

Review

Social cognition in insects

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Insects feature some of the most complex societies in the animal kingdom, but a historic perception persists that such complexity emerges from interactions between individuals whose behaviours are largely guided by innate routines. Challenging this perception, recent work shows that insects feature many aspects of social intelligence found in vertebrate societies, such as individual recognition, learning object manipulation by observation, and elements of cultural traditions. Insects also display emotion-like states, which may be linked to social behaviours such as rescuing others from danger. We review recent developments in insect social cognition and speculate that some forms of now-hardwired behaviour (e.g., nest construction) could have initially been the result of individual innovation and subsequent cultural spread, with evolution later cementing these behaviours into innate behaviour routines.

Where do you find a more richly gifted animal? ... Can the bird, this wonderful architect, compare his works to the construction of the honeybee, this masterpiece of higher geometry? Even man has a rival in the Hymenopteran. We build cities, so does he; we keep servants, so does he; we breed domestic animals ... he has his milk cows, the aphids. ... To consider the animal means to ask the disquieting question: Who are we? Where do we come from? Thus: what goes on in this tiny Hymenopteran brain? Are there abilities related to ours, is there a form of thinking? Jean-Henri Fabre 1882 [1].

Social insect societies: robotic individuals, intelligent swarms?

In social insects such as bees, wasps, and ants, we find some of the most advanced animal nesting architectures, sophisticated **division of labour** (see [Glossary](#)), forms of ‘agriculture’ as in aphid and fungus farming of ants, complex communication systems (including a form of ‘language’ using symbols, e.g., the honeybee dance), and consensus decision making where many individuals’ knowledge is integrated on a societal level. **Ethograms** have revealed that the behavioural repertoires of such insects are comparable with, or even supersede, those of many mammals [2]. Darwin named the beaver as the single non-human vertebrate whose collaborative construction abilities might rival those of social insects. He observed that a common perception was that across animals, instincts and intelligence are inversely related, but countered that in both beavers and social insects, complex instincts and intelligence actually come together. While today no-one contests that insects learn about foraging options while outside the nest, a persistent notion is that insects’ social interactions, architectures, and unique behavioural specialisations are governed by principles wholly different from mammalian societies (including humans): that **social cognition** plays no role in insects and that **complexity** arises only as the by-product of simple innate routines governing the behaviour of each individual.

While this might apply in some aspects of social insect behaviour, we also know that insects can learn, and learn from each other, about foraging options [3], predation threat [4,5], mate choice [6–8], oviposition sites [9], and nesting opportunities [10–12]. Such learning occurs not just in

Highlights

Some social wasps recognise each other’s faces and memorise information about the status of other individuals; such information can be acquired through observing interactions between familiar individuals and might involve transitive inference.

Bumblebees can learn simple ‘tool use’ techniques by observing skilled conspecifics and such techniques can spread through entire colonies in a process akin to cultural diffusion of novel innovations.

Female fruit flies copy mate preferences from other females and such preferences might be maintained over generations via conformity bias.

Given these forms of advanced social cognition in insects, we suggest investigating whether the elaborate architectures of social insect colonies might in part be the result of cultural evolution processes, even possibly in the distant past.

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insect societies, but also solitary species (e.g., [10]), and thus likely predated the advent of sociability. Indeed, the flexibility of social learning is such that insects can learn from members of other species [3,10] and robots [13,14]. Like vertebrates, insects prioritise socially obtained versus individually acquired information flexibly, depending on context [15–20].

We focus on recent developments in the field of social **cognition** of insects. We review how insects can innovate novel behaviours that potentially spread through populations by social learning. Some social wasps recognise each other's faces and individual recognition forms the basis for many complex social interactions in their societies. There might even be forms of cultural traditions in insects, for example, where mate choice preferences are acquired by observation and might be retained by a **conformity bias** for generations. We explore whether there might be unique emotional states linked to social activities of insects, such as **swarming** in honeybees or the rescuing behaviour observed in some species of ants, which may involve empathy-like states. Emotions have even been implicated as facilitating social insects' nesting constructions [21]. We build on the empirical insights reported here to speculate whether some of the highest architectural accomplishments and behavioural innovations of social insects might, at some point in their history, have emerged not just by evolutionary trial-and-error processes, but also by culture-like processes, by which new accomplishments spread rapidly within and possibly across colonies and new innovations might build on previous ones.

What do insects know about individual conspecifics?

The exploration of individual psychological differences in insects already has a century-long history (scholars interested in vertebrate 'personality' often tout this as a new perspective). African-American psychologist Charles Turner (1867–1923) identified individual variation in the speed with which displaced homing ants returned to their nests, which he thought resulted from differences in associative memory [22]. Individual variation has since been found in every study on psychological traits in social insects where such variation was not eliminated by 'averaging', for example, **neophilia/neophobia** [23,24], tendency to innovate [25,26], resource exploration and exploitation [27,28], tool use [29], visual learning tasks [30], and colour learning speed and accuracy [31–33], where a structural neural correlate was found in the density of synaptic complexes in associative regions of the brains' **mushroom bodies** [34]. But do members of insect societies also store information about other individuals' characteristics and behaviour?

One of the hallmarks of primate and other mammalian societies is individual recognition. Members attach to an individual's appearance detailed information about social status, affective relationships, fighting ability, territory boundaries, and cooperation [35]. Insect societies were until recently not thought to exhibit individual recognition, but to make only simple **ingroup/outgroup** distinctions [36], where, for example, the guards at a nest entrance can tell rightful entrants from intruders [37–42].

The view that insect societies are entirely anonymous was challenged by Elizabeth Tibbetts' discovery that some species of paper wasps can visually identify their **nestmates** based on their facial and abdominal markings [43] (Figure 1A). In these species of *Polistes* wasps, colonies are founded by several queens who fight to establish a dominance rank order; such confrontations can result in serious injury and occasionally death [44]. The winner becomes the alpha female who monopolises reproduction [45]. The ability to recognise individuals therefore allows avoiding further costly confrontations. Wasps can learn about the strength of individuals by observation alone [46]. When bystanders watched **conspecifics** fight through a transparent partition, they were less aggressive towards combatants who were seen to initiate more and receive less aggression (Figure 1B). Paper wasps therefore do not need to interact directly with fighters to

Glossary

Cognition: the processes of knowing and thinking; allows generating new information in a combinatorial manner from information acquired in separate events in the past, or spontaneously through insight. As such, it is distinct from simple information processing and associative learning processes.

