CHAPTER ONE

Putting the ecology back into insect cognition research

Mathieu Lihoreau[a], **Thibault Dubois**[a,b,*], **Tamara Gomez-Moracho**[a,*], **Stéphane Kraus**[a,*], **Coline Monchanin**[a,b,*], **Cristian Pasquaretta**[a,*]

[a]Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI), CNRS, University Paul Sabatier, Toulouse, France
[b]Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia
*These authors contributed equally to the work.

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Abstract

Over the past decades, research on insect cognition has made considerable advances in describing the ability of model species (in particular bees and fruit flies) to achieve cognitive tasks once thought to be unique to vertebrates, and investigating how these may be implemented in a miniature brain. While this lab-based research is critical to understand some fundamental mechanisms of insect brains and cognition, taking a more integrative and comparative view will help making sense of this rich behavioural repertoire and its evolution. Here we argue that there is a need to reconsider insect cognition into an ecological context in order to design experiments that address the cognitive challenges insects face in nature, identify competing hypotheses about the cognitive abilities driving the observed behavioural responses, and test them across different populations and species. Reconnecting with the tradition of naturalistic observations, by testing animals in the field or in ecologically-inspired setups and comparing

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their performances, is complementary to mechanistic research in the lab, and will greatly improve our understanding of the role of insect cognition, its diversity, and the influence of ecological factors in its evolution.

… que se passe-t-il dans ce petit cerveau d'hyménoptère? Y a-t-il là des facultés soeurs des nôtres, y a-t-il une pensée? Quel problème, si nous pouvions le résoudre; quel chapitre de psychologie, si nous pouvions l'écrire! […what happens in this little brain of Hymenoptera? Are there abilities similar to ours, is there a thought? What problem, if we could solve it; what chapter of psychology, if we could write it!]

Translated from Jean-Henri Fabre (Fabre, 1882, p. 405).

1. Past and present of insect cognition research

Famous naturalists such as Réaumur, De Geer, Latreille, Fabre, Darwin, Lubbock, to name just a few, have played a considerable role in demonstrating that insects, just like large-brained animals, are capable of adapting to new situations through various forms of learning, memory and communication. In the 20th century, the first ethologists made invaluable contributions to our understanding of these processes, through experimental manipulations and quantifications of insect behaviour in the field. Von Frisch (1915), for instance, used artificial flowers to show colour discrimination by honey bees. This approach later facilitated the discovery of the symbolic communication by which foragers advertise the location of remote feeding sites to their nestmates by displaying dances on the vertical honey combs (von Frisch, 1967). Tinbergen manipulated the visual appearance of the nests of digger wasps with pine cones to demonstrate that wasps use visual memories to orient themselves and return home (Tinbergen, 1932).

Since then, generations of talented entomologists have described a rich diversity of cognitive abilities by which insects sample, process and use information from their environment to adapt their behaviour in different contexts (e.g., mate choice, foraging, egg laying, navigation) at different levels (e.g., as individuals and as groups) and in a variety of taxa (for recent reviews see: Collett et al., 2013; Feinerman and Korman, 2017; Giurfa, 2013, 2019; Papaj and Lewis, 2012; Perry et al., 2017). This research shows that model species (especially bees and fruit flies) achieve ever more impressive cognitive tasks despite their relatively simple neural system. At the individual level, bees are capable of learning concepts (Giurfa et al., 2001), counting (Howard et al., 2018), optimising paths (Lihoreau et al., 2012b), copying others (Alem et al., 2016), innovating (Loukola et al., 2017) and even self-assessing their chances to solve a task (Perry and Barron, 2013). Some wasps can recognize the faces of their nestmates (Sheehan and Tibbetts, 2011) and fruit flies can socially transmit mate choice preferences across several generations, possibly leading to local traditions (Danchin et al., 2018). At the collective level, ants and bees in colonies often make faster and more accurate decisions than alone when selecting food sources (Beckers et al., 1990) or a nesting site (Sasaki et al., 2013; Seeley, 2010), and can efficiently solve mazes (Goss et al., 1989) or transport large food items across complex environments (Gelbium et al., 2015).

