Individual and collective cognition in ants and other insects (Hymenoptera: Formicidae)

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Abstract

Ants are regarded by many non-scientists as reflex automata, with hardwired and inflexible behaviour. Even in the modern field of complexity science, they are sometimes portrayed as an example of simple units that can nevertheless, construct collective processes and infrastructures of bewildering sophistication, through feedback-controlled mass action. However, classical studies and recent investigations both have shown repeatedly that individual ants and other arthropods can display great flexibility in their behaviour, often associated with learning. This involves not only simple conditioning to the locations of stimuli associated with food, but also more complex learning, attention, planning, and possibly the use of cognitive maps (shown in honey bees). Ants in particular have been shown to employ sophisticated behaviours not only collectively, but also individually: one example is the use of tools, which was once thought to be a uniquely human characteristic. The evolution of such skills is not well understood. Recent research has demonstrated costs of learning, and therefore only some ecological conditions may favour the evolution of advanced cognitive abilities. The diversity of ants provides a rich resource for studying the link between ecology and learning ability, as well as revealing how much can be achieved with a brain that is many orders of magnitude smaller than ours.

Key words: Cognition, learning, orientation, cognitive map, attention, planning, generalisation, collective behaviour, review.

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Introduction

We define cognition as the ability to acquire, retain, and process information (SHETTLEWORTH 2001, DUKAS 2004) – processes that largely take place in the brain. Insects have tiny brains: a honey bee brain is estimated to have about 1 million neurons (MENZEL & GIURFA 2001), compared to about 100 billion in the human brain (WILLIAMS & HERRUP 1988). Therefore it is not surprising that they are widely assumed to possess only the most basic capabilities of information processing, let alone complex mental representations of the world. Consequently, insects have largely been ignored in the fields of comparative psychology and animal cognition, where most research focuses on mammals (and occasionally on birds) (DOMJAN 1987, WASSERMAN 1993, BOYSEN & HIMES 1999, PREMACK 2007), although see DUKAS (2004) and GRIFFIN & SPECK (2004). Nevertheless, the study of insect behaviour has revealed a host of both specialised and general cognitive abilities that rival those of many vertebrates (classic studies: SCHNEIRLA 1933, 1934, 1941, 1943, VOWLES 1964, 1965, STRATTON & COLEMAN 1973, ISINGRINI & al. 1985, HARRISON & BREED 1987, COLLETT & al. 1992, JOHNSON & al. 1994, PASSERA & al. 1994; newer reviews: ROITBLAT & FERSEN 1992, WANG & SPELKE 2002, GOULD 2004, GREENSPAN & van SWINDEREN 2004, GRIFFIN & SPECK 2004, GRONENBERG 2008, REZNIKOVA 2008). Ants in particular have shown such seemingly advanced skills as tool use (MORRILL 1972,

PIERCE 1986, GRASSO & al. 2004, BANSCHBACH & al. 2006), planning for the future (FRANKS & al. 2007b), learning (SCHNEIRLA 1933, DUPUY & al. 2006, LANGRIDGE & al. 2008), teaching (RICHARDSON & al. 2007), and sophisticated decision-making both at the individual (FRANKS & al. 2003, ALEKSIEV & al. 2007) and collective level (e.g., DORNHAUS & al. 2004, PRATT & al. 2005, DORNHAUS & FRANKS 2006, FRANKS & al. 2007a, PLANQUE & al. 2007). Most of our knowledge of insect cognitive skills derives from a few model systems, especially from studies on the honey bee (ALLOWAY 1972, GOULD 1986, MENZEL & GIURFA 2001, GREENSPAN & van SWINDEREN 2004). However, as the examples cited here show, ants provide a great opportunity to study the evolution of cognitive skills, by virtue of their morphological, social, and ecological diversity, and the ease with which they can be studied in large sample sizes (compared to primates or other vertebrates), while their individual behaviour can still be observed (Fig. 1). Studying cognition in insects, particularly ants, has several benefits. First, because of the relatively small size and complexity of the insect nervous system, they provide an opportunity to link brain structure and function, and even to study properties of individual neurons. New techniques in the neurosciences have enabled researchers to investigate behaviour and the underlying neuronal processes in great detail (HEISENBERG 1998, MENZEL & GIURFA 2001,

Fig. 1: Individual labelling of ants, usually with paint marks, is crucial for discovery of individual cognitive skills (shown here: *Temnothorax rugatulus*, photograph by Alex Wild ©).

GERBER & al. 2004b, MEHREN & al. 2004, SRINIVASAN & ZHANG 2004, ROBINSON & al. 2005, GRONENBERG 2008), although we are still far from mapping a complete neural circuit for any moderately complex behaviour. Second, the immense number of insect species allows comparative studies to link cognitive abilities to ecology, and thus quantify the fitness benefits of cognitive skills such as information processing and learning (CHITTKA & al. 2004, RAINE & al. 2006a, RAINE & CHITTKA 2007b). In addition, researchers are beginning to investigate costs as well as benefits of cognition-related genes (MERY & KAWECKI 2003, CHITTKA & al. 2004, MERY & KAWECKI 2004). Eventually, a more thorough understanding of benefits as well as costs of cognitive skills should enable us to understand how and why a diversity of such skills has evolved in animals.

