زانكۆی سەلاحەدین - هەولێر

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Communication in social Insect

Research Project

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By

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SUPERVISOR CERTIFICATE

This research project has been written under my supervision and has been submitted for the award of the degree of BSc. in Biology with my approval as a supervisor.

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DEDICATION

This work is dedicated to:

The sake of Allah, my Creator, and my Master, my great teacher and messenger, Mohammed (May Allah bless and grant him), who taught us the purpose of life.

My great parents, who never stop giving of themselves in countless ways, my beloved brother and sisters, to all my family, the symbol of love and giving.

Maryam

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ABSTRACT

Communication is the foundation of all social systems and is at the heart of nearly all social activities in an insect colony. It requires a sender who produces a signal (a trait shaped by natural selection to convey information) and a receiver who responds to the signal.Social insect colonies function as highly integrated units despite consisting of many individuals. This requires the different functional parts of the colony to exchange information that aid in colony functioning and ontogeny the communication between worker castes that allows colonies to balance the number of different worker types. There are different types of communication (chemical communication ,visual communication ,acoustical communication and tactile communication)in social insects.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.

Keywords: Communication, Social insect, Pheromone, Visual communication, Chemical communication, Tactile communication, Acoustical communication.

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INTRODUCTION

Communication involves much more than simply detecting a stimulus and making one that can be detected. Communication implies the transfer of reliable information that reduces uncertainty about a signaler's identity, capability, and motivation. Thus, some modification of a stimulus is expected following its origin, whether via sensory bias or a coevolutionary process(Alem et al.,2013). Social insect colonies contain between dozens and millions of individuals,Their social organization is based on an efficient communication system which makes it possible to distinguish multimodal signals(Billen,2006).

Social insect communities are simple, autonomous, co-operative organizations that are able to coordinate effectively to achieve global goals despite the lack of centralized planning(Saleem,2011).The main purpose of communication in social insects is to provide information that reduces uncertainty about important aspects of colony life(Seyfarth et al., 2010).Social life within insect societies is regulated through a sophisticated multi-modal communication network. Complex blends of chemical compounds are integrated with vibration, acoustic, and visual signals to control the division of labor in the colony, from colony de- fence to brood care (D'Ettorre and Moore ,2008).

Studies of insect communication have revealed a great variety of mechanisms, tactics and systems, which are either chemical, visual or acoustical. Many insects like crickets, katydids, grasshoppers and cicadas produce air-borne sounds which can be heard by humans and consequently have been extensively investigated for many years(Andrej Cokl,2004).Therefore, to know and understand the modalities of intracolony communication and the roles they play is necessary for a full understanding of social insect biology.While chemical communication by various means constitutes the primary category of intracolony communication modes in social insects(Richard and Hunt, 2013).Also, signal use might strongly depend on the context (Cilia et al., 2019), so that the response to pheromones, for example, depends on the simultaneous presence

of other cues/signals or is even affected by individual experienced (Grüter and Czaczkes, 2019).With increasing social complexity, the need to communicate a greater diversity of messages arose to coordinate division of labor, group cohesion, and concerted actions. Here we summarize the knowledge on prominent messages in social insects that inform about reproduction, group membership, resource locations, and threats and discuss potential evolutionary trajectories of each message in the context of social complexity(Leonhardt,2016). This article aims to have a closer look at this communication system in social insects, and to illustrate the various modalities that characterize it with a number of examples.

Communication

Communication in social insects to a very considerable extent is mediated by the action of chemical messenger molecules or pheromones. These are produced in an impressive variety of exocrine glands, that occur all over the body of these insects. Various gland types as well as various types of pheromonal communication can be distinguished(Billen,2011).

Social insects

Social insects, are characterized by communities in which they live in permanent contact with their nest mates. Bees and bumblebees, wasps, ants and termites since long have fascinated man because of their well organized and often impressive colonies. Their social lifestyle goes along with the inevitable development of a communication system, that allows the individual members of the colony to exchange information. This social language can occur via various sensory channels, using visual, acoustic, tactile, sometimes magnetic, and especially chemical signals (Billen,2006).

