorithmic sequence learning (e.g., repeated left-right turns) has been shown, as well as suggestions of metacognitive abilities such as estimating their own uncertainty. Some evidence pointing to successful relational-concept learning (e.g., "same" vs. "different") has been reported, but not all experiments searching for this were successful. I end the review by highlighting specific areas of ant cognition that may offer large rewards for intrepid researchers. The study of advanced cognition in ants is still in its early stages, and there are many opportunities for exploration and discovery.

Key words: Review, tool use, meta-cognition, pattern learning, concept learning, cognitive control, Formicidae, Hymenoptera.

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What is advanced cognition?

There is no universally accepted definition of cognition. Different researchers use the term to denote markedly different things (Bayne & al. 2019). These definitions fall into broadly two camps: broad and narrow. Broad cognition adopts the definition given originally by Neisser (1967) and popularised by Shettleworth (2009) as "the mechanisms by which animals acquire, process, store, and act on information from the environment". Narrow cognition does not enjoy such a concise definition and is much more restrictive: Narrow cognition usually requires symbolic computation, abstract representation of information, mental model building, or information processing in the absence of current exposure to relevant external stimuli (Bayne & al. 2019). Pragmatically, many authors refer to phenomena which fall into the narrow cognition class as "advanced cognition". I shall do so here. This review will thus restrict itself to a discussion of "advanced" cognitive abilities, while remaining agnostic about whether simpler information processing should be considered cognition.

I will not discuss basic learning and memory in ants, although ants are very impressive learners (Huber & Knaden 2018, Piqueret & al. 2019, Czaczkes & Kumar 2020), and collective cognition is discussed separately (Box 1). It is important to note, however, that there is no reason to expect that advanced cognition requires complex brain structures or that "basic" cognitive abilities, such as associative learning, are neurologically simpler: Simple neural networks have been developed which can reliably perform conceptual or numerosity discrimination (Peng & Chittka 2017, Cope & al. 2018, Vasas & Chittka 2019).

Humans are equipped with very general-purpose cognitive tools, which we can deploy in a wide variety of situations. We thus tend towards an anthropogenic bias, considering general-purpose cognitive abilities as more advanced. But searching for human-like advanced cognition in insects may not be appropriate. Insects will have different cognitive approaches to us and may possibly be more limited in the breadth of their cognitive flexibility.

Box 1: Collective cognition in ants.

Ants and other social animals often exhibit collective behaviour, with emergent patterns arising from the interaction of the individual animals. For example, an ant colony can focus its foraging effort on the best of multiple food sources by stronger individual recruitment to the best food source (Beckers & al. 1990). Another collective behaviour almost exclusively confined to ants is cooperative transport, wherein a group of ants cooperatively drag or carry an item too large for a single ant to move (Czaczkes & Ratnieks 2013). Cooperatively transporting ants can even solve navigational challenges, such as bypassing barriers which the carried item cannot cross (Gelblum & al. 2016, McCreery & al. 2016) even if individual ants can (Ron & al. 2018, Gelblum & al. 2020). The topic of collective cognition has been the subject of excellent, recent reviews (Feinerman & Korman 2017, Pratt & Sasaki 2018). While impressive, to my knowledge, no example of collective cognition in ants (or elsewhere) can be considered underlined advanced cognition as none require the processing of abstract information. However, it is theoretically possible for advanced cognition to take place at the collective level. Recently, information storage in the interaction pattern of fish shoals has been described (Sosna & al. 2019). It is reasonable to expect such interaction patterns to also encode information in social insects, especially with individual ant colonies often showing idiosyncratic repeatable behavioural differences ("animal personality", Horna-Lowell & al. 2021). Collective cognition strongly intersects the new(ish) move towards embodied or grounded cognition, which argues that cognition cannot be understood purely as a process happening within a brain on symbolic representations. For a good introduction to embodied cognition, see Clark (2017), and for more ant-centric treatments, see Wystrach (2021).
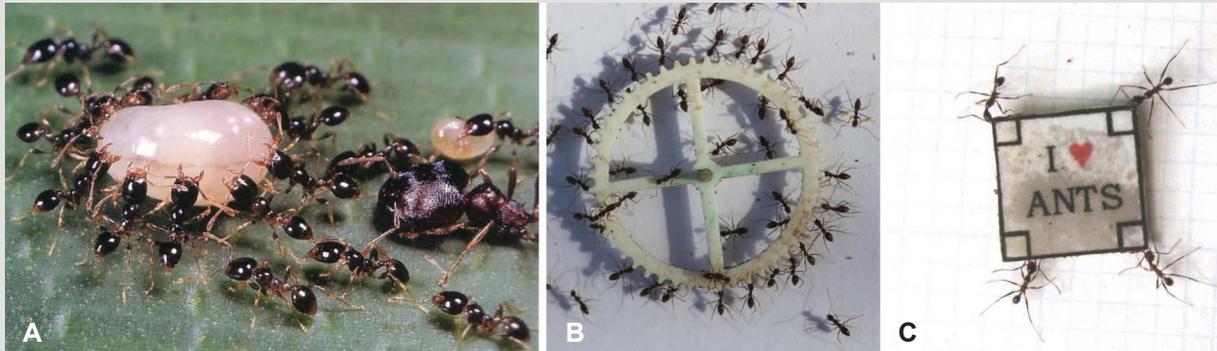
Ants cooperatively transporting an item too large for a single ant to move – an example of collective behaviour. A) *Carebara simalurensis* carrying brood. Copyright Mark Moffett / Minden Pictures. B) *Paratrechnica longicornis* attempting to cooperatively carry a cog, resulting in turning. Credit: Ehud Fonio. C) *Pheidole oxyops* carrying a standardised food item. Credit: Tomer Czaczkes.