Learning

Learning is a cognitive process that involves a change in behaviour after experience (PAPAJ & PROKOPY 1989, SHETTLEWORTH 2001). It is important to note that many behaviours that require complex computations, although using learned input parameters, are themselves innate mechanisms. For example, the neural mechanisms which ants use in a path integration orientation system (WEHNER 1987) entail the computation of a homing vector from hundreds of individual direction (MÜLLER & WEHNER 2007) and distance (WITTLINGER & al. 2006, RONACHER 2008) measurements. Honey bees (*Apis mellifera*) can accurately compute the sun's azimuth even when they have not seen the sun for hours (FRISCH 1967, SRINIVASAN & ZHANG 2004), and they do not have to learn to do this. Successive genera-

tions of monarch butterflies navigate from Mexico to North America and back without prior experience (BROWER 1996). The ability to perform certain, even complex, computations can thus be "hardwired" and heritable. However, many behaviours exhibited by insects involve learning, particularly in the contexts of orientation, choice of food sources, and other task performance.

Learning in foraging

The distribution of food sources, in both space and time, often varies between seasons and among habitats. If the occurrence of food sources is completely unpredictable, foragers have to spend much time searching, but gain no benefits from learning. If food sources can be found using unchanging, generally applicable rules or strategies, it is likely that these strategies evolve and become fixed in foragers, and there are also no benefits to learning ability. However, in most cases, food source locations, appearance, and optimal handling strategies vary at a cross-generational scale, but stay somewhat predictable within the foraging career of an individual. It is such cases that make learning adaptive: individuals can learn locally or currently optimal search locations or strategies to forage more successfully. Ant foragers have been shown to memorise both the locations of food sources and times at which they are profitable (SCHATZ & al. 1994, BEUGNON & al. 1996, SCHATZ & al. 1999b). Similarly, ant scouts can not only remember locations of new nest sites in order to immediately recruit to them (MALLON & al. 2001), but also remember previously found sites for later avoidance (FRANKS & al. 2007b). Bees have been shown to learn to associate a host of olfactory, visual, or tactile cues with food sources (see Tab. 1 for bees and Tab. 2 for ants).

Orientation and navigation

Compared to other cognitive skills, orientation and navigation are well-studied in ants and other insects. Ants are central place foragers, as they have to return to the nest with their prey. This means that all ants have to have mechanisms of finding their way back to the nest (the "central place") after a foraging trip. One mechanism for returning to the nest is path integration. Path integration means that foragers continuously update their memory of the vector (direction and distance) to the nest by measuring the directions and distances that they walk (WEHNER & al. 2006, RONACHER 2008). In principle, a path integration algorithm requires no learning to achieve this, but in reality, path integration is too error-prone to be used exclusively, as even small measurement errors can offset the homing vector. All social insects are therefore likely to at least memorise attributes of the nest entrance (FAURIA & al. 2002), to be able to identify it after returning to its general vicinity. In addition, landmarks (WEI & al. 2002, COLLETT & GRAHAM 2004) play a role in many orientation systems. Possibly, honey bees even count landmarks (CHITTKA & GEIGER 1995); although counting in ants has not yet been shown (FRANKS & al. 2006). Wood ants (*Formica rufa*), memorise snapshots of landmarks at multiple positions along a route (COLLETT & GRAHAM 2004). If the ants arrive at a site that matches their stored view, they can retrieve information on the next landmark, and thus follow their learned route back to the nest from any point along it. Maintaining a library of snapshot landmark memories may be more costly than a path

Tab. 1: Model organism honey bee: Bees, particularly honey bees (genus *Apis*), have frequently been used as model to study learning and cognition (FRISCH 1967). Their learning abilities are mainly tested in three different paradigms: 1. using the PER (proboscis extension reflex), 2. in flight arenas or Y-mazes, and 3. in training of free-flying bees to artificial food sources (feeders). In all three, bees are trained to recognise some stimuli as rewarding and others as unrewarding (sometimes even aversive stimuli are used). Bees have also been trained through complex labyrinths, and have been shown to associate cues in different modalities (SRINIVASAN & al. 1998), to be able to learn to follow signposts (ZHANG & al. 1996) as well as being able to learn the regularities of mazes (ZHANG & al. 2000). Honey bees also learn when and what to learn (ZHANG & SRINIVASAN 1994, WEI & al. 2002, PAHL & al. 2007). The structure of the honey bee nervous system, and the temporal structure of the learning process, have also been studied (MENZEL & GIURFA 2001).

