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Inter-caste communication in social insects

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Abstract

Social insect colonies function as highly integrated units despite consisting of many individuals. This requires the different functional parts of the colony (e.g. different castes) to exchange information that aid in colony functioning and ontogeny. Here we discuss inter-caste communication in three contexts, (*i*) the communication between males and females during courtship, (*ii*) the communication between queens and workers that regulate reproduction and (*iii*) the communication between worker castes that allows colonies to balance the number of different worker types. Some signals show surprising complexity in both their chemistry and function, whereas others are simple compounds that were probably already used as pheromones in the solitary ancestors of several social insect lineages.

Introduction

Insect colonies often consist of thousands – and sometimes millions – of individuals and the success of each individual depends crucially on the success of the colony [1,2]. Colonies show two kinds of division of labor. First, there is a reproductive division of labor between queens (and kings in termites) and the largely sterile workers. Second, there is division of labor among the workers for tasks like brood rearing, colony defense or foraging [1,2]. Communication between and within the different castes (queens, males and different worker groups) is fundamental for the efficient functioning of a colony. In order for colonies to respond to the often changing needs, workers – like the cells of multicellular organisms – need to respond to signals in ways that are beneficial to the whole complex system.

Most communication is based on chemical signals or pheromones that are produced by exocrine glands [1-4]. Hundreds of chemicals produced in more than 60 different glands have been identified in social insects [3,5], which has led researchers to refer to social insects as chemical factories [1]. Traditionally, pheromones have been divided into two classes, primer and releaser pheromones [1]. A releaser pheromone initiates an immediate behavioral response, whereas a primer pheromone alters more long-term endocrine and reproductive systems in the recipient [6]. However, it has become clear that there are pheromones that have both releaser and primer effects [6-8]. The pheromone signals are perceived via olfactory sensillae on the antennae [3,9-11] before being further processed by the olfactory system [12].

In this review we focus on recent advances in our understanding of inter-caste communication in three important contexts: (*i*) communication between male and female reproductives that results in mating and, subsequently, colony foundation, (*ii*) communication between queens and workers to regulate reproduction and (*iii*) communication between different functional groups of workers (sometimes called sub-castes) that allows colonies to balance the number of workers performing different tasks (for communication within castes, e.g. among foragers during resource collection or during house hunting see [13-16]). Recent research has highlighted the importance of chemical and behavioral complexity, context, and dose for communication [6]. Furthermore, the recent identification of several queen signals that inhibit reproduction in workers [7,17,18] or other queens [19] has improved our understanding of the evolution of reproductive division of labor. New tools like calcium imaging or genomics have started to reveal how pheromone signals are processed in the nervous system [12,20] and how external cues and signals induce important behavioural modifications are associated with large scale changes in the pattern of expression of brain gene (e.g. [20-22]).

Communication between males and females

Before starting a new colony reproductive individuals must find a mating partner. Chemical communication plays a fundamental role in this process and males in particular show numerous adaptations that help them find females [3]. These include large compound eyes, strong wing muscles or antennae with large numbers of odor receptors [23,24]. Most mating patterns fall into two broad categories, the “female calling syndrome” and the “male aggregation syndrome” [1,3]. In species with the “female calling syndrome”, females are often wingless and do not travel far from their natal nest (sometimes they call from within the nest). They release sex pheromones to “call” the winged males. These species typically form small colonies and mating flights do not seem to be synchronized across colonies. In some cases it is the workers that “call” males. In *Megaponera analis*, for example, males follow recruitment trails laid by workers to guide them to the nest [1]. In the stingless bee *Scaptotrigona postica*, 2-alcohols attract males from long range, but additional substances are then required to elicit copulations by males [25]. Once males have settled near a nest containing a virgin queen, the males themselves become attractive to other males, leading to large aggregations (Fig. 1a) [26,27].

Thus, male aggregations in many stingless bee species are probably the outcome of both female and male calling [26-28].