For example, they may only be able to learn some abstract concepts, but not others, or only be able to apply a concept in some situations. Of course, the same is true for humans, but we cannot easily recognise our own inabilities. Most, if not all, of the advanced cognitive abilities studied in animals are initially familiar to us via introspection, which leads to an implicit or explicit anthropomorphic assumption that they function similarly to those of humans and to a lack of studies examining non-humanlike advanced cognitive abilities (Döring & Chittka 2011). We should also be wary of conflating narrow functional definitions used in animal behaviour (e.g., personality, culture) with the broader colloquial or human psychology usage (Döring & Chittka 2011).

In this review, I will discuss only some aspects of advanced cognition which have been investigated in ants. It is thus far from an exhaustive list of advanced cognitive abilities. The available research falls into three broad categories: planning and response flexibility (including tool use and cognitive control), abstract-concept learning, and metacognition. Finally, I will end by highlighting some unstudied and understudied aspects of ant cognition, which deserve further investigation.

Planning, multi-stage tasks, and response flexibility

Directly pursuing a main objective may not always be the best option. Accessing the contents of a can, for example, may be better achieved by suppressing this main objective in favour of the secondary objective of finding a can-opener. This, however, requires a significant level of abstraction in order to plan the best course of action and acquire the best tool for the job.

Tool use

The study of tool use in animals has a long history, and the definition of tool use is contentious. While tens of

definitions of tool use exist, a broad but generally accepted one is "the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment" (St Amant & Horton 2008). The definition of tool manufacture is somewhat less contentious and can be defined as "any structural modification of an object or an existing tool so that the object serves, or serves more effectively, as a tool" (Shumaker & al. 2011). Evidence of tool use by hominids dates back from about 2.5 million years ago by *Homo habilis,* who knapped stones to make cutting flakes (Semaw & al. 1997). Tool use is famously reported in non-human primates and birds, especially corvids. Classic examples include chimpanzees (*Pan troglodytesi*) using stripped twigs to fish for termites (Sanz & al. 2009) and New Caledonian crows (*Corvus moneduloides*) manufacturing hooks to probe crevices (Hunt 1996). However, tool use is in fact quite widespread in invertebrates. For example, tree crickets (*Oecanthus henryi*) manufacture baffles to increase the volume of their songs (Mhatre 2018), and recently, Asian honeybees (*Apis cerana*) have been reported to use faeces applied to the nest entrance to ward off attacks by giant hornets (*Vespa soror*) (Mattila & al. 2020). Impressively, bumblebees can be trained to a variety of tool-using tasks, such as string pulling (Alem & al. 2016) and ball rolling (Loukola & al. 2017), and these behaviours can then even be socially transmitted. Somewhat surprisingly, a comprehensive catalogue of tool use in animals contained almost as many examples of tool use in insects (53) as in primates (65) (Bentley-Condit & Smith 2010). Proportional to the amount of research attention tool use has received in birds and primates, this implies that a very large number of tool-using insects are yet to be described. However, while all of the examples listed above are broadly accepted as true tool use, not all can be considered as arising from advanced cognition (Call 2013, Sanz & al. 2013). Many examples of tool use, such as water spitting by Archer fish (Toxotidae), are ubiquitous within a species, fully stereotyped, and inflexible. Others, like termite fishing by chimpanzees (*Pan troglodytes*), arise spontaneously and patchily within species, show wide variation in use and technique between individuals, and are considered examples of behavioural innovation and evidence of advanced cognition (Call 2013). Two main categories of tool use are described in ants: liquid collection using sponges, and stone dropping into nests. Liquid collection using sponges is especially intriguing as it is a very rare case of tool use behaviour that falls in between the fully stereotyped, inflexible category and the flexible behavioural innovation one.

Several myrmicine ants use objects to improve liquid food collection (Morrill 1972, Fellers & Fellers 1976). Items such as leaves and soil grains are gathered from the vicinity of the food source and placed onto the liquid food

Fig. 1: Tool use in ants. An *Aphaenogaster subterranea* worker placing a large soil particle into a drop of honey water. The soaked soil particle will later be retrieved and returned to the nest. Photo credit: István Maák.

(Fig. 1). The soaked items may then be adjusted and are eventually retrieved to the nest for feeding (Fellers & Fellers 1976, Lőrinczi 2014). Note that tool placement and tool retrieval are two separate tasks, often performed by different individual ants (Fellers & Fellers 1976, Maák & al. 2017); hence, I do not consider retrieval as part of tool use in this example. This liquid-soaking behaviour fulfils the definition of tool use as it alters the physical properties of another object (the food) dynamically (by soaking) to make it more transportable. Indeed, ants even adjust leaves or twigs to make tools (Banschbach & al. 2006) or adjust tools to make them easier to handle (Maák & al. 2017, Lőrinczi & al. 2018), demonstrating tool manufacture – a much rarer behaviour. Tool use in ants likely evolved from a tendency of ants to cover liquids with debris to avoid drowning or entanglement (Zhou & al. 2020). There is good evidence, however, that this behaviour is not simply a combination of defensive covering of entanglement danger and subsequent food retrieval: Ants preferentially drop tools in honey over water, even when both are covered in pine needles (Módra & al. 2020), and liquid viscosity can also affect the choice of tools (Lőrinczi & al. 2018). Ants never retrieve tools soaked in non-food liquids, such as paraffin oil or water (Banschbach & al. 2006, Lőrinczi 2014, Lőrinczi & al. 2018). Interestingly, only a small subset of active foragers (ca. 8%) use liquid-soaking tools, and whether or not an ant becomes a tool user depends in part on their pre-existing personality, with more explorative and bolder individuals more likely to become tool users (Maák & al. 2020).