Social communication can be

- Chemical

- Visual

- Acoustical

- Tactile

Chemical communication in social insects

Chemical messengers are the primary mode of intracolony communication in the majority of social insect species. Chemically transmitted information plays a major role in nestmate recognition and kin recognition. Physical and behavioral castes often differ in chemical signature, and queen effects can be significant regulators of behavior and reproduction. Chemical messengers themselves differ in molecular structure, and the effects on behavior and other variables can differ as a consequence of not only molecular structure of the chemical messenger itself but also of its temporal expression, quantity, chemical blends with other compounds, and effects of the environment.

The most studied, and probably the most widespread, intracolony chemical messengers are cuticular hydrocarbons (CHCs). CHCs are diverse and have been well studied in social insects with regard to both chemical structure and their role as pheromones. CHCs and other chemical messengers can be distributed among colony members via physical contact, grooming, trophallaxis, and contact with the nesting substrate.Widespread intracolony distribution of chemical messengers gives each colony a specific odor whereby colony members are integrated into the social life of the colony and non-members of the colony are excluded. Colony odor can vary as a function of genetic diversity within the colony, and the odor of a colony can change as a func- tion of colony age and environmental effects. Chemical messengers can disseminate information on the presence of reproductives and fertility of the queen(s) and workers, and queen pheromone can play a significant role in suppressing

reproduction by other colony members. New analytical tools and new avenues of investigation can continue to expand knowledge of how individual insects function as members of a society and how the society functions as a collective (Richard and Hunt,2013).

Termites have both non-volatile and volatile components of queen pheromones. Non-volatile polar compounds of proteinaceous origins are secreted by functional reproductives in the termites Prorhinotermes simplex, Reticulitermes santonensis, and Kalotermes flavicollis (Hanus et al., 2010). The cuticular hydrocarbon cuticular profile differs between neotenic reproductives and workers in Cryptotermes secundus (Weil et al., 2009) and Zootermopsis nevadensis.In Z. nevadensis, four polyunsaturated alkenes are present in significant amounts on reproductives but almost absent in soldiers, workers, and neotenic reproductives with inactive gonads (Liebig et al., 2009). In Reticulitermes speratus, queen pheromone consist of volatile compounds which are an ester, n-butyl-n-butyrate, and an alcohol, 2-methyl-1-butanol, and these compounds are not produced by nymphs and workers (Matsuura et al., 2010).

Pheromone

The term pheromone is derived from the Greek pherein, to transfer (carry); horman to excite. Pheromones are defined as substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction,Although the general descriptions of insect anatomy and structure as found in entomological textbooks equally apply to social insects, the development of the exocrine apparatus in the latter clearly distinguishes them from solitary insects (Figure 1). An extremely diverse array of exocrine glands is found in all social insects, with 63 different glands described so far (39 if only considering the Formicidae, 21 for the Apidae, 14 for the Vespidae and 11 for the Isoptera) (Billen,1994). Several of these glands serve 'individual' functions as the source of digestive enzymes or lubricant compounds, although the majority has a clear

functionally related to the social organization of the colony (Hölldobler and Wilson, 1990).

Some have a role in producing building material like the wax glands in bees, others secrete antibiotics like the metapleural glands of the ants, or elaborate sticky defensive substances like the frontal glands of some termite species. A major social function of exocrine glands, however, is the production of pheromones, for which many glands have become specialized. The study of exocrine glands in general, and of pheromone producing glands in particular, has long been faced with a number of practical difficulties. Because of their ectodermal origin, all exocrine glands are associated with cuticle, which has put considerable constraints on the study of gland structure. The development of plastic embedding techniques has allowed much better sectioning conditions, which have resulted in a clearer picture of the structural organization of the exocrine system compared with the information obtained from paraffin sections.