Stimulus learnt	Experiment	Species	References
Odour, tactile pattern	PER	*Apis mellifera*	reviewed by MENZEL & GIURFA (2001)
Odour, colour, visual pattern, orientation	Y-maze, flight arena	*Apis mellifera*	reviewed by WENNER & JOHNSON (1966), MENZEL & GIURFA (2001)
		Bombus terrestris	GUMBERT (2000), NEY-NIFLE & al. (2001), FAURIA & al. (2002), CHITTKA & al. (2003), DORNHAUS & CHITTKA (2004)
Motor pattern, small-scale spatial coordinates	Flight arena	*Bombus terrestris*	CHITTKA (1998)
Odour, colour, visual pattern	Free-flying	*Apis mellifera*	reviewed by FRISCH (1967)
Spatial and temporal coordinates	Free-flying	*Apis mellifera*	reviewed by FRISCH (1967); RILEY & al. (2003)
		Bombus terrestris	NEY-NIFLE & al. (2001), SALEH & CHITTKA (2007)
Generalisation of colour / odour / pattern, categorisation	Flight arena	*Apis mellifera*	reviewed by MENZEL & GIURFA (2001); STACH & al. (2004), ZHANG & al. (2004)
		Bombus terrestris	GUMBERT (2000)
Negative / positive pattern discrimination	PER	*Apis mellifera*	DEISIG & al. (2001)
Sameness / difference (delayed matching to sample and non-matching to sample)	Y-maze	*Apis mellifera*	GIURFA & al. (2001); reviewed by MENZEL & GIURFA (2001)
Motion parallax cues	Free-flying	*Apis mellifera*	LEHRER (1996)
Symmetry	Free-flying	*Apis mellifera*	GIURFA & al. (1996)

integration mechanism, but it is also more robust to errors in measurements of distance and direction, and it can be used more flexibly if the ant is displaced from its location by water, wind, or researchers (a condition under which a path integration mechanism fails completely). An even more costly mechanism of orientation may be to use a "cognitive map", i.e., a map-like representation of the relative positions of landmarks, the goal (nest or food source), and the own position of the forager (WEHNER & al. 1996, COLLETT & GRAHAM 2004, RONACHER 2008). It has been debated whether animals in general, and insects in particular, are capable of using cognitive maps. New evidence from honey bees suggests that they can (MENZEL & al. 2000, RILEY & al. 2003, MENZEL & al. 2005, MENZEL & al. 2006). Such cognitive maps would enable foragers to take novel shortcuts between sites represented on the mental map, something that is impossible if only path integration or route memories are used. Orientation is also well-studied in the desert ant *Cataglyphis* (WEHNER & al. 1996, RONACHER 2008), which, contrary to bees and even wood ants (FUKUSHI & WEHNER 2004), does not seem to employ a map-like representation of landmarks for orientation (although some authors dispute this, BEUGNON & al. 1996). Are there so few distinctive landmarks in the desert that *Cataglyphis* ants would not benefit from using geocentric maps (Fig. 2)? Comparative studies of more species should be used to develop and test hypotheses about the evolution of map-like memory for landmarks. Whether or not ants use cognitive maps for orientation or learn routes based on landmarks, it is clear that learning and memory are important aspects of foraging.

Other learning

In insects, as in other animals, individuals often perform various tasks better and faster with experience. This can occur even if the overall structure of the behaviour seems to be genetically "preprogrammed". For example, colony emigrations in the ant *Temnothorax albipennis* always have the same structure (MALLON & al. 2001, PRATT & al. 2002), but the ants have been demonstrated to perform them faster and more efficiently with experience (LANGRIDGE & al. 2004, DORNHAUS & FRANKS 2006, LANGRIDGE & al. 2008). Ants and bees also learn to navigate mazes (SCHNEIRLA 1941, 1943, ALLOWAY 1972, STRATTON & COLEMAN 1973, ZHANG & al. 1996, CHAMERON & al. 1998, ZHANG & al. 2000, REZNIKOVA 2008), or generally to orient around their

Tab. 2: Learning in foraging in ants: Compared to the tradition of research on learning in bees, research on ant learning is a nascent field. Ants often rely more on olfaction than vision, and are typically of smaller body size than bees – both factors that make research on their learning ability more difficult. Nevertheless, many species of ants are also foraging in spatially complex environments, and thus learning in the context of orientation is the best-studied aspect of learning in ants (see reviews in JUDD & COLLETT 1998, WEHNER 2003, COLLETT & GRAHAM 2004). For information on neurobiology of ants see GRONENBERG (2008). This table does not intend to list exhaustively all studies on learning in ants, but to provide examples of the approaches used.

Learning paradigm	Tested as	Context	Species	References
Odour learning	Individuals	Y-maze	*Camponotus mus, C. fellah, Formica rufa*	VOWLES (1964), DUPUY & al. (2006)
Visual discrimination	Individuals	Y-maze	*Formica rufa*	VOWLES (1965)
Visual discrimination	Individuals	Binary maze	*Cataglyphis cursor*	COLLETT & al. (1992), CHAMERON & al. (1998), SCHATZ & al. (1999a)
Motor pattern	Individuals	Binary maze	*Gigantiops destructor*	MACQUART & al. (2008)
Spatial learning (landmarks)	Group, but pheromone trails excluded	Arena	*Temnothorax albipennis, T. rugatulus*	PRATT & al. (2001), A. Schmolke & A. Dornhaus, unpubl.
Spatial learning (landmarks)	Individuals tested but others present	Field	*Cataglyphis fortis, Formica japonica*	AKESSON & WEHNER (2002), FUKUSHI & WEHNER (2004)
Spatial (path) learning	Group	Complex maze	*Solenopsis saevissima*	STRATTON & COLEMAN (1973)
Spatial (path) learning	Group, but pheromone trails excluded	Complex maze	*Formica nitidiventris (as F. "incerta")*	SCHNEIRLA (1933, 1934, 1941, 1943)
Spatial (path) learning	Group & individual	"Binary tree maze"	*Formica* spp.	reviewed by REZNIKOVA (2008)
Time of day at which reward is present	Group & individual	Laboratory & field	*Ectatomma ruidum, Formica schaufussi, Paraponera clavata*	HARRISON & BREED (1987), FOURCASSIÉ & TRANIELLO (1993), PASSERA & al. (1994), SCHATZ & al. (1994), BEUGNON & al. (1996), SCHATZ & al. (1999b)