Over the past decades, the development of new technologies and methods in neurosciences (Dubnau, 2014; Menzel, 2012) has progressively moved research in insect cognition from the description of sophisticated behaviour in the field to mechanistic investigations of cognitive processes and their neural correlates in the lab. Significant progresses in understanding insect brain organisation and function have been made using genetic mutants (e.g., GAL4/UAS, optogenetics), imaging techniques, drug injections or screening of gene expression in targeted neuropiles (Guo et al., 2019). We now have a fairly good idea of brain areas, neurons and molecular pathways involved in different forms of associative learning in model species such as fruit flies, honey bees, some ants, moths, cockroaches and crickets (Giurfa, 2013). In particular, the fruit fly *Drosophila melanogaster* has emerged as a key genetic model to address these questions both because of the relative simplicity of its nervous system (mapped at the level of synaptic connectivity, Zheng et al., 2018) and its rich behavioural repertoire both at the individual and collective levels (Sokolowski, 2010), allowing for the genetic dissection of sophisticated behaviours, such as place learning (Ofstad et al., 2011), flight control (Dickinson and Mujires, 2016), courtship (Pavlou and Goodwin, 2013), grooming (Hampel et al., 2015), memory-driven action selection (Owald and Waddell, 2015) and collective movements (Ramdya et al., 2014).

Although very insightful, the fast development of lab-based mechanistic studies has also reduced the scope of insect cognition research in several ways. First, the focus on the molecular and genetic bases of cognitive processes has limited investigations to few model species that may not express a cognitive repertoire representative of the estimated 5.5 million insect species (Stork, 2018). While it can be interesting to compare bees, ants and wasps when considering social evolution within the social Hymenoptera (e.g., Farris, 2016; Gronenberg and Riveros, 2009), the comparison with the more phylogenetically distant fruit flies may be less informative (Brenowitz and Zakon, 2015). Second, studies on the mechanisms of learning and memory often rely on hypotheses and paradigms inspired from human experimental psychology that may sometimes bias interpretations of the results, and limit the search for alternative (sometimes more parsimonious) explanations (e.g., Cheung, 2014; Guiraud et al., 2018). Third, research that is exclusively conducted in the lab presents the risk of disconnecting subjects, behaviours and cognitive traits of interest from their natural environment. Testing animals in very artificial setups in order to achieve a high level of control on information available to insects and their behavioural responses, does not always allow for the expression of the desired naturalistic behaviours (e.g., Niggebrügge et al., 2009). The questions or approaches used to study insect cognition are often very different from situations animals face in nature (e.g., study aversive learning using electric shocks, conditioning immobile harnessed insects, testing social insects in isolation). The animals themselves used for testing cognitive abilities often come from long-term laboratory or commercial cultures in which some traits may be inadvertently selected or counter selected (e.g., commercial bumblebees, *Drosophila* mutant strains). Fourth, the type and levels of stress animals are exposed to may be highly different in the lab and in the field. This can be problematic since several recent studies show that negative or positive experiences can induce emotion-like states in insects that have consequences on their behaviour and performances in cognitive tasks (e.g., *Drosophila*, Yang et al., 2013; honey bees, Bateson et al., 2011; bumblebees, Perry et al., 2016).

Here we argue that there is a need for complementing current lab-based insect cognition research with more ecologically inspired studies in order to fully understand the diversity and evolution of cognitive traits. In recent years, concepts of cognitive ecology have been embraced by behavioural ecologists and experimental psychologists working on vertebrates and proved successful to advance knowledge on the ecological role and evolution of bird and primate cognition (Dukas, 1998, 2008; Dukas and Ratcliffe, 2009; Morand-Ferron et al., 2015; Pritchard et al., 2016). In what follows, we advance that time is ripe for the development of a cognitive ecology of insects. First, we review conceptual frameworks that have been proposed for the evolution of the insect brain and cognition. We then explain how taking into account the ecological context in which cognitive traits are expressed in nature can help refine these frameworks by designing field-inspired experiments, testing wild animals, bringing lab-controlled protocols to the field, as well as comparing more species. Finally, we discuss how technological advances to study insect cognition in ecologically realistic conditions will help develop this comparative approach, by dramatically increasing the number of cognitive tasks and individuals that can be investigated.

2. The evolution of insect brains and cognition

While we are now getting a more accurate picture of what insects can and cannot do (Perry et al., 2017), and which are the brain areas and neural circuits involved in some of these cognitive operations (Giurfa, 2013), fundamental questions about why and how cognitive traits evolve in these animals remain poorly understood.

Both social and ecological factors are expected to fashion the evolution of brains and cognition (Shettleworth, 2009). Since early descriptions of the anatomy of the insect nervous system (Dujardin, 1850), many discussions about the evolution of insect brains and cognitive abilities have focused on the influence of social factors (Strausfeld, 2012). Following the "social brain hypothesis" developed to explain the evolution of large brains in social vertebrates, and in particular anthropoid primates (Byrne, 1996; Dunbar, 1998), two hypotheses were recently proposed for insects. Gronenberg and Riveros (2009) suggested that the transition from solitary to gregarious and colony-based social structures has required the expansion of brain regions related to communication, large behavioural repertoires and flexibility. By contrast, behavioural specialization in socially advanced species with division of labour may have led to reduced investment in brain regions underpinning a range of cognitive operations not required anymore, thereby predicting a quadratic relationship between increasing levels of social complexity and brain size (Gronenberg and Riveros, 2009). O'Donnell et al. (2015) proposed that group communication relaxes the need for individual information processing, resulting in a linear decrease of brain size (or brain size areas) with increasing levels of sociality.