The small size of insects, on the other hand, for long represented a considerable drawback in our chemical understanding of the glandular secretions. The availability of more sophisticated equipment and techniques in the past decades has made analysis at the monogram level possible, thus resulting in the identification of many glandular products.
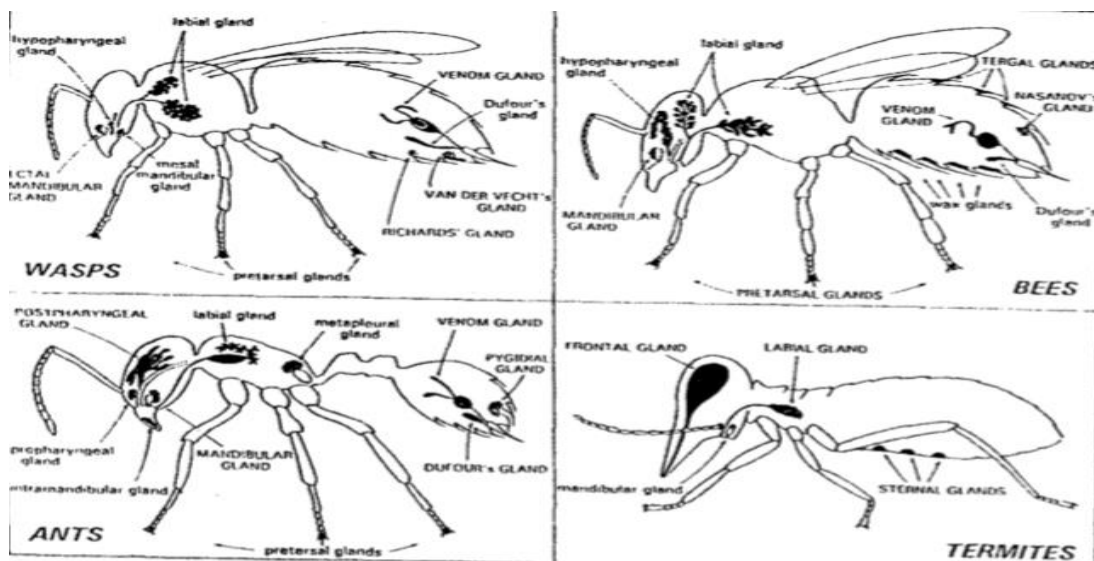
Figure 1. Schematical profile drawings showing the commonly found exocrine glands in wasps, bees, ants and termites. Glands with a pheromonal function are indicated with capital lettering.

queen pheromone (queen signals)

Signals produced by queens in eusocial colonies indicate the queen's presence and/or fertility to workers who then abandon their own reproduction and help with rearing siblings (Keller and Nonacs, 1993) (Figure 2).

Workers can further use this in- formation to control each other's reproduction by for instance destroying eggs laid by other workers (Ratnieks and Reeve, 1992). When a colony loses its queen or the queen loses fertility, the queen signal diminishes and non- sterile workers can start laying eggs themselves (Keller and Nonacs,1993). Consequently, communicating the presence and fertility of a queen reinforces reproductive division of labor and benefits the social organization within colonies.

Figure 2. A royal chamber of the West African termite Macrotermes bellicosus. The queen (white) is surrounded by the substantially smaller king (black, below the queen) and workers.

Queen pheromones are likely present in most eusocial insect species and are thought to be located on the queen's cuticle. Different species appear to use different (albeit partly structurally related) compounds as queen (Oi et al., 2015). However, only a few studies experimentally demonstrated thatputative queen pheromones actually inhibited reproductive activity in workers (Kocher and Grozinger, 2011). For example, queens of the black garden ant (Lasius niger) produce large amounts of a methyl-branched hydrocarbon in both their own and the chemical profile of their eggs, which inhibits worker aggression and ovarian activity (Holman et al., 2010). Queens of the red

imported fire ant (Solenopsis invicta) produce several compounds (two pyrones and a terpene), which inhibit reproduc- tive activity in virgin queens and reinforce helping behavior in workers (Kocher and Grozinger, 2011). Similarly, an ester and an alcohol from secondary queens and queen-laid eggs of the termite Reticulitermes speratus attract workers and inhibit differentiation of new queens (Matsuura et al., 2010).