Complexity: in behaviour, can be quantified by the diversity of distinct behaviour routines (see ethograms); in cognition, complexity can be assessed by the number of sequential or parallel steps of neural computation.

Conformity bias: frequency-dependent social learning, where the probability of acquiring a trait increases disproportionately with the proportion of other individuals who exhibit it.

Conspecifics: individuals belonging to the same species.

Division of labour: a characteristic feature of eusocial insects where different workers specialise in subsets of the tasks performed by a colony.

Emotion-like states: in animals, transient subjective states, underpinned by physiological, behavioural, and cognitive phenomena, triggered by appraisal of environmental situations, similar to emotions in humans.

Ethogram: catalogue of natural behaviours exhibited by an animal.

Genotype: the complete set of genetic material of an organism.

Ingroup: social group in which an individual identifies as being a member.

Mushroom bodies: pair of dorsal structures in the insect brain known to play a role in learning and memory.

Neophilia: the spontaneous attraction of an animal to a food item, object, or place because it is new.

Neophobia: the aversion that an animal shows to a food item, object, or place simply because it is new.

Nestmate: colony member.

Neuropil: area in the nervous system that forms a synaptically dense region.

Outgroup: social group with which an individual does not identify.

Personality: animal personality refers to consistent behavioural or psychological differences between individuals of the same species.

Phenotype: the complete set of observable traits of an organism.

Phototaxis: innate locomotory movement towards or away from light stimulus.

assess their rank. Such **social eavesdropping** allows them to acquire information about **third-party relationships**, an ability that had hitherto only been demonstrated in vertebrates [47]. Tibbetts' team also discovered that *Polistes* wasps appear to use transitive inference: the ability to infer unknown relationships between items based on known relationships (e.g., if one observes that individual A is stronger than B and B stronger than C, then it follows that A is also stronger than C) (Figure 1C) ([48], though see [49] for possible alternative explanations). Thus, transitive inference may be a mechanism used during social eavesdropping to infer the dominance status of other wasps in the colony.

Individual recognition is at least partially acquired during development: wasps that are socially isolated early in adult life do not develop face recognition skills [50]. In terms of gross neuroanatomy, there are few appreciable differences between the visual systems of face-recognising wasps and those of related species that do not use face recognition [51], but a small **neuropil** in the insect brain, the anterior optic tubercle, shows differential growth in socially exposed but not socially deprived individuals [52] (Box 1). Understanding how the neuron-to-neuron connectivities in and around this brain area might mediate face recognition should be rewarding. The work on these remarkable species of wasps shows that at least in principle, individual recognition can shape the societies of even small-brained animals. Such recognition may not be limited to just a few select wasp species, nor might it have to rely on vision only: in an example from ants (*Pachycondyla villosa*), chemosensory signals are used to identify other individual queens [53]. In other insect societies the 'missing ingredients' for individual recognition might simply be that appreciable individual differences in appearance (visual or otherwise) might be insufficiently pronounced for conspecifics' sensory systems to resolve them. Interestingly, when individual differences are highlighted with visible colour marks applied by experimenters, fruit flies and bumblebees (neither of which are known to recognise one another individually in nature) can learn to identify the bearers of reliable social information by visual cues [54]. Thus, the cognitive capacities to recognise other individuals and store valuable information about them (including which individuals make for particularly valuable role models) certainly exist in the insects.

In social animals such as many bees and wasps, a question is how psychological diversity of individuals benefits the colony as a whole [55]. Recent results show that overall colony behaviour does not emerge directly from the **genotypes** that govern behaviour [20,28,56,57]; instead, we can only understand the synergies of different cognitive **phenotypes** if we understand how genotypes influence the perception and psychology of workers and how workers with different psychologies communicate and influence each other. The historic notion that complex colony function emerges only from simple, hardwired behaviour routines, which govern local interactions between anonymous individuals, is no longer tenable.

Insect emotions in a social context?