Despite many attempts to correlate brain sizes with metrics of social complexity in different insect taxa, empirical supports for a social brain hypothesis are mixed (Farris, 2016; Gordon et al., 2019; Kamhi et al., 2016, 2019; O'Donnell et al., 2015; Riveros et al., 2012). Part of the problem may be methodological (e.g., coarse measures of social complexity and brain sizes, lack of phylogenetical approaches), thus calling for broader comparative analyses of neuro-anatomical and behavioural studies mapped on phylogenies (Godfrey and Gronenberg, 2019; Lihoreau et al., 2012a). Another difficulty in this hypothesis lies in the unverified assumption that larger behavioural repertoires require larger brains. In fact, many fundamental changes in the complexity of a nervous system may not result in measurable volumetric differences and novel behaviour can emerge from minimal rewiring of existing neurons (Chittka and Niven, 2009).

The strong focus on the importance of social factors for the evolution of brains and cognitive capacities (especially in Hymenoptera) has somehow neglected a number of alternative or complementary hypotheses that have been long developed by vertebrate biologists, such as the importance of diet (DeCasien et al., 2017), maternal care (Curley and Keverne, 2005) or spatial navigation (Jacobs et al., 1990). Ecological conditions are known to fashion the evolution of insect sensory systems and brain anatomy (e.g., vision (Briscoe and Chittka, 2001), and olfaction (Hansson and Stensmyr, 2011)). However, the links between ecological constraints and cognitive capacities have been little explored. In an attempt to test these alternative hypotheses in Hymenoptera, Farris and Schulmeister (2011) made a careful evaluation of the architecture of the mushroom bodies (central brain structures involved in various forms of visual, olfactory and bimodal memories (Strausfeld, 2012)) in a wide diversity of species and mapped their lifestyles and neural structure onto an established phylogeny. This analysis showed that relatively enlarged mushroom bodies, with elaborate structure and visual and olfactory inputs, evolved 90 million years prior to sociality, in solitary parasitoid wasps (Farris and Schulmeister, 2011). Presumably, the challenge of acquiring spatial memories for locating prey and provisioning larvae may have placed much higher cognitive demands in these first parasitoids than in their herbivorous ancestors. Only later, this cognitive adaptation to spatial orientation may have favoured the evolution of central place foraging and the development of large societies sustained by highly efficient visuo-spatial foragers (Farris, 2016).

3. Towards a cognitive ecology of insects

The emerging field of cognitive ecology provides a theoretical and methodological framework to study the ecology and evolution of animal cognition (for reviews see Dukas, 1998; Dukas and Ratcliffe, 2009). This involves designing new hypotheses and experiments based on field observations, testing wild animals, bringing lab-controlled experimental protocols into the field, taking into account the social context of the cognitive task, and comparing large numbers of species with known ecologies and phylogenetic relationships. While this approach has so far mainly been used for vertebrates, especially birds and mammals (Dukas, 2008; Morand-Ferron et al., 2015; Pritchard et al., 2016), below we highlight some key recent examples in insects.

3.1 Identifying new questions and hypotheses from field observations

Field observations are necessary to identify the types of problems animals must solve in their everyday life and how they might do so. The natural environment often contains much more relevant cues for the animals than typically assumed which structures the kind of information they can acquire. Observing freely moving insects in their natural environment is thus fundamental to design questions, identify competing hypotheses and develop experimental protocols, be the research later conducted in the lab.