nest (CAPALDI & al. 2000). Specific handling routines at the food source are also often learnt, especially in bees, where flowers vary in morphology and thus the handling they require – different individuals may even develop different techniques even for the same kind of flower (HEINRICH 1979, LAVERTY 1994, CHITTKA 1998, RAINE & CHITTKA 2007a). Ants foraging on resources that require handling, such as seed-harvesting ants and predators, may also learn handling strategies, but this has not been tested. Bumble bees and certain butterflies also forage along more or less constant paths ("traplines"), learnt independently by each individual (PAPAJ & PROKOPY 1989, WILLIAMS & THOMSON 1998, SALEH & CHITTKA 2007).

Social insects may also have to learn the odour of their colony (JAFFÉ 1987, MOREL & al. 1988, DOWNS & RATNIEKS 1999), or even learn to recognise individual nestmates, sometimes visually (TIBBETTS 2002). In some insects, even mate acquisition and recognition of competitors may require learning, although in many such cases habituation or sensitisation, rather than associative learning, may be sufficient (PAPAJ & PROKOPY 1989). It is not known whether this is the case in any ant species. Finally, even though reactions to pheromones are often thought to be hardwired behavioural rules, in some cases they are not: bumblebees will learn to interpret the "footprint pheromone" on flowers as signalling the presence or absence of a reward (SALEH & CHITTKA 2006, SALEH & al. 2006, 2007); and in ants

of the genus *Camponotus*, workers may learn the specific hydrocarbon signature of their queen, and discriminate against others (ENDLER & al. 2005). Overall, it is clear that learning is as indispensable for insects as it is for vertebrates: indeed it can be argued that every major category of behaviour in insects has been shown to be influenced by learning in at least one species, and learning occurs in every insect order so far tested (ALLOWAY 1972, PAPAJ & PROKOPY 1989).

Complex forms of learning

Learning can be categorised as "procedural" or "declarative". Procedural learning involves memorising a certain course of action, e.g., when a stimulus is associated with a particular response. Declarative learning, by contrast, implies that a property of the environment is memorised. Declarative knowledge can then affect an animal's actions in several contexts (SHETTLEWORTH 2001). Declarative learning is considered to be a harder problem than procedural learning, and its presence in any animal is controversial (SARTER 2004). However, there are many cases in which insects arguably seem to acquire knowledge that can be used differently in different contexts. For example, bees will extend the proboscis when smelling a learned flower scent (GIURFA & al. 2001), but in a different context, such as when encountering the same flower scent in the hive, it will induce them to fly to a known food source (WENNER

Fig. 2: Ants encounter the problem of orienting in a complex environment particularly during foraging trips. The challenges faced by the ants, and the possible solutions, however vary enormously with the habitat: some habitats may lend themselves to using landmarks or patterns on the horizon for orientation, whereas some desert ants rely more on path integration because of the lack of landmarks (Top photograph: Alex Wild ©; bottom photograph: Tobias Merkle ©).

& JOHNSON 1966, FRISCH 1967). Knowledge about food source attributes also modulates other behaviours: if learned visual stimuli are not sufficient to discriminate food sources, honey bees deposit additional scent marks to guide them (GIURFA & al. 1994). Both bees and wasps may also perform "learning flights" around new food sources or around a familiar site if landmarks have changed (LEHRER 1996, WEI & al. 2002), indicating that in this context, bees "know what they know", and actively seek to learn more if necessary (WEI & al. 2002). Bees can also use prior knowledge about which stimuli they are likely to encounter to recognise poorly visible or camouflaged objects (ZHANG & SRINIVASAN 1994).

Tool use

It may seem obvious that even a small-brained animal like an ant must be able to learn to return home or to profitable food sources. Tool use, on the other hand, whether innate or learnt, was only discovered in non-human primates in the 1960s (in chimps: GOODALL 1964, WHITEN & al. 1999). Ants followed soon after this in the 1970s (MORRILL 1972, FELLERS & FELLERS 1976), but have received far less public attention. The known instances of tool use in ants fall into two categories, food transportation and competition /

aggression. To transport liquid or gelatinous substances, ants of the genera *Aphaenogaster* and *Pogonomyrmex* have been observed to drop leaf fragments, pellets of sand or mud, or pieces of dried wood into the pool of food. These objects were transported back to the nest after they had been soaked with the food substance, and some authors claim that this increases the amount of food that can be transported by each ant (FELLERS & FELLERS 1976).