Beyond doubt, queen pheromones have been most intensively studied in the European honeybee Apis mellifera, wherein the queen mandibular pheromone (QMP) represents the most complex queen pheromone or pheromone cocktail examined so far. It comprises at least nine components (five fatty acid derivatives, two alcohols, and two phenolics) that regulate worker ovarian activity, inhibit rearing of new queens and juvenile hormone synthesis in workers, delay the transition from nursing to foraging, attract workers and males, and coordinate swarming (Kocher and Grozinger, 2011). Thus, QMP can act as both a sex pheromone and a social coordinator.

In other insects, various hydrocarbons are positively correlated with ovarian activity and therefore candidates for queen pheromones, e.g., in paper wasps (Polistes dominulus, Sledge et al., 2004), termites (Weil et al., 2009), and ants (Pachycondyla inversa, D'Ettorre et al., 2004; several Lasius species, Holman et al., 2013).

Dance of honey bee (*Apis mellifera)*

Honey bee (Apis) dance communication is arguably the most lauded of all forms of animal signalling. Bees dance to signal the location of valuable resources to their nestmates, and dances are effective in recruiting additional foragers to those resources (Seeley, 1995).Dance is unique to the genus Apis .In European honey bees (*Apis mellifera)*, dances are performed in the contexts of foraging and nest site selection. On returning to the hive, successful A. mellifera foragers sometimes perform highly stereotyped dance movements (Fig. 3). For resources more than a few hundred metres away from the nest, the dance can be described as a repeating figure-of-eight movement performed on the vertical surface of the comb hanging inside the hive (Fig. 3). At the junction between the two loops of the figure of eight, the bee takes a stride and leans

forward, vibrating her wings and waggling her abdomen rapidly from side to side in the famous and distinctive 'waggle run' of the dance (Tautz et al., 1996). The wing vibrations produce both acoustic signals and jets of air directed behind the dancing bees (Michelsen, 2012).

Features of the waggle run correlate with the distance and direction of the resources found by the forager. As these dances appear to represent quantitative information about the position of foraging sources in a new (and apparently arbitrary) form compared with the original information, they have been described as 'symbolic communication' (Couvillon, 2012). For foraging resources located close to the hive (typically less than 100 m), the duration of the waggle phase is extremely short; consequently, the figure-of-eight form deforms into a sickle or round shape, but the very brief waggle phases of these dances still contain some directional information (Gardner et al., 2008).
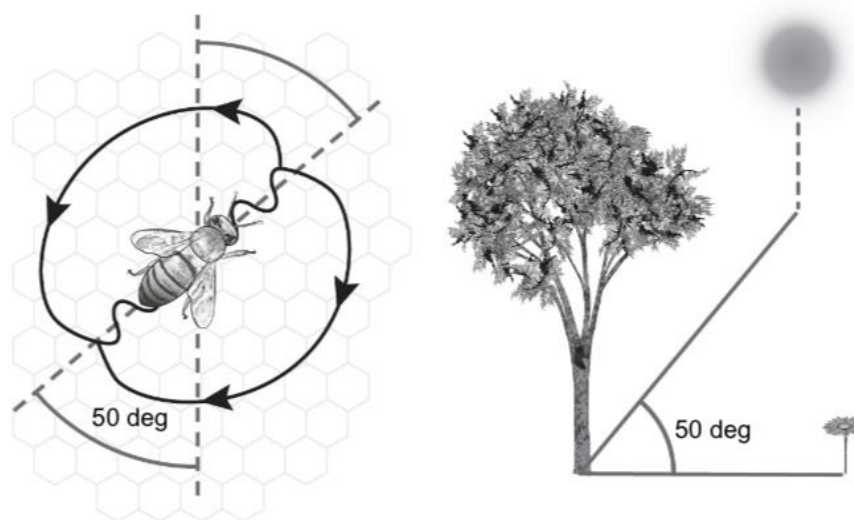
Figure 3. Schematic diagram of the waggle dance of Apis mellifera. Dances advertise resources found by foragers. The dance is usually executed on vertical combs inside the hive (left). The angle of the waggle phase of the dance relative to vertical on the comb corresponds to the direction to the advertised resources on departure from the hive relative to the solar azimuth (right). The duration of the waggle phase correlates with the amount of optic flow experienced during the flight to the resources. At the end of the waggle phase, the forager loops back to the beginning and repeats the movement.