Field observations are particularly important in insect navigation research since spatial orientation behaviours are not always easily expressed in lab setups with limited spatial scales and the incomplete set of environmental cues. In bees, field observations have recently moved the focus on simple nest-feeder navigation to more complex multi-destination route learning and optimisation (Lihoreau et al., 2013). In an attempt to study long-distance pollination by orchid bees in the Costa Rican rain forest, Janzen (1971) observed that some individuals often visited the same set of plants each day, probably in the same order. Given that bees are assumed to visit hundreds of flowers during a single foraging trip (von Frisch, 1967), this anecdotic observation has initiated several research programs investigating how bees develop routes between many familiar sites (Lihoreau et al., 2012b; Ohashi et al., 2007; Woodgate et al., 2017), for how long route memory is effective (Thomson, 1996), and how individuals achieve this behaviour while minimizing competition with other nectar foragers (Ohashi et al., 2008; Pasquaretta et al., 2019). In ants, field observations have raised new questions about how insects use environmental cues to solve orientation challenges. In the Australian desert, thermal turbulences due to solar heating of the ground create frequent wind gusts and it is not rare to see ants getting blown away from their familiar route. Even a small displacement of a few meters (i.e., several hundreds of body lengths for an ant) constitutes a big challenge for the ant to relocate its original position. Based on this observation, desert ants, *Melophorus bagoti*, were observed reorientating in the field after being experimentally displaced by wind gusts from a leaf blower into a dark pit (Wystrach and Schwartz, 2013). When released at windless unfamiliar locations, ants headed in a compass direction opposite to the one they had been blown away, thus functionally increasing their chance of returning to familiar areas. The encoding of wind direction relative to sun position occurs before being displaced, while clutching the ground to resist the wind (Wystrach and Schwartz, 2013). Field observations that ball-rolling dung beetles, *Scarabaeus lamarcki*, also appear to use wind in addition to the sun for spatial orientation have raised the question of how insects may use multimodal compass cues for navigation and inspired lab experiments in which sun and wind cues can be delivered in a tightly controlled manner (Dacke et al., 2019). In this setup, beetles were found to register information provided by the sun and the wind, and directional information can be transferred between these two sensory modalities, suggesting that beetles combine in the spatial memory network in their brain. This flexible use of compass cue preferences relative to the prevailing visual and mechanisms scenery provides a simple, yet effective, mechanism for enabling compass orientation at any time of the day when one type of cues may not be available (Dacke et al., 2019).

Field observations can also been pivotal to understand cognitive processes in populations of animals, such as the collective decisions underpinning the onset of insect swarms (Bazazi et al., 2008; Simpson et al., 2006). During population outbreaks Mormon crickets, *Anabrus simplex*, form marching bands of several kilometres long, comprising millions of individuals moving en masse (Sword et al., 2005). Observations of migratory bands indicated that many dead insects were left behind, as well as some carcasses of small vertebrates, suggesting that sedentary herbivorous crickets swarm in response to a local depletion of key nutrients (Simpson et al., 2006). Giving migrating crickets a choice between artificial diets varying in their nutritional composition in the field demonstrated that crickets in migratory bands are deprived of protein and mineral salts, which triggers their cannibalistic interactions. The crickets are in effect on a forced march, whereby individuals move ahead to try to eat conspecifics while escaping cannibalism by others behind them (Simpson et al., 2006).

3.2 Testing wild animals

Running experiments on wild animals offers the opportunity to assess important inter-individual variations in behaviour and cognition that are potentially shaped by environmental conditions, thereby providing a link between cognitive performances and the ecological context (Morand-Ferron et al., 2015).

In fruit flies, *D. melanogaster*, the utilization of wild-caught individuals for behavioural experiments has revealed the existence of natural allelic variations of the gene *foraging*, which encode a cGMP-dependant protein kinase (PKG) that affects the motor behaviour and social interactions of larvae and adults (Sokolowski, 1980). Sitter flies (for^S) are more sedentary and tend to aggregate within food patches, whereas rover flies (for^R) move more within and between food patches and are less gregarious (Sokolowski, 2010). These two natural behavioural variants are maintained at appreciable frequencies (ca. 70% rovers, 30% sitters) in nature (Sokolowski, 1980) and in the lab through negative frequency dependent selection (Fitzpatrick et al., 2007). Rovers and sitters also show important differences in their cognitive abilities. Rovers express stronger proboscis extension responses following a sucrose stimulation of their tarsi and show slower habituation of this response after multiple stimulations than sitters (Scheiner et al., 2004). Rovers develop better short-term aversive olfactory memory but poorer long-term memory than sitters (Mery et al., 2007). Interestingly, these two behavioural variants also differ in their ability to use social information. In a spatial task, where flies must learn to locate a safe zone in an aversively heated arena (i.e., invertebrate version of the Morris water maze), rovers rely more on personal information whereas sitters tend to primarily use social cues (Foucaud et al., 2013). These results suggest that both the utilization of information types and the cognitive performances of the two genotypes are co-adapted with their effects on foraging behaviour: the highly exploratory rovers could particularly benefit from fast learning based on individual information, whereas the more sedentary sitters should benefit more from social information and good long-term memory.