Species with larger colonies frequently exhibit a “male aggregation syndrome”, whereby males from many colonies gather at specific sites where they are later joined by females [3]. In these species mating flights are usually tightly synchronized between many colonies thereby decreasing the probability of inbreeding and hybridization between closely related species. In species such as some *Camponotus*, *Atta* and *Acromyrmex*, the departure of both sexes from the nest is coordinated by the release of mandibular pheromones by males as they leave the nest. This, in turn, triggers the mass exodus of females [3]. Honey bee (*Apis mellifera*) drones gather at congregation areas (ranging from 30 to 200 m in diameter) where they wait for virgin queens [23,29]. A modification to this pattern of male aggregations is found in bumble bees where males patrol flight paths which they mark with labial gland secretions [30]. In *Bombus terrestris,* and probably other *Bombus* species, females are preferentially attracted to flight paths marked by many males, hence selecting for males to aggregate to attract females [3]. Another alteration to the “male aggregation syndrome” is found in many polistine wasps, where males mark objects in their territories with scent by dragging their legs or abdomens over the substrate or release pheromones into the air [31,32].

How females locate male aggregations is not well understood but males’ mandibular glands have been implicated as the source of the sex attractant in numerous ant genera and conclusively demonstrated in several *Pogonomyrmex* species [1,3]. The main compound found in mandibular glands in *Pogonomyrex* (4-methyl-3-heptanone) seems likely to play an important role in female attraction [3], although controlled experiments are needed to confirm this. Once females have found the aggregation female-derived pheromones are thought to attract males at close range. In *Formica lugubris*, for example, the source of the attractant is the females Dufour’s gland, which contains undecane (90%), (Z)-4-tridecene (4%), and tridecane (4%). Synthetic undecane causes a strong male response similar to the response observed in nature [33]. One of the first identified sex pheromones is the honey bee “queen substance”, which originates from the queens’ mandibular glands [34]. Mandibular gland extracts of honey bee queens attract drones from a distance of ~50m [3,29]. The most active compound (9-keto-(E)-2-decenoic acid or 9-ODA) is almost as active as the whole blend [34]. Interestingly, Asian honeybee species also use 9-ODA as the main male attractant [35]. However, differences in the timing and location of mating flights and visual cues of sexual partners seem to limit heterospecific sexual encounters [3]. After mating, queens of some species quickly become unattractive to males. This can be caused by changes in the queens’ cuticular hydrocarbon (CHC) profile (e.g. *Leptothorax gredleri* [36]) or by tactile signals produced by the queen (e.g. *Pogonomyrmex* spp. [1]).

Communication between queen and workers

An important prerequisite for the functioning of social insect colonies is the ability of queens to signal their presence and good health. To this end queens produce a chemical signal that often has several effects, among which are the inhibition of the rearing of new reproductives [6,37], attraction of workers to the queen (Fig. 1b) [6,37], the suppression of worker reproduction [6,7,17,38-40] and chemical marking of eggs, which allows workers to recognize whether eggs are queen- or worker-laid [39,41]. The absence of the queen signal, which generally is associated with the death of the queen, usually elicits important changes in the colony, including the rearing of new queens [42] or the activation of worker ovaries to produce male brood. There has been considerable controversy about whether queen signals are manipulative tools allowing queens to prevent workers from reproducing or whether they are cooperative signals that allow workers to increase their fitness [5,43-45]. The idea behind the second hypothesis is that because worker reproduction may impose costs for colony productivity, workers may increase their inclusive fitness by not reproduction in the presence of the queen [39,46]. Several lines of evidence support the hypothesis that queen signals are indeed honest signals of fertility, rather than an attempt by the queen to manipulate the workers [47]. First, the “honest signal” hypothesis predicts a positive correlation between signal production and fertility and there is increasing support for this prediction in ants [48,49]. A possible explanation for this positive correlation is that queen signals are derived from chemical by-products of ovarian development [38,41,47]. Second, comparative studies show that workers often ignore queen signals and try to reproduce in the presence of a fertile queen if it is in their genetic interest to do so [47,50]. Third, the “queen manipulation” hypothesis predicts an evolutionary arms race between queens and workers that leads to the rapid evolution of chemical signals [43,45]. Contrary to this prediction, recent research suggests that structurally related non-volatile hydrocarbons function as conserved queen signals in several lineages of social insects, including ants, wasps, bumble bees and stingless bees [17,18,38,47,51], but see [52], suggesting that queen pheromones are derived from ancestral communication systems that were already present in the common solitary ancestor of ants, wasps and bees (with the exception of the honey bee, see below) [17,47]. However, definitive evidence for queen pheromones being honest signals will require a better mechanistic understanding of how the compounds affect workers and queens, for example whether queen-produced pheromones exclusively bind to antennal receptors (which would support the view that they are honest signals) or whether they also enter the worker circulatory system and mediate hormonal changes directly affecting reproduction (which would be consistent with pheromonal queen control) [43].