As discussed above, tool use in animals can be separated into stereotyped behaviour or as arising from innovation, with ant tool use being a rare example of an intermediate category. Tools are used in a relatively stereotyped way, for a single purpose, by a phylogenetically-distinct group of species, with naïve individuals showing tool-use behaviour without previously observing tool use (Tanaka

& Ono 1978, Maák & al. 2020). However, tool use is only performed by a small subset of foragers in a colony and correlates with individual ant personality (Maák & al. 2020): More explorative workers which respond to novel prey items more strongly in personality tests are more likely to perform tool use, and if the tool users of a colony are removed, one can reliably predict the new tool users to emerge based on a personality score (Maák & al. 2020). This implies that tool use in these ants is to some degree not a fully hard-wired behaviour and involves a cognitive component.

Moreover, the steps required for tool use require several abilities which might require non-trivial cognition: In order to successfully use soaking tools, an ant which locates a liquid food source must first suppress its feeding response (showing self-control or delayed gratification, see below). It must then keep the location of the food source in working memory while searching for an appropriate tool. This demonstrates that (some) ants can maintain an ultimate goal in mind for sometimes extended periods of times while undertaking a required sub-goal which is spatially displaced from the original goal location. This may reasonably be considered simple planning – a mental representation of the problem in which the current state, the goal state, and the actions necessary to reach one from the other are constructed (Morris & Ward 2004). However, this behaviour could also be achieved by a series of simple "if" rules: If liquid food is found, remember the location and begin a search for tools. If a tool is found, return to the food location. Tool use behaviour is also notably flexible in that ants can use tools not found in nature (such as sponge pieces) and can modify tools by ripping them into smaller pieces before use (Maák & al. 2017). Ants also seem to select the tool type in response to the qualities of the tool and the food source, for example, preferentially using larger sponge pieces on viscous honey but smaller soil pieces on less viscous honey water (Lőrinczi & al. 2018). While impressive, this flexibility does not necessarily imply understanding of how the tools work – the ants may have hardwired criteria for matching tool properties with food properties and for modifying hard-to-handle tools, much as large prey items are dissected or recruited to if they are too hard to move (Robson & Traniello 1998, Yamamoto & al. 2009).

Ants have also been reported to build siphons to extract dangerous liquids from containers and make them safe for consumption, which is sometimes referred to as tool use (Fellers & Fellers 1976, Zhou & al. 2020). However, it is unclear whether this is a side-effect of simply covering liquids to make them safe.

Several species of ants, including *Tetramorium caespitum* and *Conomyrma bicolor,* were reported to drop stones and soil particles onto ground-nesting bees to lure them out of their nest (Lin 1964, Schultz 1982) or to block a rival colony from foraging (Möglich & Alpert 1979). Especially the stone-dropping behaviour used to lure guard bees out of a nest may suggest some cognitively advanced behaviour, since, much as in the tool-based liquid collec-

tion, the ants must leave their goal (the bee nest), maintain the main goal in their working memory, and suppress it in order to complete a sub-goal (stone collection). Again, however, this behaviour could be achieved by a series of "if" rules.

Cognitive control, response flexibility, and self-control

Cognitive control is the repression of an instinctive, preferred, or dominant response in favour of a more appropriate learned response when the two responses conflict (Botvinick & al. 2001). For example, in literate, humans reading the meaning of the word **blue** or red is the preferred response, but with effort, we can force ourselves to name the print colour – although this is uncomfortable and comes at a cost to accuracy and response speed (Stroop 1935, Dreisbach & Fischer 2012, Littman & al. 2019). Ants are well-able to perform cognitive control: They can suppress the pheromone-trail following response when it conflicts with their own memory of a food source location (Harrison & al. 1989, Aron & al. 1993, Grüter & al. 2011). This does not merely represent a hierarchy of information source use since ants can dynamically choose to ignore pheromone trails or not depending on whether the trail is likely to lead to a better food source than the ant is currently exploiting, information they can gain from interacting with returning foragers on the trail (Fig. 2) (Czaczkes & al. 2019). However, while ants can readily learn to ignore pheromone trails, they cannot learn to avoid them (Wenig & al. 2021). Much as in humans (see above), in ants, exerting cognitive control seems to come at a cost to response speed and accuracy (Czaczkes & al. 2021). There is a lively debate in cognitive psychology as to whether cognitive control demonstrates higher-level cognitive processes (Braem & al. 2019). Some argue that cognitive control requires executive control: a self-monitoring cognitive element to repress preferred responses in favour of correct ones (Botvinick & al. 2001). Others argue that the hallmarks of cognitive control – increased response times and error rates – can be explained by associative learning mechanisms alone (Mayr & al. 2003).