In the context of competition, the genera *Dorymyrmex* (as "*Conomyrma*"), *Tetramorium*, and *Messor* were observed to drop small pebbles or soil pellets down the nests of a competitor (either another ant colony or a ground-nesting bee; PIERCE 1986). In the case of *Messor*, this prevented the competitor colony from foraging, possibly leading to a competitive advantage for the stone-dropping colony. In the case of *Tetramorium*, soil pellets dropped onto bees often precipitated an attack and the death of the bee (PIERCE 1986).

It is debatable whether building sophisticated nest structures (HÖLLDOBLER & WILSON 1990, ANDERSON & MCSHEA 2001, HANSELL 2005), or using other individuals to achieve a goal (larvae as weaving tools; other ants as "pothole plugs" or bridges; HÖLLDOBLER & WILSON 1990) also constitutes "tool use" (PIERCE 1986). Ant nest architecture certainly can be very sophisticated, with large structures that facilitate ventilation and temperature regulation, and specific storage chambers for food and refuse (HÖLLDOBLER & WILSON 1990, HANSELL 2005).

Mental representation and manipulation

We define cognition here as the ability to acquire, retain, and process information (see also SHETTLEWORTH 2001, DUKAS 2004), and the mind as the sum of such processes occurring in an animal's nervous system ("The mind is what the brain does": MINSKY 1986). But what information is actually stored, how is it processed, and why have these abilities evolved? How is learned information represented in the brain, and how does it influence subsequent behaviour? We advocate the use of terms such as "representation" and "decisions" when describing insect (or, indeed, human) cognitive function, because they have clear operational definitions which do not differ between research on vertebrate an invertebrate animals. We believe that rather than being overly preoccupied with definitions, scientists should focus their attention on "the ecological theatre and the evolutionary play" (HUTCHINSON 1965), i.e., the link between environment and behaviour (ALLEN & HAUSER 1991, SHETTLEWORTH 2001). Unabated reductionism may not suffice: describing brain function in terms of interactions of neurons is important, but insufficient to describe cognitive abilities as we, as yet, understand rather little about how behaviour can be created with neural circuitry. Just as physicists analyse the hydrodynamic properties of fluids at a higher level than their constituent atoms, even though fluids are just atoms and their interactions, cognitive biologists need to analyse their systems above the level of neurons and their interactions. Although, of course, only analyses that combine all levels are completely satisfying, several lines of evidence support the notion that the description of insect behaviour may not be possible in terms of very simple neural networks. The learning abilities demonstrated in insects cannot be explained by assuming a set of separate modules, each conditioned to react to a particular stimulus

(MENZEL & GIURFA 2001). Insects can react differently to the same stimulus depending on context (FAURIA & al. 2002). They can form abstract categories (ROITBLAT & FERSEN 1992, GIURFA & al. 1996, 2001, ZHANG & al. 2004) and generalise from learned stimuli to other stimuli and contexts (CHENG 1999, LIU & al. 1999, GUMBERT 2000, STACH & al. 2004). Bees can solve a negative pattern discrimination task, in which a combination of individually rewarded stimuli is not rewarded (DEISIG & al. 2001), which cannot be explained by parallel modules specific to each stimulus. Instead, these findings suggest that information is (or can be) processed centrally. Even stimuli of different modalities (such as visual and olfactory) can be processed together (as shown in context learning (WENNER & JOHNSON 1966, SRINIVASAN & al. 1998) and matching-to-sample tasks (GIURFA & al. 2001), and neurobiological studies have shown that such multi-modal integration is likely to occur in the mushroom bodies, a part of the insect brain that receives input from several other brain regions (HEISENBERG 1998). *Temnothorax* ants have been shown to assemble multiple kinds of information about different nest site attributes into one quality judgement using weighted-additive decision-making, the most advanced strategy for integrating information (FRANKS & al. 2003).

As already mentioned above, studies of orientation superbly reveal the advanced processing of stored information. When orienting in their home range, insects often use vector navigation to find their way back to their nest, particularly on routes that they have used many times (RILEY & al. 2003, FUKUSHI & WEHNER 2004), but some species may also use "cognitive maps", which enable them to compute novel shortcuts (see above). These orientation mechanisms are in certain ways surprisingly similar to those demonstrated in humans (WANG & SPELKE 2002). Outside the insects but still within the arthropods, spiny lobsters (*Panulirus argus*) have even been shown to perform true navigation (homing from a completely novel location with no learned landmarks) using magnetic cues, which may effectively serve as a kind of global positioning system (BOLES & LOHMANN 2003).