Wild populations are characterised by natural levels of genetic diversity that can greatly impact behavioural variability in cognitive tests. Experiments with German cockroaches, *Blattella germanica*, from different laboratory strains showed that individuals can discriminate between conspecifics with different genetic backgrounds, favouring aggregations with partners from the same strain (Rivault et al., 1998; Rivault and Cloarec, 1998) but mating with partners from different strains (Lihoreau et al., 2007). Intra-strain (kin) discrimination, however, could only be demonstrated in studies using wild-caught cockroaches sampled in separate geographic areas, showing that behavioural discrimination is based on quantitative differences in chemical signatures (i.e., cuticular hydrocarbon profiles) correlated with the genetic distance between individuals (Lihoreau et al., 2016a). The potential lack of genetic diversity in lab cultures maintained for long periods of time (highly inbred, no information about genetic background) may be a reason why kin recognition has been observed so rarely in insects (Fellowes, 1998; van Zweden and D'Ettorre, 2010).

3.3 Bringing experimental protocols into the field

Insect cognition research is largely based on well-defined paradigms designed to investigate specific cognitive traits (Giurfa, 2013). While this provides the advantage of allowing the identification of what animals can do, it may not, however, always reflect what animals actually do in the wild (Pritchard et al., 2016).

Firstly, important stimuli yielding information necessary for the expression of targeted behaviour may be absent in the lab. This is well illustrated by studies on visual cognition. Bees are capable of various forms of visual associative learning and memories used to locate and discriminate flowers, as well as developing routes between them (Avarguès-Weber et al., 2011). To control for the visual experience of bees, the spatial distribution of flowers and their rewarding value, bees spatial foraging strategies have been studied in the lab using artificial flowers in small flight arenas, flight rooms or greenhouses. In many bee species, foragers allowed to exploit an array of artificial flowers over several consecutive hours tend to develop repeatable flower visitation sequences (Lihoreau et al., 2010; Ohashi et al., 2007; Saleh and Chittka, 2007), a behaviour called "trapline foraging" (Thomson et al., 1997). Replicating these experiments in the field, using a harmonic radar to record the flight trajectories of individual bees at much larger ecologically relevant spatial scales, revealed that bees establish routes minimizing travel distances between all flowers and the nest based on long-term memories (Lihoreau et al., 2012b; Woodgate et al., 2017). In this case, both the increased spatial scales (e.g., longer travel distances associated to higher energetic costs) and the access to celestial cues (e.g., sun compass) have dramatically accelerated the dynamics of route formation and improved the optimization performance of bees in the field setup.

Another major advantage of adapting lab experiments to the field is to avoid potential sources of stress inherent to lab conditions. Even if insect species can be brought into the lab and the spatial scale and the information available to the insects were appropriate for understanding the behaviour of interest, the insect itself may still experience the lab task very differently than if it were presented with an analogous task in the wild. Again, research on bee visual cognition provides a good illustration of how lab-based protocols can be adapted to the field to tackle this problem. One of the most common paradigm for investigating learning and memory in honey bees is the conditioning of the proboscis extension reflex (PER), which tests for associations between an unconditional stimulus (sucrose reward) and a conditional stimulus (e.g., colour or scent) in harnessed bees (Takeda, 1961). This approach thus has the advantage of enabling the control for the timing of stimulus presentation (e.g., sequence of stimulus exposure, number of trials, inter-trial duration). However, while PER conditioning has been incredibly insightful to study olfactory cognition at the behavioural, neurobiological and molecular levels (Giurfa and Sandoz, 2012), it has always given poor or contrasted results with visual stimulations (e.g., some authors report the necessity to amputate antennae to obtain good learning, Kuwabara, 1957; Niggebrügge et al., 2009) and have never reached the usual levels observed in free-flying bees (Avarguès-Weber et al., 2011). Considering that bees predominantly use vision in flight, motion cues probably provide more natural visual context that participate to maintain a close dependence between visual and motor processing, and the immobilization of the bee in visual-PER studies undoubtedly disrupts this feedback loop (Avarguès-Weber and Mota, 2016). To address this issue, Muth et al. (2018) developed a field version of PER conditioning with freely moving insects in which animals reach high performance levels. This new protocol allows for testing visual associative learning and memory of different species of bees in a less stressful environment, while controlling for stimulus presentation as well as allowing tests in field conditions on wild populations (Muth et al., 2018).

3.4 Taking into account the social context

The difference between the lab and the natural conditions under which an animal usually learns is sometimes not just physical (Pritchard et al., 2016). While many standard cognitive tests are performed on isolated insects (Giurfa, 2013; Menzel, 2012), key model species such as *Drosophila*, honey bees, and ants live in groups (Sokolowski, 2010; Wilson, 1971). A number of social factors may thus influence what the insects can learn or how they express their behaviour.