Fig. 2: An outgoing *Lasius niger* forager (right) inspecting a returning forager (left). Ants respond flexibly to pheromone trails, choosing to follow them or their own memory, depending on information about food qualities available in the world, which they can gain by contacting returning ants. Photo credit: Stephanie Wendt.
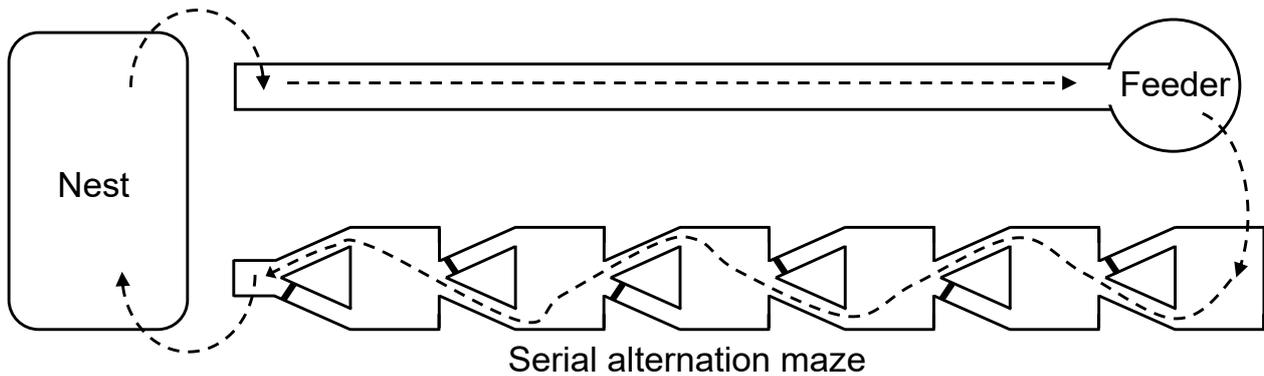
Fig. 3: A serial alternation maze, as used in Macquart & al. (2008). By testing ants on a maze with more sub-units than a training maze, the ability to learn abstract algorithmic sequences (e.g., alternating left then right, as shown here) can be tested. By placing cues in each sub-unit, multiple cue exposures can be achieved for each round trip, as in Beugnon & Macquart (2016).

Ants can also demonstrate self-control or delayed gratification. In a classic study, young children were offered a single marshmallow immediately but were promised two marshmallows if they waited for several minutes (Mischel & Ebbesen 1970). Most children failed at this temporal-delay task. While primates and ravens perform well on such tasks (Evans & Westergaard 2006, Osvath & Osvath 2008, Kabadayi & Osvath 2017), other vertebrates such as rats and pigeons fare less well (Tobin & Logue 1994). In a spatial-delay scenario, ants successfully forego feeding at an acceptable food source in order to feed at a known, higher-quality food source further away (Wendt & Czaczkes 2017). However, spatial delay may be an easier task than temporal delay for some animals (Stevens & al. 2005), and such more natural foraging tasks may make self-control more likely (Blanchard & Hayden 2015), perhaps since the subject needs not constantly suppress the urge to take the reward (Mischel & Ebbesen 1970). Temporal delay also may be more cognitively demanding, requiring mental time travel – a representation of the future in the brain. The tool-use scenario above also demonstrates that ants can also suppress immediate rewards in favour of other goals.

Finally, ants demonstrate broad learning flexibility in that they are able to learn to perform tasks which are unlikely to have important fitness consequences in nature. For example, Turner, one of the first researchers to consider ants as cognitive entities (Turner 1907a), demonstrated that ants can be trained to drop off surfaces to reach a reward (Turner 1907b), a feat only recently replicated by Riberio & al. (2009), who also managed to train ants to take one-way return routes to the nest (Ribeiro & al. 2009). Ants can also be trained to locate rewards on the basis of thermal, magnetic, or vibrational cues alone (Kleineidam & al. 2007, Buehlmann & al. 2012). However, some clear limits have been found: *Pogonomyrmex* ants cannot learn to remain passive and not to leave a safe zone to avoid punishment and so seemingly cannot learn passive avoidance (Abramson 1981). *Lasius niger* cannot learn to associate surface roughness with a reward (Bernadou & Fourcassié 2008).

Abstract pattern, concept, and association learning

Learning and comprehension of abstract patterns and concepts is often considered a hallmark of "advanced cognition" (Giurfa & al. 2001, Zentall & al. 2008, Avarguès-Weber & al. 2012). The term abstract refers to non-absolute, non-physical attributes of the word, such as infinite algorithmic sequences, numbers and ordinal positions, relative concept categories (same vs. different, above vs. below), or non-categorical, non-physical concepts (e.g., democracy, fairness).

Algorithmic sequence learning

By an "algorithmic sequence", I refer to a sequence of situations which can continue indefinitely following a set pattern – for example, alternating left and right. While learning a sequential series of views underlies positional image matching – a common navigational strategy in insects, which ants (and other Hymenoptera) excel at (Collett & al. 2003, Graham & Collett 2006), this does not require the encoding of abstract concepts since the images all arise from and are grounded in the physical world. However, *Gigantiops destructor* shows some success at learning simple, abstract algorithmic sequences (Macquart & al. 2008). Ants were trained to return to their nest via a linear series of eight chambers with two exits (Fig. 3). After training, two additional chambers were added to test for pattern extrapolation. Ants trained on simple repeat choices (e.g., "always left") continued the pattern successfully in both chambers in 95% of trials, much as bees do (Zhang & al. 2000). However, this may reflect visual associative learning. Ants trained on simple alternation patterns (e.g., LRLRLRLR, with L = left and R = right) showed 85% extrapolation accuracy in the first novel chamber but dropped to random choice in the second. Performance deteriorates further in more complex double alternation patterns (e.g., LLRRLLRR): Most ants choose correctly in the first novel chamber (71%) but then alternate immediately in the second, rather than repeat the choice a second time (14% correct choices). It may be that the ants have realised they overshot the usual maze end

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after the first novel chamber and were deploying searching behaviours, although this fails to explain the discrepancy between the single and double repeat results. Note that these tasks can also be solved with a series of rules, that is, "if you chose left last time, choose right now". This does not require abstraction but does require remembering one's own abstract actions, not just previously experienced views grounded in the real world.