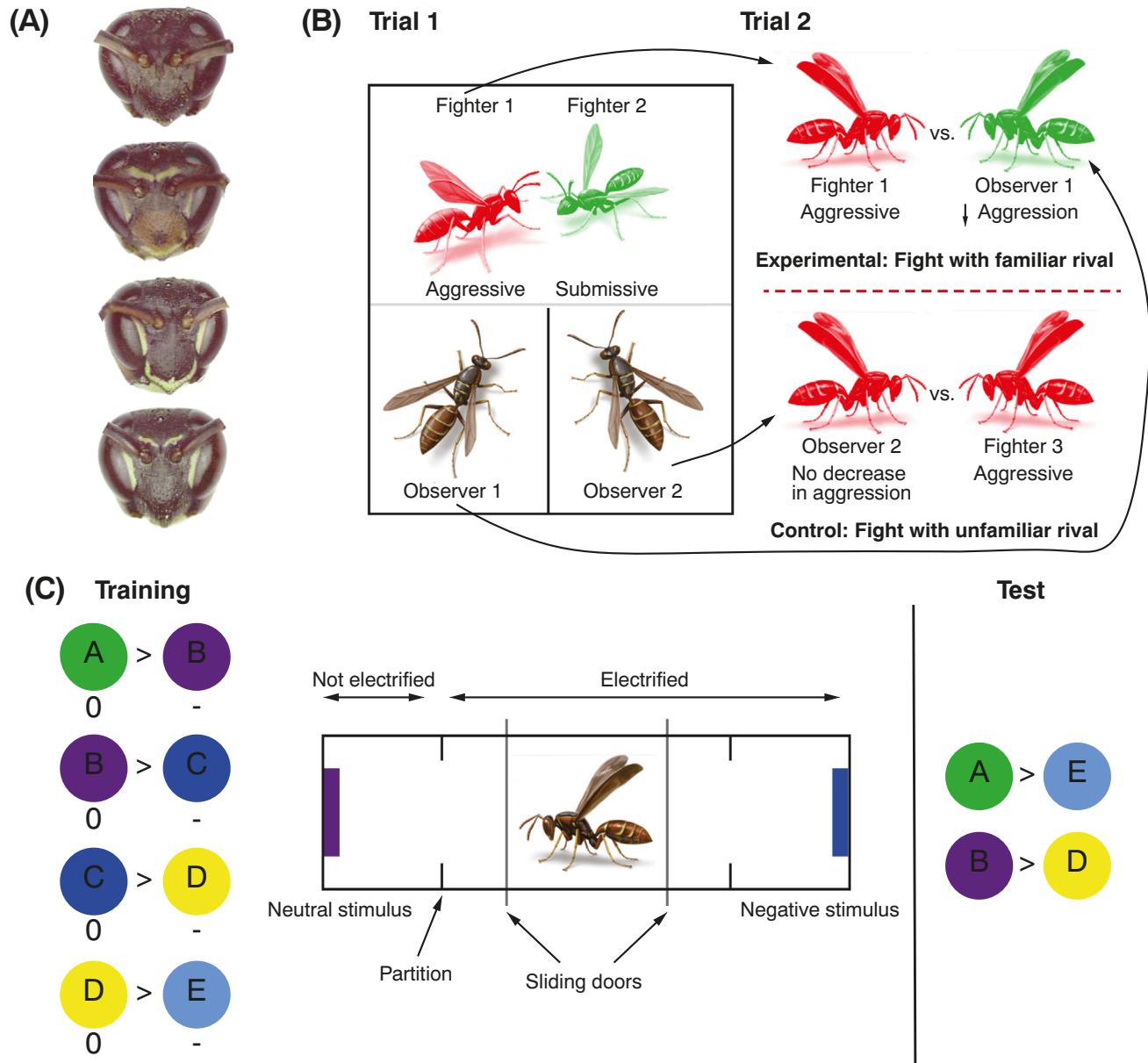
In 1764, the eminent Swiss naturalist Charles Bonnet suggested that bees' consciousness and feeling drove their proclivity to 'prepare useful things', resulting in the 'symmetry, strength and convenience' of the honeybee comb constructions [21]. Such views have been ridiculed by more recent generations of scholars entrained in searching for parsimonious interpretations of behaviour and, indeed, there was no evidence for sentience in insects at the time. However, recent work indicates that insects display positive and negative **emotion-like states**, at least when the same criteria are applied as are used for diagnosing emotions in vertebrates [58–63]. This makes it plausible that social insects attach positive affective states to being around nestmates, these nestmates' wellbeing, and building functional structures and negative affective states to, for example, damage to their colony, hunger in their brood, and attacks by predators. Having a range of basic emotions might be part of most animals' 'survival tool kit': natural

Social cognition: (see also cognition) knowledge of, or acquiring information from, other individuals in an animal's environment; distinct from 'swarm intelligence', which describes emergent phenomena that arise as a by-product of hard-wired interactions between individuals.

Social eavesdropping: the extraction of information by a bystander about the quality of the observed signalers using information contained in the signal exchange.

Swarming: in insects, group migration from an old nest for a new one.

Third-party relationship: the interaction and relationship between conspecific group members in which the observer is not directly involved.



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Figure 1. Cognition and individual recognition in *Polistes* paper wasps. (A) Portraits of four *Polistes fuscatus*. From [43]. (B) Social eavesdropping to assess potential rivals. In Trial 1, bystander wasps observed a pair of unfamiliar conspecifics fighting. In Trial 2, bystander wasps were paired with a fighter they had previously observed (experimental) or an unfamiliar fighter (control). When bystanders interacted in Trial 2 with the same individual as observed in Trial 1 (experimental), they were less aggressive towards the fighter they had previously observed as being aggressive (aggressive fighter). In contrast, when bystanders interacted in Trial 2 with an individual different from the one observed in Trial 1 (control), there was no modulation of aggression. Bystanders who observe a conspecific fight therefore use this information to modulate their subsequent behaviour. Modified from [46]. (C) Testing for transitive inference. First, wasps were trained to discriminate four pairs of colours (A_0B , B_0C , C_0D , and D_0E ; 0 no shock, – electric shock): one colour was associated with the electrified part of the arena (negative stimulus), while the other colour was associated with a safe zone (neutral stimulus). Wasps chose the correct colour (neutral stimulus) more. Then, individuals were tested on novel pairs without training (A versus E , B versus D). Consistent with transitive inference, wasps chose A over E and B over D . This implies that wasps organised the trained stimuli into the implicit hierarchy $A > B > C > D > E$. Modified from [48].

Box 1. Insects and the social brain

The social brain hypothesis holds that group living requires exceptional cognitive abilities and, therefore, larger brains (or enlargements of brain regions that mediate social intelligence). In primates, some scholars have reported correlations between group size and brain size or relative neocortex volume ([97], but see [98,99]). Insects offer an ideal model to test the social brain hypothesis; their societies range from species with a handful of individuals to many millions and include a wide variety of types of social complexities and varied behavioural and cognitive repertoires [100,101].

Sayol *et al.* [100] found no correlation between sociality and relative brain size in a range of bee species. Overall brain size is simply not an informative measure for any form of computational complexity [102,103]. Since neurons are computational units of the brain, one might hypothesize that their number should allow at least some prediction of computational complexity [104]. Godfrey *et al.* [101] analysed body and brain mass, nuclei number, and cell density in the brains of a range of Hymenoptera. However, an inspection of their data reveals no difference between solitary and social species, nor a correlation between any of these parameters and social group size. It may be that without any information on how neurons are wired into functional circuits, how many and what types of connections there are, or how many sequential processing stages, neuron numbers in themselves are as uninformative as overall brain size in predicting cognition.