Alarm signaling

Alarm signals frequently have visual and auditory components, especially in birds and mammals (Leavesley and Magrath, 2005), but chemical alarm signals are also widespread. Most alarm pheromones likely have evolved from compounds originally having other functions.

Specifically, it has been proposed that alarm pheromones may evolve either from chemicals involved in defense against predators or from compounds released upon injury (Wyatt, 2003). To the extent that these compounds serve as reliable cues to the presence of predators, potential receivers should evolve to detect them and respond in ways that enhance fitness. The acquisition of a true signaling function then entails further evolutionary elaboration of the cue specifically in response to selection acting on its role in communication (Maynard Smith and Harper, 2003).

Sexual pheromone

The trail pheromone substance 3,6,8 dodecatrien-1-ol (2) already described as a trail pheromone of termites from the sternal gland, has been suggested to be also the sexual attractant pheromone of the termites Pseudacanthotermes spiniger (Bordereau et al., 1991) and Reticulitermes santonensis (Laduguie et al., 1994).

P. spiniger has ten times more of the substance in the glands of alate females than of males, and more than in the glands of workers.Although a number of substances have been identified in the mandibular glands of sexual ants, where these are different from the substances found similarly in workers, we are not aware of any examples where these have definitely been shown to act as sexual attractant pheromones. On the other hand there is plenty of evidence that they exist and for their origins. The difficulties of bioassays have held back their isolation.

Primer pheromone

Primer pheromones undoubtedly play a central proximate role in establishing and maintaining the sophisticated social structure of ant colonies. Such basic processes as caste determination and reproductive development appear to be regulated by pheromones, produced primarily by queens (Hölldobler and Wilson ,1990).Despite their importance in shaping the structure and function of ant colonies, no ant primer pheromones have been identified and little specific information exists about them. The main obstacle in studying ant primer pheromones has been the lack of sensitive, reliable bioassays. As with research on any semiochemicals, the key to sustained progress is an effective bioassay. In contrast to the effects of releaser pheromones, e.g., sex attractants, trail following and alarm behavior, which in many cases can be assayed in a matter of minutes, primer pheromones have much more subtle physiological effects which may not be apparent for several days or weeks.

Traditionally, several lines of evidence have suggested the occurrence of primer pheromones. In many instances, the presence of a queen is clearly associated with some inhibitory effect on development or reproduction, e.g., the development of new queens (gynes) or reproduction by workers. This together with the lack of obvious aggression or other behavioral displays by queens that could serve as cues has implicated the presence of pheromones. However, the presence of a queen has other correlates besides possible chemical cues that could be involved in producing primer effects, e.g., tactile cues and source of eggs which affects the worker to larva ratio.Therefore, demonstration of the involvement of queen primer pheromones requires carefully designed experiments to exclude other possible non chemical cues.Strong evidence for the involvement of pheromones comes from showing activity with queen corpses, excluding any role for behavioral cues, together with proper controls to exclude possible tactile cues associated with a queen. This level of evidence in ants has only been approached in a handful of cases.Even stronger evidence involves the demonstration of biological activity with extracts of queens. This level has only recently been achieved in studies of the fire ant Solenopsis invicta .