Reznikova and colleagues report that various *Formica* species can communicate sequential path-choice instructions to foraging team-mates, in a phenomenon they dub "distance homing" (reviewed in Reznikova 2008). Moreover, it is reported that ants can extract regularities in a sequential pattern and use these to compress the information required for transfer. However, the cognitive abilities reported in this body of work (including precise numerosity discrimination up to the mid-hundreds and symbolic communication) are so far advanced from other cognitive abilities reported for other insects or even great apes, corvids, or cetaceans that there is not yet consensus as to whether these results can be accepted at face value. It is thus not yet fully clear whether or not ants (or any other insect, for that matter) can learn abstract algorithmic sequences.

Abstract relational concepts

In a series of now classic experiments, honeybees have been shown to learn abstract concepts such as "same vs. different", "above vs. below", "larger vs. smaller", or "odd vs. non-odd" (Giurfa & al. 2001, Avarguès-Weber & al. 2012, Avargues-Weber & al. 2014, Muszynski & Couvillon 2015). While convincing alternative explanations have been raised for some of these findings (Guiraud & al. 2018), current consensus suggests that at least some bees can successfully learn some abstract concepts. Most tests of abstract conceptual learning rely on visual inspection of the stimuli. It is thus perhaps not surprising that one of the few studies strongly suggesting concept learning in ants was conducted on the highly visual *Gigantiops destructor* (Fig. 4).

Beugnon & Macquart (2016) trained *Gigantiops destructor* foragers in a serial chamber maze to go left when they saw a wide bar in the centre of the chamber and right when they saw a narrow bar. After ants successfully learned this, they first experienced three exposures to wide or narrow bars followed by three exposures to a novel intermediate-width bar. Ants which had first seen narrow bars responded to intermediate bars as if they were wide. The reverse (though admittedly non-significant) trend is seen when ants are first exposed to wide bars then experience novel intermediate-width bars. This strongly implies that the bars are perceived not in terms of absolute width but rather relative to the other bars. This is doubly impressive as the stimuli are presented sequentially – the ants must thus compare a currently-present stimulus with a remembered stimulus they know to be different. However, as no transfer to novel shapes was conducted, alternative explanations based on association to absolute widths cannot
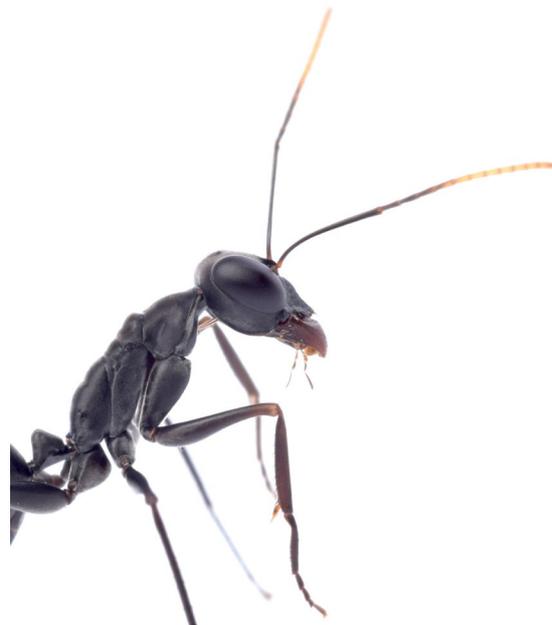

Fig. 4: The highly visual *Gigantiops destructor* can learn simple repeated patterns of left and right but might use associative learning to do so. Note the very large eyes, making this species very useful for conducting vision-based cognitive tasks. Photo credit: Philipp Hönle.

be ruled out. Moreover, while this study demonstrates relative perception of width, it does not demonstrate that ants can learn the abstract concept of "bigger" or "smaller".

The abstract concept of same vs. different can be tested for using non-visual paradigms, making it well-suited for testing in more olfaction-focussed ants. Oberhauser & al. (2020) trained *Lasius niger* ants in a match-to-sample experiment, wherein ants were allowed to walk onto a runway with a scented stem and had to choose the Y-maze arm with either the same odour ("sameness" training) or a different odour ("different" training) to find a reward and avoid a quinine punishment. Odour pairs were cycled every visit in a continuous transfer design. After 48 visits, ants trained to follow the different odour made 65% correct decisions. However, ants trained to follow the "same" odour made the incorrect choice more than half the time. It is thus unlikely that *L. niger* ants can learn the concept of same vs. different. Instead, the ants resorted to developing alternative heuristics, such as "always go left", to solve this task. Intriguingly, different individuals developed different heuristics, with fewer than half the ants choosing truly randomly. Some ants even used a heuristic which was moderately <u>worse</u> than random choice, implying that truly random choice may be equally or more cognitively challenging than the development of a simple behavioural rule.

Counting and symbolic communication

Numerosity perception is the ability to perceive how many items are in a group. There seems to be a threshold in numerical discrimination ability at around 3 - 6, which is widespread in the animal kingdom, from humans to

honeybees (Starkey & Cooper 1995, Gross & al. 2009, Howard & al. 2019b). Below this threshold, a process of immediate recognition of the number, known as subitizing, occurs. Above this threshold, counting, that is, sequentially incrementing the number, occurs. Readers may readily test this distinction by attempting to rapidly state the number of symbols in the following groups: (●●♦) - (●●♦♦♦) - (●●♦♦♦♦) - (♦●♦●). However, more commonly, animals (and humans, if they do not make an explicit cognitive effort) simply sense magnitude about this threshold, which does not involve recognising discrete numbers.