A better approach is to identify specific brain areas, the dimensions and function of which are associated with certain social capacities, and then examine the neural circuits within and around them. Jernigan *et al.* [52] found that an area in the central brain of a face-recognition wasp species, the anterior optic tubercle, grows differentially in size only in individuals with early social exposure, but not socially isolated wasps (Figure 1). The anterior optic tubercle visual processing centre lies on the pathway that connects two of the insects' visual ganglia, the medulla and lobula, to the central brain. In other insects, this relay station processes both polarised light as well as topographic and nontopographic inputs [105]. An interesting future project will be to analyse the neuronal network connectivities in this and adjacent brain areas in wasp species that recognise conspecific faces versus those that do not, and within face-recognising species, to identify how individual social experience leads to changes in these circuits.

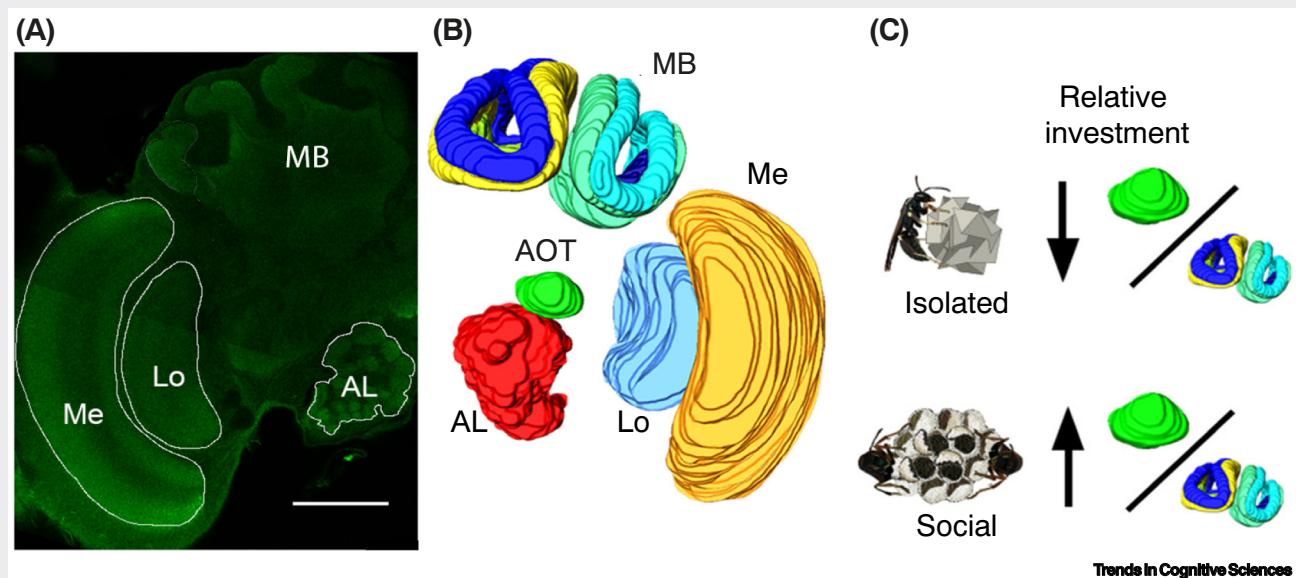


Figure 1. The anterior optic tubercle (AOT) in isolated and social wasps of a face-recognising species. Frontal view of the brain of *Polistes fuscatus*, with one hemisphere shown as immunofluorescent image (A) and the other as a reconstruction allowing volumetric measurements (B). (C) The AOT shows relative enlargement (compared with the MBs) when individuals are embedded in a social setting during development, but not in isolated wasps (figure modified from [52]). Scale bar 250 µm. Abbreviations: AL, antennal lobes (principal olfactory relays); Lo, lobula (visual ganglion); MB, mushroom bodies (association centres); Me, medulla (visual ganglion).

selection might not look kindly upon individuals that do not know fear, parents who are indifferent to the loss of their offspring, or social animals for whom it does not 'feel rewarding' to be in their social setting. The question of whether insects have emotion-like states linked to the social context is little explored.

An interesting test case is whether social insects experience empathy when encountering injured nestmates whom they subsequently rescue. Empathy is an affective state involving the ability to feel, recognise, and/or understand the emotional states of others, for example, one currently experiencing distress [64]. The phenomenon has been especially well-studied in rats, where

multiple studies have shown that animals will try to alleviate the situation of conspecifics in various forms of peril [65]. Rescue behaviour is also found in social insects, where it has been particularly well researched in ants. English politician and entomologist John Lubbock (1834–1913) found that such helping behaviour is differentially dedicated to nestmates: he experimented with inebriated ants and found that nestmates would be carried home where they could sleep off their intoxication, whereas unrelated conspecifics would be unceremoniously dumped in a puddle [66]. However, the question of whether the behaviour is directed to relatives or others is irrelevant to whether helping is accompanied by positive emotions that function to make the act of helping a rewarding experience in itself, thus promoting its frequency and ultimate benefits to colony fitness.

More recent work shows that ants will rescue nestmates from collapsed tunnels or predators, or when ants raid other insect colonies such as termite nests [67–71]. Rescued individuals have a higher chance of survival and ultimately benefit the colony [68,70]. In one study [72], ants were trapped by a tether around their waist and their abdomen covered with fine-grained sand as well as pebbles. The behaviour displayed by rescuing ants is superficially similar to rodents (Figure 2): both exhibit frenzied behaviour, pull on the extremities of a trapped individual, and attempt to bite the restraining structure [73]. Yet, interpretations of the insect work were strictly mechanistic and did not invoke empathy. This inconsistency has been recognised and further tests to diagnose empathy should be useful in both ants and rodents [73]. It is, however, important to point out that, even in humans, the most advanced and flexible forms of empathy are built on more basic forms and remain connected to core subcortical and neurohormonal mechanisms associated with affective, parental, and social attachment processes [74].