One challenge for large colonies is an efficient distribution of the queen signal. Research in ants and termites shows that the signal is located on both the queen and on her eggs [7,19,37,39]. This means that the queen presence can be felt in parts of the nest where the queen is not present (Fig. 2a). In honey bees, eggs are not carried around, but there are specialist “messengers” whose role is to actively distribute the queen pheromone in the colony [42]. Small amounts of pheromone are also transmitted via the wax comb (Fig. 2b) [53]. Again, 9-ODA plays an important role but, unlike in the attraction of drones, worker attraction requires the combined presence of four additional mandibular compounds (some strains may require even more compounds) [6,54]. The combination of 9-ODA and these four compounds constitute the queen mandibular pheromone which has been shown to alter the pattern of expression of several hundred genes in the brain of adult workers [20,55], including genes implicated in the dopamine pathways [56] and genes associated with the behavioral maturation of workers from nurses to foragers [20].

Communication between worker sub-castes

Division of labor among workers is an important reason for the ecological success of social insects [1,2]. A key challenge for a colony is to allocate an appropriate number of workers to the different tasks. The number of soldiers in a colony, for example, should match the level of threat a colony faces [57,58]. Research has shown that pheromones that function as negative and positive feedbacks play a crucial role in balancing the number of workers performing different tasks. In honey bees, for example, the number of workers that progress from nurse duties to foraging duties as they age depends on the number of foragers already present in the colony [59,60]. Foragers produce ethyl oleate, which acts as a chemical inhibitory factor delaying the onset of foraging [61]. The removal of foragers leads to increased levels of juvenile hormone (JH) titers, which is correlated with the onset of foraging behavior [62]. Ethyl oleate is synthesized *de novo* and is present in highest concentrations in the bee’s crop. Thus, behavioral maturation and the propensity to become a forager is modulated via trophallaxis [61], a form of food exchange that plays a prominent role as an information channel in various contexts [63]. A pheromone produced by larvae has a similar effect: colonies treated with a synthetic blend of this pheromone show delayed foraging activities compared to workers in untreated control colonies [8].

Colony defense is another important task and many species rely on a specialist soldier caste for their safety [1,2,64,65]. Colonies in some species are able to adjust soldier production according to the dangers in the environment [57,58]. An overproduction of new soldiers is prevented because the presence of existing soldiers inhibits the production of new soldiers. Such soldier inhibition has been in demonstrated in aphids [66], termites [67] and ants [68] but the pheromones causing this effect have not yet been identified.

Caste specific response to pheromones

Recent research has started to elucidate caste-specific differences in the olfactory system that underlie caste-specific responses to pheromones. For instance, males, queens and workers differ in the number of sensory sensillae on the antennae [69,70] and in the expression of a range of odorant receptors (ORs), some of which are known to respond to components of queen pheromone [9,71]. The number of sensory sensillae, in turn, has been shown to correlate with the number of glomeruli, the functional units of the antennal lobes (AL, the primary olfactory center) [69]. In honeybees, queens and workers show morphological differences in both the primary (AL) and secondary (mushroom bodies) olfactory center: queens have smaller glomeruli and fewer microglomeruli [72]. In several ants and the honeybee, males and females differ in the number and size of glomeruli in the antennal lobes. Females have more glomeruli, but males have some large macroglomeruli that are less common or absent in the female castes [12,73-75]. Additionally, glomeruli in males may contain different types of innervations than in queens and workers [73]. Odors, including pheromones, trigger specific activity patterns in the glomeruli [12,76-78]. This was shown in honeybees where harnessed individuals were simultaneously exposed to floral or pheromonal odors while measuring by calcium imagin the spatio-temporal excitation patterns evoked in the glomeruli [12, 76-78]. These studies showed that odor identity in the AL is coded in odor-specific activity patterns that involve the combined activity of a number of glomeruli and that different classes of odors tend to activate different glomeruli.