Insects have thus been shown to learn in complex ways, to categorise, to generalise, and to integrate information from the different senses; they have been shown to teach, adapting their behaviour to the progress of their "student" (RICHARDSON & al. 2007), and use tools. Some authors argue that classical conditioning alone may prove that insects also possess some kind of consciousness or inner perspective (GRIFFIN & SPECK 2004), because conditioning seems to be impossible without consciousness in humans (LOVIBOND & SHANKS 2002); however, this is controversial (LOVIBOND & SHANKS 2002, GRIFFIN & SPECK 2004). What about other complex mental processes, such as attention, planning, and anticipation? It seems that certain species of arthropods, for example jumping spiders (genus *Portia*), can anticipate and plan their route to a food source (TARSITANO & JACKSON 1997, TARSITANO & ANDREW 1999, GREENSPAN & VAN SWINDEREN 2004). A motionless spider can follow a pathway visually from a food source back to its own position, suggesting that the spider's attention is directed to the various parts of the path in turn (TARSITANO & ANDREW 1999). Ants have also been shown to use "latent learning", i.e., to memorise information that

is currently irrelevant but may be used later – a behaviour that may also be called "planning" (FRANKS & al. 2007b). Indeed a neurobiological correlate of anticipation, as well as an "attentive response" to salient stimuli, has been found in *Drosophila* and other insects (GREENSPAN & VAN SWINDEREN 2004).

Attention to particular stimuli may be necessary for any type of learning (GRIFFIN & SPECK 2004), because it restricts perception to relevant stimuli (GREENSPAN & VAN SWINDEREN 2004). This suggests constraints in the ability to process information immediately, or in parallel. Such constraints have been suggested in foraging bees exhibiting flower constancy (visiting only one type of flower even when other rewarding flowers are closer than the chosen flower type (WASER 1986). A possible explanation for this behaviour is that only one flower type can be retained in a readily accessible "working memory". In other words, bees may form a "search image", which can be more quickly recognised than other learned stimuli. Indeed bees were found to hesitate for longer if they were forced to switch between flower types, even if they were experienced at handling both types (CHITTKA & al. 1997). Search images, and a cost to switching between prey types, have also been demonstrated in jumping spiders (JACKSON & LI 2004). These results suggest that the ability to concentrate, i.e., to attend only to stimuli of likely relevance, has an effect on learning and information processing in insects and spiders. Even seemingly advanced cognitive processes, such as planning, anticipation and attention, can thus be demonstrated experimentally in arthropods. Such studies may enable researchers to identify neural structures necessary for these aspects of information processing.

Cognitive limitations

Insects, like vertebrates, do not learn everything equally easily. When learning the colours of food sources, bees can learn some colours after only one exposure, but take extended training to learn others (GOULD 1986, MENZEL & GIURFA 2001). Moreover, stimuli of certain modalities are quickly associated with an accompanying reward, whereas stimuli in other modalities are learnt only after a long time or never (FRISCH 1967). Such findings demonstrate that animals are predisposed to learn certain things and not others. This highlights the role ecology has played in the evolution of learning ability.

What is the memory capacity of an insect? Under ideal conditions, bees can memorise odours, colours, and required handling techniques for several flower types and retain these memories for life (GOULD 1986, PAPAJ & PROKOPY 1989, CHITTKA 1998). Bees may also be able to learn 40 - 50 different spatio-temporal food source coordinates (GOULD 1986). Butterflies, on the other hand, may only be able to remember one flower type at a time (LEWIS 1986, PAPAJ & PROKOPY 1989). However, even in bees the temporal schedule of learning trials and the similarity of stimuli or tasks may cause interference and thus limit learning performance and memory retrieval (STANTON 1984, LAVERTY 1994, CHITTKA 1998, FAURIA & al. 2002, WORDEN & al. 2005). This indicates that correct suppression and retrieval, not memory capacity *per se*, limits the number of associations bees can make (CHITTKA 1998).

Collective intelligence

In addition to solving complex problems individually, social insects are also said to possess "collective intelligence" (FRANKS 1989). In insect colonies, problems that exceed the information collection and processing capabilities of individuals are often solved collectively. For example, a colony of honey bees can effectively survey an area of more than 100 km^2 for resources or nest sites, although individuals only have a body length of 15 mm (SEELEY 1998). A colony of *Temnothorax albipennis* ants can move out of a destroyed nest site and into the best new one among many alternatives, even if each individual ant has only visited one or two sites (FRANKS & al. 2002). Indeed there are several ways in which colonies can make collective decisions (FRANKS & al. 2002, JEANSON & al. 2004). All social insect colonies achieve an allocation of individuals to tasks which is both adaptable to changing demands and robust to loss of a large proportion of the workforce (SEELEY 1998, PAGE & ERBER 2002), something that engineers are striving to replicate. How do the insects achieve this?

Social insect colonies benefit particularly from their ability to collect and distribute large amounts of information. Recruitment and communication enable individuals to use information collected by their nestmates, and specialised information channels are often used to disseminate information to the appropriate individuals (SEELEY 1998, DORNHAUS & CHITTKA 2004). This extends the sensory abilities of individuals enormously. Information may also be stored in the nest or in pheromone deposits en route to or on food sources (SEELEY 1998, DORNHAUS & CHITTKA 2004), complementing individual memory. Task allocation is achieved with algorithms that make use not only of variation among individuals, but also of their capabilities of changing behaviour through learning (PAGE & ERBER 2002, WEIDENMÜLLER 2004). The algorithms used to achieve distributed problem solving by colonies of social insects may be very similar to those employed when the brain solves problems through the actions and interactions of neurons. Collective strategies thus enable insects to surpass even the good cognitive abilities that they possess as individuals.