A regrettable trend in the exploration of emotion in animals is that most studies use human emotions as a benchmark and then search for analogues in animals. This neglects the possibility that, just as sensory systems differ profoundly between animals depending on their environmental needs, animal emotions might also include affective states wholly different from those known to humans (however difficult these might be to diagnose). For example, German biologist Hugo von Butteli-Reepen (1866–1933) pointed out over a century ago the possibility of a form of ‘swarm intoxication’, a specific emotional state associated with the swarming process found in honeybees when a large number of bees and the old queen leave the hive in search for a new home [75]. He observed that this state appeared to involve reduced aggression, increased positive **phototaxis**, retrograde amnesia for the location of the previous nest, and possibly a form of enjoyment as inherent in play behaviour. Classifying such states in a manner that is not simply anchored in the human emotional world, and exploring their neural and hormonal correlates, is important in the study of the inner world of insects. For example, exploring whether reward pathways in the brain are activated when social insect workers provision their young, groom the queen, or engage in other social interactions, will be valuable [76]. The questions of whether emotions strengthen the cohesive forces in insect colonies, contribute to their organisation of labour, and orchestrate learning from each other, thus potentially contributing to cultural processes (see later), merit further investigation.

Culture and tradition in insects?

Many forms of social learning reported so far focus on tasks encountered daily in these animals' lives, for example, to identify the most rewarding floral resources, or the most suitable mates [3–20]. One of the hallmarks of human cultural traditions, however, is that they involve phenomena that are demonstrably remote from those for which our species might have innate predispositions. Might it be possible to monitor the spread of non-natural behaviours in insects, problem-solving strategies that are not typically displayed in nature?

In one study, the diffusion of such a skill, never encountered by any bee in its entire evolutionary history, through an entire forager population was tested [25]. Bumblebees learned to solve a string-pulling puzzle, where an artificial flower was displayed under a transparent plate (Figure 3A). The only way to reach the reward in the flower was to pull on a string attached to the flower and protruding from under the plate. More than 100 individuals were tested, but only two ‘innovated’ and pulled the flower from under the table spontaneously. Most naive bees, however, learnt the task by observing a trained demonstrator (either directly interacting with the demonstrator, or by watching from a distance through a glass screen). This led to a veritable cultural diffusion: the phenomenon observed in humans when a new innovation spread rapidly to a large fraction of a population. When a colony was ‘seeded’ with a single knowledgeable individual, the skill spread swiftly to the majority of foragers of the colony. There were several sequential sets ('generations') of learners, so that previously naive observers first acquired the technique by interacting with skilled individuals and, subsequently, themselves became demonstrators for the next 'generation' of learners, so that the longevity of the skill in the population could outlast the lives of the earliest competent string-pullers (Figure 3B). Impressive though they may seem, these results were explicable by a combination of attraction to conspecifics, associative learning (learning that conspecifics signify reward), and trial-and-error learning (to figure out the actual string-pulling technique); this combination might indeed suffice for the cultural spread of foraging techniques.

However, a more recent experiment indicated that there might be a form of outcome awareness in bumblebees learning object manipulation techniques by observing skilful demonstrators. Such outcome awareness was first suggested for ants by Charles Turner [77] and has more recently been discussed in the context of intentionality in insects [78,79]. Such intentionality might be important in the cultural spread of new object manipulation techniques. In one set of experiments, bees learned to move a ball to the centre of a circular platform to gain access to a reward, in a task equivalent to token or tool use [80] (Figure 3C). To see if observers understood the desired outcome of the task, a simple trick was played on the trained demonstrators. Three balls were placed into the arena at different distances from the target location and the best solution to solve the task would have been to move the closest ball to the centre. However, the two closest balls had been glued to the floor and so the demonstrators learned that they could only ever move the furthest ball. Naive observers were each given three opportunities to watch the demonstrator move the furthest available ball to the goal. Note that the observer had no own experience with ball-rolling herself, she merely witnessed the procedure thrice. When subsequently tested alone, observers spontaneously used the ball closest to the centre. Thus, rather than simply ‘aping’ the demonstrators in moving balls over long distances, observers solved the task more efficiently, using the ball positioned closest to the target, even if it was of a different colour than the one previously observed by the naïve bee. They typically did so on the first trial, leaving no room for trial-and-error learning. This spontaneous improvement on the strategy displayed by the demonstrator indicated that bees had a form of understanding of the desired outcome of the task and tailored their actions accordingly. Irrespective of the mechanisms, this work shows that the technique of object manipulation can be spontaneously improved by social learners without further trial-and-error processes, potentially leading to rapid cultural improvements of problem solving over short time periods.

Such cultural processes may not be limited to insects living in close-knit societies. In a study on fruit flies, it was discovered that mating preferences can be learnt by observation and may be maintained within populations for several generations [8,81]. The researchers coloured the males in non-natural dyes and found that females that watched a green or pink male mate with another female through glass would subsequently prefer males of the same colour. These results are far from trivial, as they suggest that the observing female identifies what she sees on the other side of the glass as a mating couple of her own species (not, e.g., a predator eating a fly, or a

strange 12-legged arthropod). On some level, she also appears to comprehend that the successful individual is a male whose features are worth memorising, even though the colourful individual looks different from any naturally occurring fruit fly. When a female observed that males of one colour or another were in the majority, no matter how slight that majority, a 'conformist bias' was observed, a significant preference for males of the majority colour. Female flies, like many adolescent humans, seem to acquire their partner preferences from the majority choices that can be observed around them. This suggests that fruit flies engage in extensive sampling before forming their own mate preference; conformity can only emerge when individuals have sampled a substantial fraction of the preferences expressed by others around them. Such a conformist bias in learning has previously been found in chimpanzees [82] and also some species of birds [83,84] and fishes [85].

We have learnt in this section that some of the key ingredients of culture and tradition are found in insects. This includes the ability to learn by observation how to manipulate objects and how to choose mates. We have seen that innovations and acquired skills can propagate rapidly through populations and could potentially be maintained over multiple generations by conformist bias. Why then are such cultural processes not observed in the wild in insects, even though the required cognitive ingredients exist and can enable culture-like processes laboratory settings? One possibility is that the required long-term field observations over multiple colonies or populations simply have not been performed yet. Another possibility is that in seasonal insects living in temperate habitats (such as bumblebees), populations collapse in the winter and any acquired knowledge dies with the workers that have accumulated it. For example, some species of bumblebees practice 'nectar robbing', biting holes into the spurs of long-tubed flowers to extract nectar more easily, but without necessarily touching the reproductive parts of flowers. This technique spreads by social learning [86,87], but this spread must occur *de novo* every year. We suggest that culture-like phenomena, even possibly cumulative culture, could be rewardingly explored in the tropical stingless bees, whose colonies persist for years, often decades, and which feature some of the most remarkable nest architectures and behavioural innovations anywhere in the animal kingdom [88,89] (see Box 2). There is extensive

Box 2. Culture in stingless bees?