Numerosity discrimination, especially of lower numbers via possibly subitizing, has been extensively studied in many vertebrates (reviewed in Brannon 2005, Beran 2017) and more recently invertebrates, especially honeybees (reviewed in Skorupski & al. 2018, Giurfa 2019, Howard & al. 2019b, Gatto & al. 2021). Honeybees have been found to be rather adept mathematicians at low numbers: They can demonstrate proto-counting (sequential tallying of landmarks up to 4) (Chittka & Geiger 1995, Dacke & Srinivasan 2008) and recognise a number of specific elements (up to 3), without relying on the shape, colour, or pattern of the elements (Gross & al. 2009).

However, very little work has been done on ants. While ants can clearly estimate magnitude and compare options or groups based on this abilities (Tanner 2006, Cammaerts 2008, Cronin 2014, d'Ettorre & al. 2021), it is unclear whether they can learn the concept of a discrete number or subitize. Recently, d'Ettorre & al. (2021) examined ordinality – the ability to learn the position of an item in a sequence – in the ant *Camponotus aethiops*. Ants were trained to locate a reward in a linear runway with 5 identical landmarks, with the reward always under a specific landmark in the sequence (e.g., the third landmark, the first landmark, etc.). The relative position of landmarks to each other was varied so that only the order was informative. After 8 training visits, ants tested in an unrewarded situation searched preferentially in the vicinity of the correct landmark in the series, suggesting that the ants learned the ordinal position of the reward. While a transfer test would provide stronger evidence for the concept of a number order having been learned, this finding does suggest that ants can learn such ordinal positions (proto-counting) with relatively few training visits when no other helpful cues are present.

Work by Reznikova and colleagues (reviewed in Reznikova 2008) has reported astounding use of complex symbolic communication by *Formica polyctena* and *Formica sanguinea*, as well as in *Formica pratensis* (see Novgorodova 2006). They report that in these species, scouts can transmit a series of required left and right turns to recruits. The length of time required to communicate a message is a function of the complexity of the message, with longer or more complex routes requiring longer information transfer. This ability is also claimed to allow ants to convey explicit, precise numbers rather than magnitudes. If true, this would imply that the ants are using explicit symbolic representations for each number. Over a series of experiments, scouts were allowed to find a reward on one branch of a comb-like maze with 25 or more unrewarded branches. After returning to their foraging group, communicating, and thereafter being removed, the foragers immediately chose the correct tooth in 117 / 152 cases (summarised in Reznikova 2008). However, these findings stand in strong contrast to work on numerosity perception and symbolic communication in other non-human animals. Honeybees, the insect most extensively studied in terms of cognitive abilities, struggle to learn to discriminate very low numbers. For example, Howard & al. (2019b) found that bees were no better than chance after 20 trials learning to discriminate numbers between 4 and 8, and peak performance did not rise over 75% correct after rewarded 50 trials, falling to under 70% correct in unrewarded trials. With extensive training, honeybees seem capable of learning specific numbers and even perform simple arithmetic calculations (Chittka & Geiger 1995, Giurfa 2019, Howard & al. 2019a, Howard & al. 2019c). However, it is very difficult to disentangle symbolic, conceptual number learning from relative magnitude learning (MaBouDi & al. 2021). Similar difficulties mar attempts to ascertain whether ants and bees can learn the concept of zero (Howard & al. 2018, Cammaerts & Cammaerts 2019), and whether or not insects can gain a symbolic or categorical understanding of numbers is a hotly debated issue. A strength of the approach taken by Reznikova and colleagues is that there is a separation between the animal being trained and rewarded and those being tested. Thus, contamination by a hidden continuous variable can be ruled out. Then again, the ability to communicate complex symbolic information, let alone use it, is in itself seemingly well beyond the abilities of most animals studied. It is possible that such advanced symbolic cognition has evolved in the group of ants due to unique selective pressures on them, much as some birds show spatial memorization abilities which far surpass our own (Balda & Kamil 1992). However, we thus might expect similar, if less extreme, cognitive abilities to be more widespread than they seem to be. To my knowledge, the only published independent attempt to replicate simple contact-based directional communication in the ant *Lasius niger* failed (Popp & al. 2017). It is also possible that advanced numerical and symbolic abilities are only present in a small subset of workers, hence the apparently poor performance of other taxa. I remain agnostic, although a little sceptical, about whether any insect has a symbolic representation of numbers or patterns and whether they can communicate these concepts.

Metacognition and predictions of accuracy

Metacognition is "thinking about one's own thinking". This is commonly assumed to require a higher (second-order) mental process, which acts to examine or manipulate a lower-level mental process. An example would be examining a problem such as 189 + 98.25 = ? and being confident that you could solve it before even attempting to. An often-examined subcategory of metacognition is

metamemory, in which certainty in one's own memories are examined ("I'm pretty sure I remember the way home from here"). A hallmark of metacognition is being able to respond to uncertainty in a rational manner. The two main approaches to the study of metacognition is looking for demonstrations of information seeking on difficult tasks or looking for evidence of selective task abandonment in more difficult tasks (Hampton 2009, Shettleworth 2009). However, the study of metacognition has been plagued (or sharpened) by many alternative explanations which do not require direct examination of memory content or internal information processing (reviewed in Smith & al. 2008, Hampton 2009, Shettleworth 2009). For example, honeybees have been reported to selectively opt out of difficult perceptual above or below discrimination tasks (Perry & Barron 2013), but the authors stopped short of claiming a metacognitive ability since the behaviour could also be explained using associative mechanisms. Specifically, the bees may have learned to associate intermediate configurations with the opt-out response, effectively learning three associations rather than two associations and the use of an uncertain "opt out" response. Additionally, this task involves assessment of a public information source (external cues) rather than of private information (internal processes or memory), which arguably would require only perceptual responses, not higher-order representation (Hampton 2009).