Some behaviours are simply not expressed out of the social context. In an attempt to test the hypothesis that division of labour in social insects emerges from inherent inter-individual variation in response thresholds to environmental stimuli (i.e., the response threshold hypothesis, Beshers and Fewell, 2001), the behaviour of individual ants, *Temnothorax rugatulus*, was compared in different social contexts. When isolated, ants show highly variable responses to task-associated stimuli and these responses are not correlated to their behaviour in the colony, suggesting that testing ants outside of a social context alters the meaning or salience of the experimental stimuli and thus the observed behavioural response (Leitner et al., 2019). These social effects on insect cognition can also be developmental. In many gregarious insects, prolonged periods of social isolation can have dramatic developmental consequences and induce long-term behavioural disturbances known as "group effects" (Grassé, 1946). In the German cockroach, *B. germanica*, individuals experimentally reared in isolation during nymphal development show lower exploratory activities, foraging behaviour, and abilities to process social stimuli as adults (Lihoreau et al., 2009). This isolation syndrome can be partially rescued through social contacts artificially provided to cockroaches through mechanical stimulations (Lihoreau and Rivault, 2008; Uzsak and Schal, 2013).

Social interactions can also modulate learning and memory performances. In *D. melanogaster* social interactions facilitates the retrieval of olfactory memory (Chabaud et al., 2009). Flies trained to associate an electric shock to an odour in a T-maze develop two forms of long-lasting memories depending on inter trial intervals: long-term memory (LTM) is formed after spaced conditioning (short intervals), whereas anaesthesia-resistant memory (ARM) is formed after massed conditioning (long intervals) (Margulies et al., 2006). However, flies have higher ARM scores when tested in groups than in isolation (Chabaud et al., 2009). This social effect is independent of the social condition of training, of the experience of other flies in the group and is specific to ARM, indicating that it does not simply result from aggregation dynamics. Presumably, trained flies produce stress signals (e.g., CO_2, Yang et al., 2013) that alarms their conspecifics and enhances their attention or motivation to respond during memory retrieval. In honey bees, *A. mellifera*, social condition during breeding influences olfactory learning. Adults raised in large groups show better learning but no higher memory scores than conspecifics raised in small groups or in complete isolation (Tsvetkov et al., 2019). These differences are correlated with changes in dopamine levels in the brain suggesting that social interactions modulate learning through the biogenic amines.

Being in a group can also dramatically improve the speed and accuracy of decision-making through collective acquisition and processing of information, a phenomena known as "swarm intelligence" (Couzin, 2009; Feinerman and Korman, 2017; Seeley, 2010). In house hunting ants, *T. rugatulus*, collective decisions for the selection of a new nest site emerge from a competition between recruitment efforts by different individuals in the form of tandem running (i.e., an experienced ant drags a naïve ant towards a site) at different sites (Franks et al., 2002). When given a choice between potential nest sites varying in quality (e.g., light intensity), ant colonies can effectively compare a larger option set than individuals (Sasaki and Pratt, 2012) and are less vulnerable to irrational preference shifts induced by decoys (Sasaki and Pratt, 2011). However, this social advantage varies with the difficulty of the task (Sasaki et al., 2013). For a difficult choice (i.e., small differences of light intensity between nests), solitary ants have a relatively high probability of accepting the worst nest, because they rely on quality dependent acceptance probabilities that differ little for similar nests. Colonies do much better because the colony's choice emerges from a competition between recruitment efforts accentuated by a positive feedback loop and a quorum rule (Sasaki et al., 2013). For an easy choice (i.e., large differences in light intensity between nests), acceptance probabilities diverge rapidly with comparison, allowing solitary ants to make the right choice with high probability. Thus in this, case social information only adds little benefit to colonies.

3.5 Comparing species

Rigorous comparisons of the cognitive performances of individuals of the same species or different species that are either closely or distantly related can greatly enhance our understanding of how cognition is shaped by natural selection (Godfrey and Gronenberg, 2019).