We speculate that if culture-like processes in the wild exist anywhere in insects, they are most likely found in the stingless bees. The colonies of this monophyletic group of 500+ social species (all of which lack a stinger) can exist for decades and swarms establishing new nests can take acquired knowledge with them. In these bees, we find some of the most impressive nesting architectures anywhere in the animal kingdom and the highest diversity of such architectures.

For example, some species of the genus *Partamona* build highly visible, funnel-shaped nest entrances, constructed from white river sand glued together with resin [88]. Homecoming bees fly into these entrances at full speed, collide with the concave interior, and slide into the nest. As a colony defence against, for example, insect invaders, some species build 'fake nests' containing diluted (valueless) honey and empty brood pots (Figure 1). Some build vertical honeycombs (one-sided and two-sided versions exist), some parallel horizontal ones, and others build spiral-shaped constructions. Feeding specialisations can likewise be extraordinary: while most species visit flowers, some are obligatory kleptoparasites (stealing food from colonies of other species) and others specialise in eating carrion [89,106].

It is typically assumed that these behavioural adaptations are innate, that they have come about by evolutionary trial-and-error processes, not individual innovation and subsequent cultural spread. Curiously, however, the stingless bees' behavioural diversity does not easily map onto a phylogenetic tree (e.g., closely related species often have distinct architectures and nesting habits). More intriguingly, there is variation within species: some can facultatively build spiral-shaped or parallel horizontal combs, colonies of some species build a protective sheath around the brood (involuticum) whereas other colonies of the same species do not, and the (mostly) carrion-eating species *Trigona hypogea* can also switch to hunting for live prey [89].

The situation is thus somewhat reminiscent of chimpanzees, where distinct forms of tool use are found in different wild populations [107]. It remains to be tested whether the remarkable behavioural adaptations found in stingless bees are at least in part the result of individual innovations and subsequent cultural processes. We do not suggest that they are wholly cultural, but it is plausible that there has been an interaction between genetic and cultural evolutionary processes, that some behavioural adaptations originated by individual innovation and selection subsequently favoured bees that copied or further improved these innovations with the highest efficiency.