Intermediate between these two levels is showing that queen corpses lose their activity after rinsing with an organic solvent (Vargo and Passera ,1991), which treatment presumably removes chemical but not tactile cues from the body. Finally,

irrefutable evidence for the involvement of primer pheromones comes from the identification of one or more biologically active compounds and the demonstration of activity with synthetic material, a level that has yet to be achieved for any ant.Even if we lack much detailed information about ant primer pheromones, there is considerable circumstantial evidence from many species giving us a good indication of the roles they play in ant colonies.There appear to be two main effects of primer pheromones in ant colonies: (1) on larval development, where they influence caste determination in female larvae; and (2) on reproductive activity of colony members, where they inhibit ovary development and/or oviposition. Much of this circumstantial evidence has been reviewed elsewhere(Hölldobler and Wilson ,1990).

Aggregation and signaling pheromone

Studies have shown that several mechanisms enable insects to form cohesive groups (Wertheim et al., 2005). In some cases, an insect benefits from the presence of conspecifics, and so may signal to attract them. If the recipient of the signal benefits from responding, there is a basis for a communication system. If the sender doesn't benefit from attracting conspecifics, it should not emit an active signal, but try to remain cryptic and give as few cues as possible to its' position. Likewise, if a recipient does not benefit from responding to a signal, it should not do so. Thus, for a communication system to exist, both sender and recipient must benefit (Smith and Harper, 2003).

A signal may be intercepted by parties other than the intended recipient, e.g. parasites and predators. Several species of parasitoid wasps use mating and aggregation pheromones emitted by their prey as a cue to find them. Competitors may also intercept a signal. In some cases, a pheromone emitted to attract a mate is used as a cue to find a suitable food resource by conspecifics of the same sex as the emitter of the signal.The

balance of cost and benefit for aggregating is situation-dependent. A bark beetle female overhearing the volatile chemical mating call of another female may choose to follow the signal to try and find a suitable host (Schlyter and Birgersson, 1999).

Visual communication in social insects

Visual cues in the meaning of inter individual signals are not common in social insects. Well-developed sight can be important in some cases, however, such as visual tracking of the leader by foraging stingless bees (Nieh, 2004). Also for partner location, prior to mating, the males' big compound eyes can help in find- ing the females (Fig. 5A). More common is the use of well-developed eyes for orientation purposes. The sun compass in honeybees (Fig. 4). Similar examples among the ants deal with orientation in Cataglyphis desert ants, where the elegant pioneer work of R. Wehner's group in Zürich illustrated how these ants detect polarized light and orient themselves through their amazing visual capacities (Wehner, 2003). In several other ant and termite species, however, visual cues play no role at all, as is exemplified by the total absence of eyes (Fig. 5B).
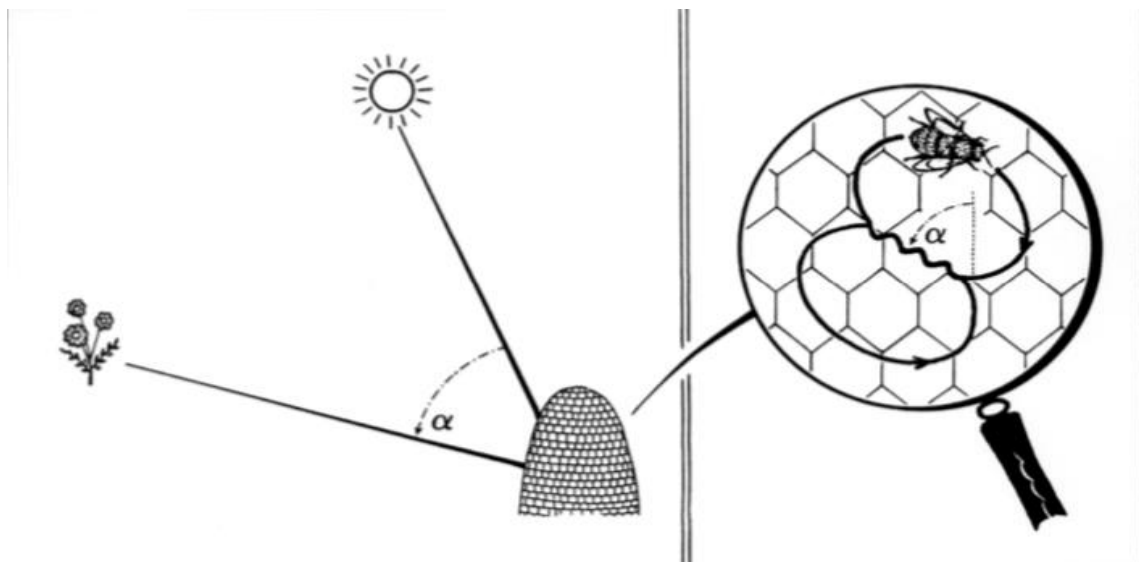
Figure 4. Schematical representation of the honeybee waggle dance, that contains information from the dancing bee towards its surrounding nest mates about the angle and distance to be flown between the nest and the discovered food source. The angle (α) between the sun and the position of the food source is the same angle as that of the central part of the dance figure with the vertical axis. The