Studying the evolution of cognitive skills

Why are so many examples of learning known from bees, and not from other species? Why are some behaviours more likely to change with experience than others? There is certainly a bias in the species and behaviours that have been investigated. Honey bees are familiar, easy to keep, and commercially relevant, so they are overrepresented in insect cognition research (Tab. 1). However, there are other well-studied insect models (PAPAJ & PROKOPY 1989), and researcher bias is unlikely to be the only explanation. Bees are a group whose ecology may make the ability to learn particularly adaptive. Bees forage for resources that are extremely variable in appearance and handling requirements (HEINRICH 1979), and they are central place foragers (having to transport food back to a fixed point, the nest), making spatial learning essential. The hypothesis that flowers are so variable that learning is required for their efficient exploitation is supported by the impressive learning abilities of butterflies, which, in common with bees, forage for nectar (LEWIS 1986, PAPAJ & PROKOPY 1989). The corollary of this hypothesis predicts that species of insects that encounter less variable resources will not have evolved sim-

ilar learning ability. More comparative studies of ecology of learning are needed to quantify possible benefits of advanced cognitive abilities in different species (JACKSON & CARTER 2001, CHITTKA & al. 2004, RAINE & CHITTKA 2007b).

Ants would be an ideal model system to address this issue. Ants are also central-place-foragers, and thus employ sophisticated orientation mechanisms. On the other hand, ant species differ substantially in foraging strategies, and the group contains both species who forage on stable resources (such as extrafloral nectaries on trees and cacti) and species who forage on patchy and variable resources, such as seeds or insect prey. Ants, as a group, therefore provide a unique opportunity for phylogenetically controlled analysis of the evolution of learning and other cognitive skills.

The evolution of learning will depend not only on its potential benefits, but also on the costs of learning and on the availability of sufficient heritable variation on which selection can act. Indeed, substantial costs to maintaining the ability to learn (WILLIAMS & HERRUP 1988, MERY & KAWECKI 2003), and to the learning process itself (MERY & KAWECKI 2004) have been shown in the fruit fly *Drosophila*. For learning to evolve, benefits have to exceed costs. Variation in learning ability is often de-emphasised, yet it is extremely common both among individuals (LAVERTY 1994, SCHEINER & al. 2001), among colonies (RAINE & al. 2006b), and among populations (JACKSON & CARTER 2001, CHITTKA & al. 2004). A large amount of this variation is likely to be heritable (SCHEINER & al. 2001, PAGE & ERBER 2002, MERY & KAWECKI 2004). Heritable interindividual and between-population variation is the raw material for selection. The presence of such variation implies that selection has not acted to maximise learning, but that the capacity to learn is maintained to maximise benefits while minimising costs (WILLIAMS & HERRUP 1988). Quantifying costs and benefits for different species is a promising area for new research. It will be necessary to identify not just the genes involved in learning and their pleiotropic effects, but also the ecological variables that make learning beneficial for some species and not for others.

Variation in performance in cognitive tests should be a subject for study in its own right, not just because it is important to understand variation in order to understand the evolution of cognitive traits. Differences in behaviour between individuals may represent different strategies, and the problem solving capabilities of individuals may be underestimated if this is ignored. For example, individual bumble bees can be either slow and accurate or fast and error-prone in selecting a trained colour from a set of distractors, but they also adapt their strategy to the difficulty of the task and the cost of errors (CHITTKA & al. 2003, CHITTKA & DYER 2004). Similarly, MERY & KAWECKI (2004) suggest that *Drosophila* flies from different (artificial) selection lines vary in their investment in learning versus productivity. Differences in individual task performance may thus result from a diverse repertoire of problem solving strategies: future studies should investigate this thoroughly.

How can we study cognition in ants

A variety of methods have been used to assess the learning abilities of insects. The PER (proboscis extension reflex) paradigm used in honey bees (see Tab. 1) has also been used in flies (AKAHANE & AMAKAWA 1983) to condition
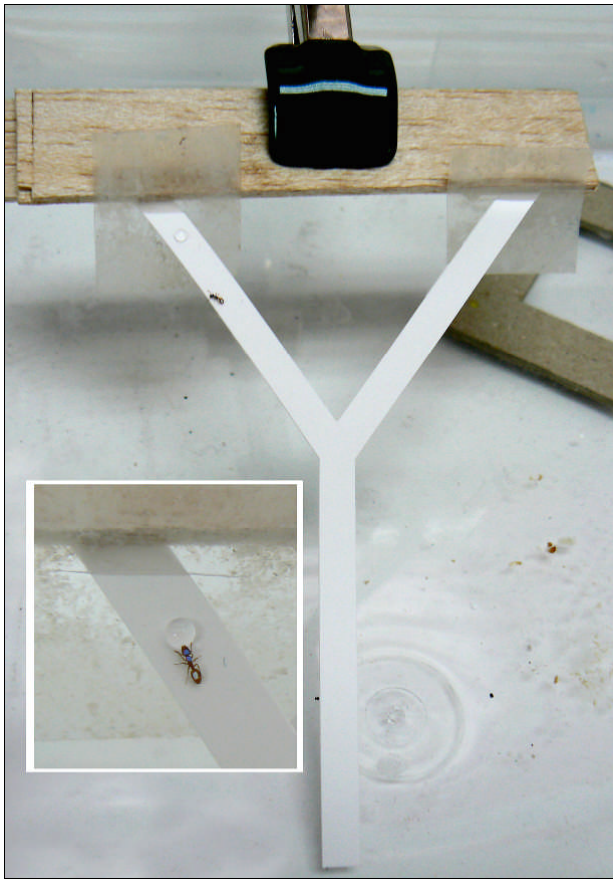
Fig. 3: A common setup for studying simple learning in insects is a Y-maze; here shown as a bridge-Y-maze with a reward on the left arm (a drop of sugar solution) and a worker of *Temnothorax rugatulus* (photograph by Lesley Rentz ©).