Studies of closely related species with known ecologies is a powerful means to tease apart selective forces that drive the evolution of specific cognitive traits. In paper wasps such comparison demonstrates the importance of sociality in the evolution of visual cognition (Sheehan and Tibbetts, 2011). Queens of *Polistes fuscatus* cooperate to found, defend and provision their colony. These wasps live in strict hierarchical societies in which individuals recognise every other colony members based on long-term memories of facial masks (Sheehan and Tibbetts, 2008). By contrast, queens of *P. metricus* found colonies alone and do not require face recognition. When presented images of normal wasp faces, manipulated wasp faces, simple geometric patterns or caterpillars (i.e., the typical prey of these wasps) in an aversive conditioning paradigm in a Y-maze, *P. fuscatus* wasps learn to recognize correctly configured wasp faces more quickly and more accurately than they did with other images, indicating that learning is specific to faces in this species (Sheehan and Tibbetts, 2011). *P. metricus* wasps, however, perform better in pattern and caterpillar discrimination. In terms of gross neuroanatomy, there are no discernible differences between the visual system of *P. fuscatus* and closely related species that do not show face recognition (Gronenberg et al., 2008). It is therefore likely that the neural circuitry used by insects for prey recognition has been co-opted for face recognition, provided minor adjustments. In parasitoid wasps that lay eggs in animal hosts, differences in the spatial distribution of preys seems to determine major differences in olfactory memory dynamics (Smid et al., 2007). *Cotesia glomerata* and *C. rubecula* wasps coexist in the same environments and lay their eggs in caterpillars. These parasitoids are known to learn to associate plant odours with the presence of caterpillars during an oviposition experience on a plant (Lewis and Takasu, 1990). When wasps of both species are trained to oviposit on caterpillars on a neutral host plant and then given a choice between the neutral host plant and their preferred host plant (cabbage), *C. glomerata* show memory formation and consolidation after fewer trials than *C. rubecula* (Smid et al., 2007). This difference in memory dynamics reflects the difference in foraging ecology of the two species: *C. glomerata* exploits gregarious hosts and may benefit to learn from one massed experience on a single encounter with a plant, whereas *C. rubecula* exploit solitary hosts and may use more experiences and more time to evaluate information from many different plants before long-term memory is formed.

Comparing distantly related species can help identify cognitive traits that are conserved or are convergent across insect lineages. For example, in recent years, the finding that many insect taxa are capable of social learning, suggests that this cognitive ability once thought to be unique to vertebrates has evolved several times in insects. Forms of social learning have been demonstrated in insects exhibiting various levels of social organisation, including social bees that can learn new flower preferences (Worden and Papaj, 2005) or foraging techniques (Alem et al., 2016; Loukola et al., 2017), gregarious fruit flies that can learn preferences for oviposition sites (Battesti et al., 2015) or mating partners (Danchin et al., 2018), or even solitary field crickets that learn about the presence of danger (Coolen et al., 2005). This comparative research indicates that insect social learning is not a specific adaptation to social life but may rather involve fundamental associative learning processes used in an asocial context by many species (Leadbeater and Dawson, 2017).

4. Future directions

Perhaps with the exception of navigation research (Collett et al., 2013), ecologically-inspired studies of insect cognition are still relatively scarce, presumably because of the technical difficulties to run controlled experiments with many insect species in their natural environment (e.g., fast moving animals, large spatial scales, large numbers of individuals, etc.). However, several technological advances to quantify cognitive performances on freely moving insects in the field, or in field-realistic virtual environments in the lab, hold considerable promises for the development of an integrative insect cognitive research combining field and lab approaches.

4.1 Automated quantification of cognitive performances

A major limitation of current insect cognition research is that many experiments involve long learning protocols (e.g., training sessions over several days, Perry et al., 2016) with relatively low levels of success (e.g., low learning scores, Avarguès-Weber and Mota, 2016), often resulting in small sample sizes that do not enable for analyses of variability in cognitive traits. Developing a truly comparative analysis of cognitive performances within individuals through time, as well as between individuals, population and species, requires the development of non-invasive automated systems to record behavioural data on large numbers of insects over long periods of times.

This can be achieved by automatizing cognitive protocols. Although many standard protocols have been improved for automatically controlling the presentation of conditioned and unconditioned stimuli to animals (e.g., appetitive olfactory conditioning in bees Giurfa and Sandoz, 2012; aversive visual conditioning in bees, Kirkerud et al., 2013; and aversive olfactory conditioning in *Drosophila*, Jiang et al., 2016), the full automation of experimental setups for conducting cognitive tests is still rare. A recent successful example includes the development of arrays of automated feeders fitted with tracking systems to test flower choices, spatial learning and social interactions in freely flying bees in the lab (Ohashi et al., 2010) and in the field (Lihoreau et al., 2016b). In this approach, a large number of insects can self-train for several consecutive days without the intervention of an experimenter (Pasquaretta et al., 2019).

Advances in automated movement tracking systems now also enable to quantify the behaviour of individual insects, while walking or flying, at various spatial and temporal scales, in the lab and in the field. These include computer vision (e.g., Pérez-Escudero et al., 2014), radio frequency identification (e.g., Stroeymeyt et al., 2018), telemetry (e.g., Kissling et al., 2014), and radar tracking (e.g., Riley et al., 1996). Recent studies have begun to complement these behavioural measures with continuous recording of fitness data, population dynamics and environmental conditions (e.g., Crall et al., 2018). In bee research, for instance, connected hive systems (i.e., bee hives equipped with sets of sensors) can be used for the continuous monitoring of colony traits (e.g., temperature, humidity, weight, sound, traffic of foragers, social interactions, nectar and pollen collection) and environmental conditions (e.g., weather, air pollution) (Bromenshenk et al., 2015). This technological advance has opened the door for a real-time assessment of the link between insect cognitive performance, in-nest behaviour, colony health status, environmental quality and stress exposure (Meikle and Holst, 2015).