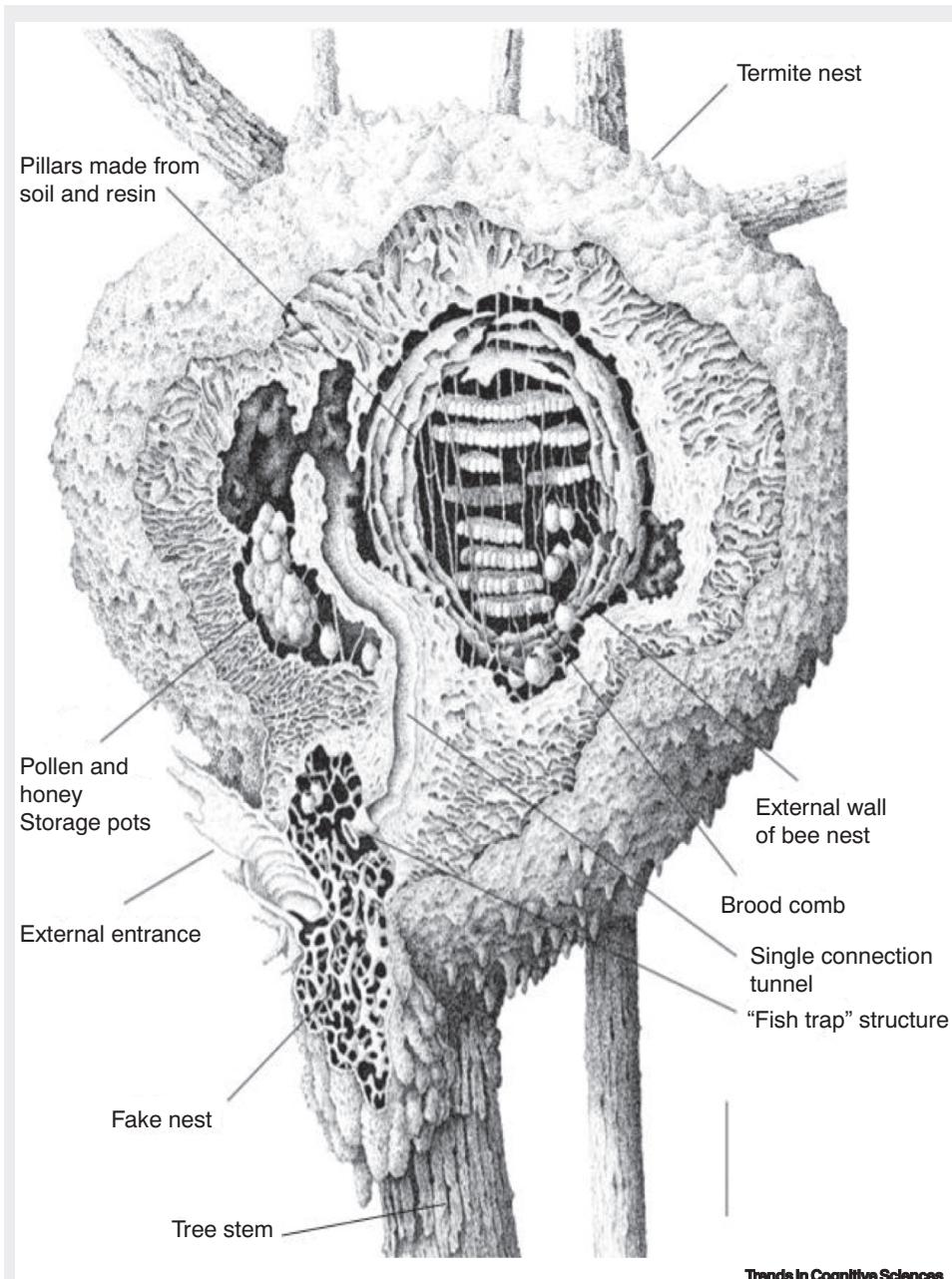


Figure I. Innate behaviour or innovation and culture in nest construction in stingless bees? The nest of *Partamona pearsoni* is built into a live arboreal termite nest and have multiple anti-intruder contrivances. The nest is surrounded with a shell made from resin, to keep the termites at bay. External insect interlopers (coming in through the entrance) first encounter a vestibule ("fake nest") that contains a three-dimensional maze, honeypots that are empty or filled with diluted honey, and an aggressive defence force of *Partamona* guard bees. The actual nest cavity is spatially separated from the entrance area; it contains horizontal combs supported by pillars made from soil and resin. Food is stored in a separate chamber. The construction of such architectures is traditionally thought to be innate, but the diversity within species combined with perennial colonies and the ability to learn by observation (documented in other bee species) make a form of cultural phenomenon plausible, at least in the early stages of the evolution of such structures. Scale bar: 5cm. Drawing by João M.F. de Camargo; from [88].

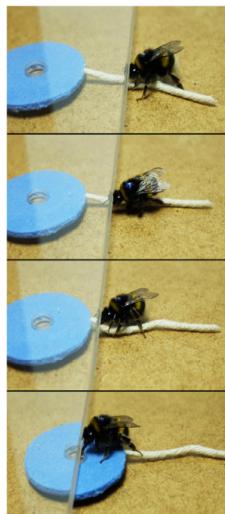


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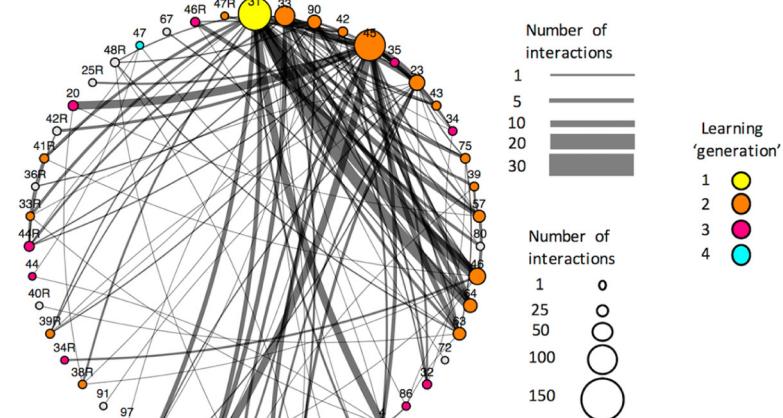
Figure 2. Rescue behaviour of trapped ants might involve physical problem solving and empathy. From [72,108]. (A) An ant is tethered to the substrate with a string around its waist and its abdomen further covered with sand and small gravel. The individual emits a distress pheromone signal (green wavy lines). (B) A helping ant (black) attempts to free the buried abdomen of the trapped individual (grey), by grabbing pebbles with the mandibles and carrying them backwards. (C) One ant brushes sand away from the abdomen of the trapped individual with her front legs, while another helper attempts to pull on the extremities of the tethered ant. (D) After the debris has been fully removed, a helping ant attempts to sever the tether by biting it. The diversity of these behaviours might require some form of comprehension of the desired outcome: an understanding of the anatomy of the trapped individual, specifically where the (invisible since buried) abdomen is located; a distinction of the appropriate actions for various objects (pebbles, sand, strength of biting on limbs versus tether, to avoid injury to the trapped ant), and an understanding of where the ant's body ends and the tether starts. Moreover, the frenzied behaviour of the rescuing ants is reminiscent of the behaviour of rodents in comparable situations, where such behaviour has been linked to empathy (sensing that the trapped individual is in distress and helpers likewise experiencing distress as a result). Partially synchronising the emotional responses of trapped individual and rescuer might be a mechanism to facilitate prioritising and expediting the rescue response.

variation not just between, but also within species in diet, nest architecture and preferred locations, and possibly colony defence and communication [88,89]. It is at least plausible that some such variation might be (or at some point have been) of a cultural nature, not (just) a heritable one. The mode of colony propagation of stingless bees, where groups of experienced bees (and new queens) move from established colonies to new nesting locations, often while keeping in touch with their native colonies [88,89], could further facilitate the cultural retention of behavioural innovations.

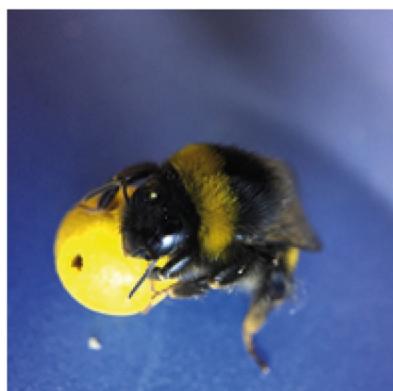
(A)



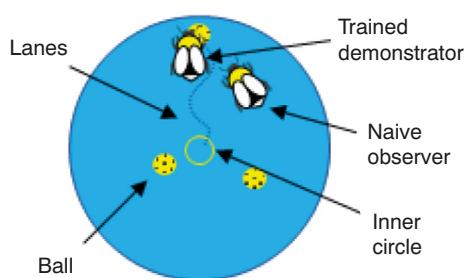
(B)



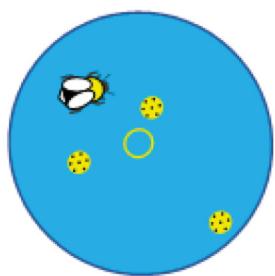
(C)



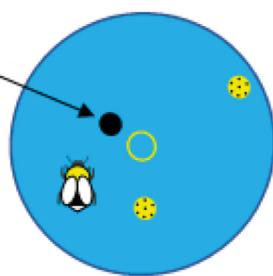
Training Social demonstration



Test



Generalisation test



Trends in Cognitive Sciences

(See figure legend at the bottom of the next page.)