them to olfactory or tactile stimuli. In addition, flies (particularly *Drosophila*) have been trained in various learning paradigms, using odours or visual patterns (colour, contrast, stationary and moving) as conditioned stimuli, and (uncomfortable) heat, visual or mechanical shaking in a flight simulator, or food as reinforcers (WOLF & al. 1998, GERBER & al. 2004a, b). Flies have also been trained to vary or suppress courtship behaviour (WOLF & al. 1998, MEHREN & al. 2004), in spatial and motor learning tests (WOLF & al. 1998), and in tests of oviposition site choice (MERY & KAWECKI 2003, 2004). Studies of butterflies and other phytophagous insects have tested for learning in oviposition and foraging contexts (LEWIS 1986, PAPAJ & PROKOPY 1989). Cockroaches have been trained in different mazes (ALLOWAY 1972). Among other arthropods, jumping spiders have been shown in a set of beautiful studies to learn complex routes to food (TARSITANO & JACKSON 1997, TARSITANO & ANDREW 1999) and use trial-and-error learning for prey capture (JACKSON & CARTER 2001), and hermit crabs have been shown to use learning when selecting shells (MESCE 1993).

Some of these methods may be more suitable for research on ants than others. In the past, learning in ants has been studied particularly in Y-maze (Fig. 3) and other variations of mazes (ALLOWAY 1972, DENEUBOURG & al. 1987,

DUPUY & al. 2006), or in other spatial tasks where the ants had to remember the location of a food source (A. Schmolke & A. Dornhaus, unpubl.). Usually in these setups the ants are required to learn visual landmarks or proprioceptive cues (SCHATZ & al. 1994, CHAMERON & al. 1998, FRANKS & al. 2007b). However, there is a lack of studies employing other modalities, such as olfaction or tactile learning. Furthermore, ants have yet to be tested in more complex paradigms, such as delayed-matching-to-sample tests. Learning may also play a big role in task specialisation within colonies, and individuals may improve their performance at various tasks with experience, but this has not been comprehensively studied.

The future of insect cognition research

Most research on insect cognition to date has been conducted on a few model organisms, such as *Drosophila* and the honey bee. Because the neurobiology and genetics of these model organisms are studied intensively, this enables researchers to investigate the relationship between cognition and the neurological circuitry in great detail. Indeed an understanding of actual networks and the functions of individual cells has begun to emerge for the insect brain (HEISENBERG 1998, MENZEL & GIURFA 2001, GERBER & al. 2004a). In addition, studies of many other insect species have revealed a diversity of specialised and general cognitive abilities. As the diversity of cognitive abilities is recognised and explored, new possibilities arise to study the evolution of such abilities by linking them with the species' ecology (JACKSON & CARTER 2001, CHITTKA & al. 2004). Not only is it a fascinating insight that many cognitive functions can be solved by brains several orders of magnitude smaller than ours, but the diversity of lifestyles of insects and other arthropods also provides a unique opportunity to study the evolution of such abilities.

Zusammenfassung

Oft werden Ameisen als "Reflexmaschinen" mit inflexiblen, angeborenen Verhaltensmustern angesehen. Viele neue Studien zeigen jedoch, dass sowohl Ameisen als auch andere Arthropoden durchaus lernen können und komplexe kognitive Fähigkeiten einsetzen. Dazu gehören nicht nur einfaches Konditionieren auf Stimuli, die mit Futter assoziiert sind, sondern auch gerichtete Aufmerksamkeit, Planung und kognitive Karten zur Orientierung. Besonders Ameisen (verglichen mit anderen Insekten) zeigen natürlich interessante kollektive Verhaltensweisen; aber sie können auch als Individuen Werkzeuge benutzen, eine Fähigkeit, von der man bis vor einiger Zeit dachte, dass sie Menschen vorbehalten ist. Das "wie" und "warum" der Evolution solcher Fähigkeiten ist noch nicht gut untersucht. Neue Studien zeigen, dass die Fähigkeit zu lernen kostspielig sein kann, und dass sie darum vermutlich nur unter besonderen ökologischen Bedingungen evolviert. Ameisen, mit ihrer hohen Diversität in Lebensstil und Arten-

reichtum, sollten in Zukunft eine Goldgrube der Kognitionsforschung sein: Sie können als Modellsystem dienen, in dem das Verhältnis von Ökologie und Lernvermögen untersucht wird. Sie zeigen auch, wie viel kognitive Fähigkeiten und Lernvermögen mit einem Gehirn möglich sind, das mehrere Größenordnungen kleiner ist als unseres.

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