Concluding remarks

Communication systems are a prerequisite for the functioning of complex biological systems in general and animal societies in particular. Yet, despite decades of research we still have a superficial understanding of the identity of the chemicals and the corresponding receptors that are involved and their location of action. The development of new molecular tools has started to shed light on these mechanistic questions and future work will allow us to gain a better understanding of how systems of chemical communication evolved to regulate the behavior and physiology of individuals and societies.

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Conflict of interest statement

Nothing declared.

References

*of special interest

**of outstanding interest

*10. This study shows a link between the expression of the antennal receptor *AmOR11* and behavioral sensitivity to a major compound of the honey bee queen pheromone, 9-ODA.

*11. The authors identify and study the olfactory sensillae on antennae that allow ants to identify other individuals based on cuticular hydrocarbons.

**17. The authors newly identify 3 queen pheromones (in an ant, a wasp and a bumblebee) and provide a phylogenetic analysis that reveals the conserved nature of queen pheromones in many social insect species.

*37. The authors report the identification of the first pheromone that inhibits reproduction in termites.

*47. The authors review the debate about queen pheromones and their function as either honest signals vs. tools of worker manipulation.

*52. The findings presented in this study challenge the finding that queen pheromones in bumblebees are conserved across species and groups of species.

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Figure 1

Figure 1. (a) A male aggregation in the Neotropical stingless bee *Tetragonisca angustula*. Aggregations of several hundred males are usually found close to a nest that contains a virgin queen or will soon contain a virgin queen (Photo by C. Grüter). (b) A fire ant (*Solenopsis invicta*) queen and her retinue workers. The workers feed and groom the queen and remove her eggs (Photo by W.R. Tschinkel).

Figure 2

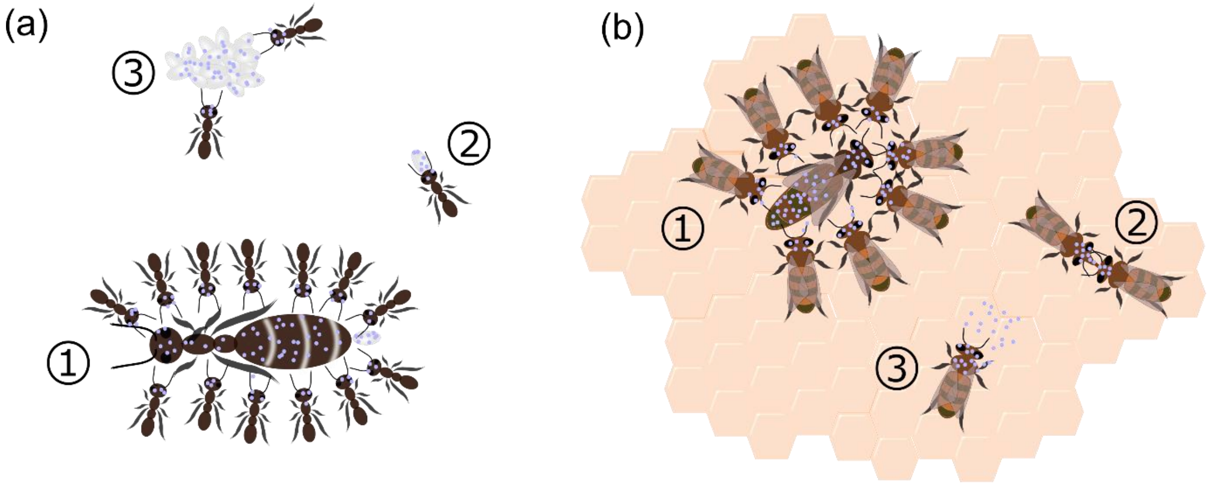

Figure 2. Distribution of queen pheromones (indicated as blue dots). (a) In ants and termites, workers acquire queen pheromone by physically interacting with a queen, e.g. during grooming or feeding (1), when carrying queen-laid eggs (2) or when contacting egg piles (3). (b) Honey bee workers acquire queen pheromone when contacting the queen (1), when interacting with workers that had recently been in contact with the queen, e.g. via trophallaxis with "messenger" workers (2) or via the wax comb (3).