Ants show many behaviours that are consistent with metacognition. When navigating home, ants rely both on internal idiothetic information (path integration, PI) and external cues (visual panoramas and odour plumes) (reviewed in Wehner 2003, Knaden & Graham 2016). When these cues conflict, ants tend to take an intermediate course (Wehner & al. 2016). Intriguingly, they seem to weigh the cues differently depending on their level of certainty (Wystrach & al. 2015). Specifically, the further an ant walked, the weaker its PI information is weighted. Similarly, when desert ants fail to find their nest entrance, the further the ant walked, the larger the search pattern they conduct (Merkle & Wehner 2010). However, it is not clear whether the ants are using their level of uncertainty directly or rather using their PI vector as a proxy for uncertainty. Indeed, if ants are confined to walking in a small pot rather than walking freely, they do not under-weight their PI information – either the integrator is paused while trapped in the pot or the vector is being used as a proxy for uncertainty (Wystrach & al. 2015). Regardless, it is clear that the ants can integrate some part of their private information, be it uncertainty or a PI vector length, and use it to inform a decision in a different but related domain, namely direction. Within the navigation domain, information from multiple sources can be integrated and translated with surprising flexibility (Schwarz & al. 2017). However, it is unclear how flexible the use of private information between different domains is: Could ants use PI vector, for example, in a non-navigational setting, for example, as a contextual cue for an olfactory discrimination task? It is also noteworthy that the ants attempt to compromise between PI and visual cues even if they provide wildly different directions. This implies that the ants do not realise that the information could stem from two different sources or that one could be completely compromised.

Ants also seem to respond to apparent uncertainty in ways not linked to their path integrators. When leaving the nest for the first time, *Ocymyrmex* desert ants perform a spiral walk around their nest, interspersed with regular pirouettes, in order to learn the retinoscopic view from around the nest. The number of pirouettes drops steadily with increasing experience (Müller & Wehner 2010). This implies that the ants are responding to their lack of knowledge by seeking out more information or, conversely, to their strong information by suppressing information acquisition. Again, it is not clear whether it is the lack of information which is being responded to directly or a proxy of this, such as the ants' own cuticular hydrocarbon profile, which will change with exposure to light and heat (Wagner & al. 2001). Such information acquisition behaviours in the face of uncertainty are reported in bees and wasps after first encountering a food source or experiencing difficulties in returning to a known food source or the nest (Zeil 1993, Wei & al. 2002), but again, these behaviour patterns could emerge by responding to proxy cues, such as prior extensive searching, without the animals directly interrogating the qualities of their memory.

Ants also respond to apparent uncertainty in ways other than changing their movement: They deposit more trail pheromone in difficult navigational situations or on hard-to-learn routes (Fig. 5). For example, pheromone deposition as well as pheromone following increase as light levels decrease (Beugnon & Fourcassie 1988, Fourcassie & Beugnon 1988, Jones & al. 2019). However, as mentioned above, mechanisms for uncertainty assessment which rely on a response to external cues are not strong evidence for metacognition (Hampton 2009). Similarly,

Fig. 5: A marked *Lasius niger* forager depositing a dot of trail pheromone. Note that the gaster is curled downwards and the tip is being pressed onto the surface. Ants decrease pheromone deposition when they are more likely to make navigational errors, consistent with a metacognitive ability. Photo credit: Julia Giehr.

Box 2: Unstudied and understudied topics in ant cognition.

Episodic-like memory: Episodic memories are wholistic representations of unique, past events, including what occurred, where it occurred, and when it occurred (CRYSTAL 2010). In other words, it is the ability to remember and re-experience a singular past event. Ants can form both aversive and appetitive multi-modal memories given only one exposure to the stimulus (DEJEAN 1988, DE AGRÒ & al. 2020), suggesting that they possess the abilities to learn unique events holistically. But is the unique event re-experienced during recall?

Planning, prediction, and foresight: Humans are well-able to foresee looming problems in the short term and take corrective action. The cooperative retrieval of prey by ants (Box 1) could be used as a test for forward-planning. For example, *Paratrechina longicornis* have been observed clearing obstacles out of the way of a large, cooperatively retrieved food item (E. Fonio & O. Feinermann, ongoing study, find a video of the behaviour here: <https://youtu.be/WAbqalnhFIU>). Does this clearing happen consistently? Does it happen as long as a pheromone trail is present or only if the obstacle is really in the way?

Mental time travel: The world changes in predictable ways, and we are capable of understanding that a bowl of ice cream left on a table will no longer be as desirable a few hours later. There are good ecological reasons for ants to be able to perform forward mental time travel, for example, to understand that a previously depleted food source has refilled. But can they?