High-throughput monitoring of insect behaviour can only be insightful if combined with modern statistical methods to automatically analyse behavioural data. Machine learning and statistical physics are increasingly used to run unsupervised behavioural classification enabling to handle large behavioural datasets, discover features that humans cannot, and develop standard metrics for comparing data across species and labs with only few prior assumptions (Brown and de Bivort, 2018; Egnor and Branson, 2016).

4.2 Virtual reality on freely moving insects

The development of ecologically inspired lab-based experiments in which animals can express naturalistic behaviours under tightly controlled conditions is complementary to field research. While many classical protocols for testing learning and memory in the lab requires to immobilize insects (e.g., Giurfa and Sandoz, 2012), recent progresses in virtual reality techniques now provide unprecedented opportunities to test freely behaving animals in complex ecologically relevant virtual environments, in which cues can be manipulated independently, in ways that would be impossible to achieve in traditional experiments (Stowers et al., 2017). These new systems, in which the natural sensorimotor experience of animals is conserved, facilitate detailed investigations into neural function and behaviour. Virtual reality for freely moving animals has recently been used to elicit naturalistic object responses (e.g., make objects appear, disappear, or even be at apparent distances) in freely walking and flying insects. For instance, flying bumblebees, *Bombus terrestris*, can be trained to search for virtual feeding platform or avoid virtual obstacles displayed on a screen on the ground of a flight arena just as they would with real objects (Frasnelli et al., 2018).

Future developments of technologies to measure neural activities in freely moving insects will considerably advance investigations of brain function underpinning these naturalistic behaviours (Marescotti et al., 2018). Combining these technologies to virtual reality will allow researchers to study the mechanistic basis of behaviour under conditions in which the brain evolved to operate, thereby facilitating the dialogue between field and lab cognitive experiments in ecologically relevant conditions.

5. Concluding remarks

In the 1980s and the 1990s, the intersection of behavioural ecology and experimental psychology led to the new field of cognitive ecology (Dukas, 1998; Dukas and Ratcliffe, 2009) as researchers began to base their hypotheses on the natural history of different species to test predictions about the cognitive abilities of these animals. This approach has been taken with success by scientists working on large-brained animals (Morand-Ferron et al., 2015), but is still little embraced by entomologists. We argue that there is a need for developing an ecologically inspired research on insect cognition to develop a comprehensive understanding of both its mechanisms and evolution.

Beyond behavioural ecologists, such approach will benefit to the broad community of researchers interested in insect cognition. Considering the ecological context of cognition will likely help ethologists to make sense of the rich cognitive repertoire of insects observed in the lab (e.g., What does it mean for an insect colony to have optimistic and pessimistic foragers? Why should insects count?) and perhaps refine mechanistic explanations by asking alternative hypotheses inspired from field observations. Ecological considerations of cognition may also help neurobiologists and experimental psychologists interested in the evolution of cognition to understand the role of environmental factors in shaping animal behaviour and cognitive abilities. As the cognitive abilities of more species are studied in the environment in which such processes evolved, a truly comparative study of cognition becomes at reach. Importantly, the ecologically-inspired approach is complementary with land-based mechanistic explorations. Some of these explorations can also be performed in the field, for instance using selective drugs (Sovik et al., 2016) or inhibitor of gene expression (Cheng et al., 2015) to identify physiological pathways underpinning cognitive operations in conditions where animals may be in better position to fully express their cognitive repertoire.

Ultimately the dialogue between ecologically-based and lab-based approaches will help develop a more integrative understanding of insect cognition with the potential to illuminate broader scale ecological phenomena. For instance, detailed studies of the sublethal effects of pesticides on bee learning and memory (Stanley et al., 2015) combined with field monitoring of population dynamics (e.g., Henry et al., 2012) have provided a robust explanation for colony collapse and the broader declines of pollinator populations (Klein et al., 2017). Growing evidence show that cognitive processes observed in individual organisms result from complex interactions between components at different levels of organisation (gut microbiota, group, parasites and pathogens, environmental stressors) (Couzin, 2009; Cryan and Dinan, 2012). Considering these ecological interactions and their consequences throughout levels of organisations is a major challenge for insect cognition research in the decades to come.

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