Ants might provide another interesting test case in this regard; the colonies of many ant species can persist for dozens of years [90]. Many species of ants have sophisticated learning abilities [91], including social learning in some contexts [92], and exhibit intriguing within-species variation in nesting architecture [93,94]. This should provide fertile ground for the spread of new useful innovations as well as their retention over many years, in turn perhaps facilitating natural selection to consolidate innovations that were acquired culturally into heritable ones.

Concluding remarks

An alien visitor searching for signs of intelligent life on Earth perhaps 3 million years ago would likely not have found ancient hominins particularly noteworthy, just another mammal living in small groups, foraging opportunistically from plants, and perhaps showing some group coordination in hunting. But she would have been impressed with elaborate constructions by termites that were hundreds of times the height of an individual worker; by organised and well-maintained ant highways, where leafcutters would carry plant materials to grow tasty fungi in their gardens; by bees choosing a new home using a symbolic language and consensus decision making; and in all these species, communally organised brood care and efficient division of labour where dozens of different tasks were each performed skilfully by specialists within their colonies. The scientist might have returned 100 000 years later and been disappointed that bees, ants, termites, and humans were still basically in the same state as before and concluded that neither insects nor humans were capable of cultural evolution, that their behaviour was only governed by innate routines that evolve but slowly. But perhaps the scientist's visits to the planet were simply ill-timed to observe major cultural advances in either type of animal.

Had the alien scientist run a battery of cognitive tests on humans and insects, she might have been surprised that with proper training, both early humans and some insects could manipulate objects for a reward, could learn such tasks by observing another trained individual, and spontaneously improved the technique (indicating a level of understanding of the goal). Moreover, she may have discovered that both humans and certain insects recognise one another individually and can therefore identify individuals that make particularly useful role models. In both taxa, she might have seen evidence that individuals work together on certain tasks and even help one another when in trouble, but she might have concluded that the responses to other individuals' distress could parsimoniously be explained by hard-wired responses not accompanied by emotion-like states. But given all these cognitive abilities, the alien scientist would have been puzzled; why could hominins not even build basic shelters for their brood when left to their own devices, and why could the (then) much more advanced social insects not take first steps to build vehicles or control irrigation?

We have learned that insects feature some of the crucial cognitive abilities both to 'invent' new foraging techniques, to communicate, and to learn from each other, facilitating the cultural spread of newly acquired information. There is not yet a demonstration that such abilities can prevail over multiple biological generations in nature. Could there be (or could there at some point have been)

Outstanding questions

Does social cognition co-opt neural-cognitive mechanisms that have evolved in individual cognition (requiring perhaps relatively minimal tweaks to existing circuits at the transition from a solitary to a social lifestyle)? Or are wholly new neural modules required for some forms of social cognition?

Can we use the miniature brain of insects as a model to understand the minimal neural circuitry that is required for face recognition? What evolutionary transitions are required in visual neural circuits to turn a non-face-recognising wasp ancestor into one that does have this ability?

Might some unique evolutionary innovations found in social insects (e.g., nesting architectures, foraging preferences) initially have emerged by individual innovation and subsequent cultural spread, with evolution only later cementing these behaviours into innate behaviour routines?

Do insects have emotional states related to social affiliations, that, for example, make social stimuli feel rewarding? Might there be emotional states that are specific to the biology of insects, with no parallel in the vertebrate world?

Do the most sophisticated forms of cognition in insects occur among the social species and, if so, is this because social life imposes selection pressures on the brain that also mediate other (nonsocial) forms of intelligence?

How do insects of multiple different 'personalities' synergistically generate adaptive colony behaviour, including nest construction, climate control, colony defence, and foraging, and how can it be ensured that a colony contains the right level of diversity?

Figure 3. Social learning of tool use in bumblebees. (A) String-pulling by bumblebees. The image series shows a forager pulling a string to gain access to a blue artificial flower under a transparent Plexiglas table; the centre of the flower holds a droplet of sucrose solution [25]. (B) Diffusion of string pulling in a bumblebee colony. Nodes represent individual bees. Thickness of lines represents the number of interactions between two individuals. Size of nodes indicates number of interactions of that individual bee with any other bee. Colour represents learning 'generation' of that bee: orange for a first-order learner (learning from the first skilled 'yellow bee', top position); pink for a second-order learner (interacting with first-order and lower); turquoise for a third-order learner (interacting with second-order and lower) [25]. (C) Ball rolling. Top left: bumblebee worker moving a ball. Top right: the task is to move a yellow ball to the centre of the round blue area (the inner circle marked in yellow). An experienced worker (demonstrator) has learned that only the furthest of three balls can be moved (the others are glued down). A naive observer watches. Bottom left: the observer is subsequently given the choice between three mobile balls. Rather than choosing the furthest ball (the one it has seen the demonstrator move), it picks the one closest to the centre. Bottom right: even if the bee is faced with a novel black ball, it still chooses the optimal solution of picking the closest ball [80].

a cumulative culture in insects, where a behavioural innovation builds on an earlier one that is already widespread in a population (see [Outstanding questions](#))? It is perfectly conceivable that a culture of string-pulling bees might subsequently apply their skill towards a wholly new task (e.g., home construction) but it is not actually easy to conceive of realistic challenges where this might be truly beneficial. Thus, the absence of a particular behavioural capacity in wild animals is not evidence that the ability is ‘hard to evolve’, or for the lack of adequate levels of intelligence, but might in many cases simply reflect the absence of relevant natural challenges. It is also plausible that if our alien scientist had inspected Earth millions of years earlier, she would have discovered that elements of social insects’ behavioural innovations that are now largely hardwired (e.g., the honeybees’ dance language, or ants tending aphid colonies) might in its earliest stages have spread via social learning (cf. the Baldwin effect [95], perhaps initially mediated by epigenetic processes [96]). Pinpointing the neural-molecular bases for social-behavioural capacities will facilitate an understanding of their past evolution and possible future evolutionary trajectories in these fascinating animals. In addition, leveraging the power of studying miniature nervous systems, with the advantage of understanding the neuron-to-neuron connectivities that mediate social cognition, will be a promising avenue of future research.

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Declaration of interests

No interests are declared.

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