distance is encoded in the frequency of performing the dance figure (the further the food source, the slower the dance).
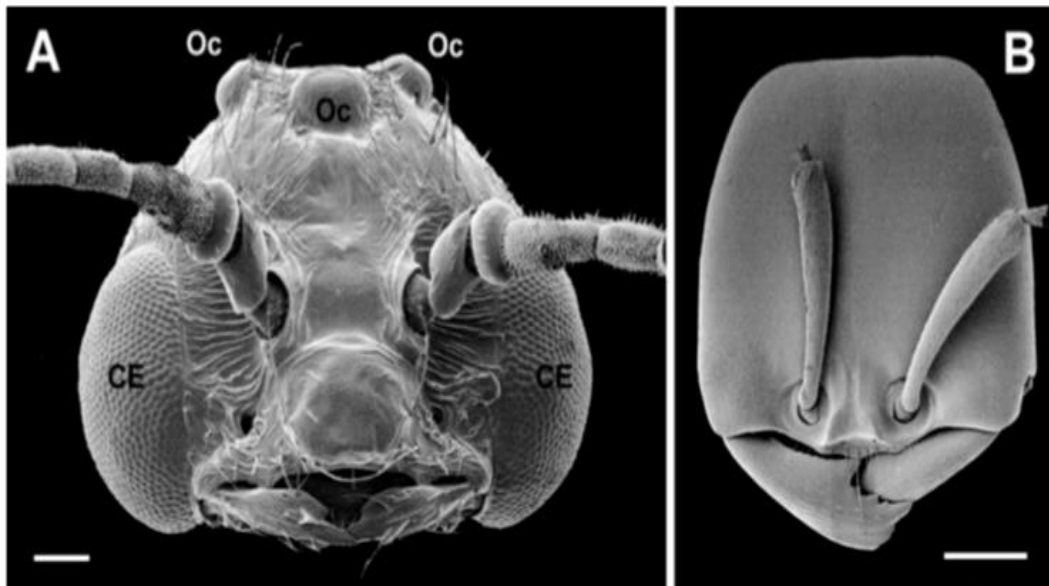

Figure 5. Scanning micrographs of the head in frontal view, showing the large compound eyes in a male of Solenopsis invicta (A, scale bar 100 μm), in contrast to the completely blind workers of Dorylus army ants (B, scale bar 500 μm). CE = compound eye, Oc = ocelli.

Acoustical communication in social insect

Stingless bees, by vibrating their wings and thoracic muscles, are equally known to produce sounds, that may be used to communicate information about distance and quality of food sources (Nieh ,2004). In the wingless termites (Röhrig et al., 1999) and ants, acoustic signals can be produced by knocking body parts onto the substrate (also known as drumming), and can elicit various behavioural responses (Hölldobler, 1999). Many ant species stridulate, which involves rapid movements of a scraper (situated at the posterior dorsal margin of the postpetiole) against a region with parallel ridges on the anterior surface of the first gastral tergite (Fig. 6). There is controversy, however, whether ant stridulatory signals are transmitted through the air (Hickling & Brown,