Counting and numerosity perception: The lively debate as to the numerical abilities of bees is driven by the presentation of visual patterns (HOWARD & al. 2019a, MABOUDI & al. 2021). Very few such attempts have been made in ants, either in a visual or a non-visual modality (but see CAMMAERTS & CAMMAERTS 2019, 2020 for controversial examples carried out at the collective level and D'ETTORRE & al. 2021 for an example of possible subitizing). Many ant species are partially or wholly subterranean and may be well suited for non-visual tests, much as blind cave fish are a good model for testing non-visual numerosity in vertebrates (BISAZZA & al. 2014). Adapting the methods used by CARAZO & al. (2012) for testing numerosity assessment in flour beetles may be a promising approach.

Reasoning and drawing conclusions by analogy: Transitive inference has been studied in social insects with mixed success and always with visual cues (BENARD & GIURFA 2004, TIBBETTS & al. 2019) but, to my knowledge, not in ants.

Theory of mind: This is the ability to ascribe mental states, such as beliefs or emotions, to other individuals. Classic animal tests for this ability include responding differently to food items depending on whether competitors are watching. For example, Ravens (*Corvus corax*) differentiate between knowledgeable and ignorant competitors. After being allowed to hide food items either in the presence of a competitor or not, ravens preferentially retrieved items hidden in the company of a competitor when that competitor was present. Ants experience strong scramble competition from other ants (PARR & GIBB 2010) – would ants invest more foraging effort into food sources which they know have been discovered by competitors?

ants deposit more pheromone after making a navigational error or experiencing an environmental change (CZACZKES & al. 2013, CZACZKES & HEINZE 2015), but such retroactive responses may be responses to external stimuli or to the ants' own recent behaviour rather than an interrogation of internal mental processes. More intriguing, however, is that ants on the way to a food source decrease pheromone deposition if they will go on to make an error (CZACZKES & HEINZE 2015) – that is, before they can assess the success of their navigation attempt. This implies prospective meta-memory. However, again, ants may be responding to their own behaviour, for example, noting that they are walking in a more sinuous manner and so reduce pheromone deposition. Alternatively, and perhaps more likely, ants may be vacillating between "knowing" and "not knowing" and depositing no pheromone if they are in a "not knowing" or naïve state (BECKERS & al. 1993). Taken together, there is as yet no incontrovertible evidence that ants (or any other insect) can perform metacognition. However, ants show many behaviours consistent with a metamemory

ability, and experiments specifically designed to address this question are likely to be rewarding. While it may be impossible to rule out all non-metacognitive explanations in any one experiment, sufficient evidence of behaviour consistent with metacognition in different domains would make a strong case and shift the burden of proof to the lower-level explanations (SMITH & al. 2012).

Unstudied and understudied aspects of ant cognition

Many classical themes in the study of advanced cognition have received little or no attention in ants and often lack any examination in insects. This is a shame since attempting to examine advanced cognition in ants and in insects in general is a valuable service to the endeavour of comparative psychology. Attempting to translate research on humans to animals, especially invertebrates, can lead to clearer thinking, sharper paradigms, or provides an impetus for offering more parsimonious accounts of a process

(Kacelnik & Marsh 2002, Jurczyk & al. 2021). Ants offer a particularly valuable model in this regard since they have a very different sensorium to that of humans. Humans are overwhelmingly visual, and almost all advanced cognition tasks are based on visual discrimination, which the current major models of insect cognition, flies and bees, excel at. Most ants, then again, rely heavily on chemical and tactile senses. This can force a major rethink in how problems are tackled. For example, the principle test for a Theory of Self is the Mirror Test, wherein a mark is placed on an animal (or baby) where it cannot be seen directly, such as the forehead, and the subject is then shown a mirror (Gallup 1970). Undue attention being given to the mark and attempts to examine the mark directly, not in the mirror, are taken as evidence of a concept of self. The visual mirror test has been carried out on ants (Cammaerts Tricot & Cammaerts 2015), but this work has been strongly criticised (Gallup & Anderson 2018). But what would such a test look like for a non-visual creature? Indeed, an "olfactory mirror" design has been recently proposed (Horowitz 2017) and discussed (Gallup & Anderson 2018). Similarly, tests for numerosity perception and Theory of Mind (understanding that other animals have intentions, motivation, or knowledge different from one's own) are overwhelmingly visual, although there is no need for this to be so. For example, in an elegant experiment, numerosity perception and proto-counting were demonstrated in the beetle *Tenebrio molitor* by quantifying mate guarding by males after contact with a varying number of "competitor" males (Carazo & al. 2012). Developing methods for studying these topics in ants will help sharpen our understanding of these concepts, regardless of whether ants possess these attributes.

With this in mind, in Box 2, I provide a non-exhaustive list of advanced cognitive abilities which have been unstudied or understudied in ants and invite the readers to imagine, and perhaps conduct, tests for these.

Conclusion

Ants are ubiquitous in almost all ecosystems and offer a very broad range of ecologies, from lone night-time hunters to herders and farmers. They may thus support a wider range of cognitive abilities than the standard models of advanced insect cognition, the honeybees and bumblebees. The cognitive abilities of ants do not consistently line up with those of honeybees and bumblebees, making it imprudent to rely on those species as a guide to what insects can or cannot do. Many species of ants are predominantly chemosensory and tactile, thus offering a very different sensorium to the visual tasks commonly used in cognition research. This poses fresh challenges for study but offers new possibilities. Ants are also often very fast learners and very easy to work with – in my experience at least, much more so than bees or flies. Taken together, ants offer an important opportunity for studying cognition in invertebrates from fresh angles. Moreover, ants are understudied compared with the standard model organisms and offer such a range of ecologies that there are probably a lot of low

hanging fruits waiting out there for intrepid researchers who are willing to reach for them.

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