2000), or whether ants are deaf and detect acoustic signals through substrate- born vibrations (Roces & Tautz ,2001).
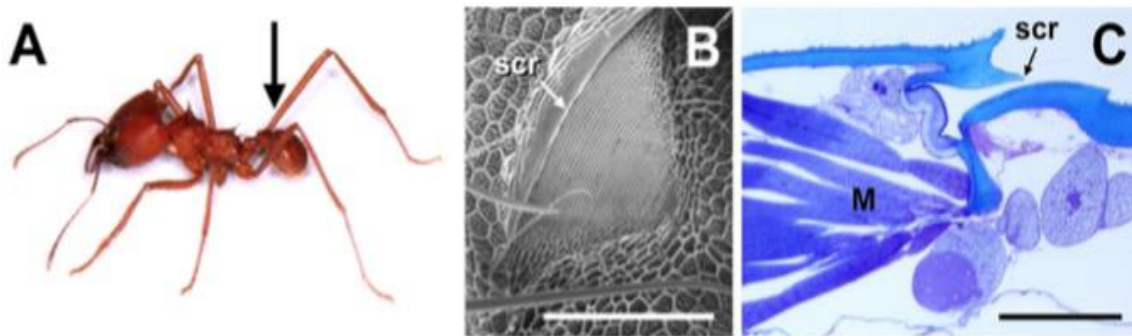
Figure 6. A. Worker of Atta sexdens rubropilosa, the arrow indicates the position of the stridulation apparatus. B. Scanning micrograph of the stridulation apparatus in a A. s. rubropilosa minor worker, showing the posterior dorsal margin of the postpetiolus functioning as a scraper (scr) and the triangular region with parallel ridges at the anteriodor- sal side of the first gastral segment (scale bar 100 μm). C. Longitudinal section through the junction between the postpetiolus and the first gastral segment of a A. s. rubropilosa worker. Note postpetiolar muscles (M) that cause up and down jerking of the gaster and hence sound production as the postpetiolar margin rubs over the ridges on the dorsal side of the gastral segment (scale bar 100 μm).

Tactile communication in social insect

Tactile contacts can form an important element in communication, although they are inevitably limited to interactions between two or just a few individuals. A very common example of tactile communication is found in the antennation and grooming between nest mates. Also the inter individual exchange of liquid material via trophallaxis (Fig. 7) is largely based on tactile interactions with mainly the antennae and the forelegs involved (Lenoir & Jaisson ,1982).

Figure 7. Tactile contacts with antennae and forelegs during trophallactic food exchange between workers of Vespula germanica (A) and Formica sanguinea (B) (wasps photograph by Dr. Tom Wenseleers).

Vibration communication

Vibrations and sounds, collectively called vibroacoustics, play significant roles in intracolony communication in termites, social wasps, ants, and social bees. Modalities of vibroacoustic signal production include stridulation, gross body movements, wing movements, high- frequency muscle contractions without wing movements, and scraping mandibles or tapping body parts on resonant substrates. Vibroacoustic signals are perceived primarily via Johnston's organs in the antennae and subgenual organs in the legs. Substrate vibrations predominate as vibroacoustic modalities, with only honey bees having been shown to be able to hear airborne sound. Vibroacoustic messages include alarm, recruitment, colony activation, larval provisioning cues, and food resource assessment (Richard and Hunt,2013).

Vibroacoustic communication occurs in social

Hymenoptera and is widespread in Isoptera(Cocroft and Rodrı guez, 2005). In some situations, such as alarm signaling in termites (Kirchner et al., 1994), substrate vibrations can disseminate information quickly, and vibrational behaviors are the major means of communication in Poloists paper wasps (Jeanne, 2009). In these and other cases among social insects, modalities of vibroacoustic communication are not a second-best substitute for chemical communication but instead have high adaptive value on their own merits. Accordingly, vibroacoustic communication is receiving increased attention for the important roles it plays in the lives of social insects (Casacci et al., 2013).

CONCLUSIONS

Seeing social insects as simple organisms that follow simple behavioural rules during communication processes has been fruitful, and improved our understanding of the collective organization of colony life. However, a closer look reveals that the behavioural strategies of insect workers are far from simple. In fact, they show a diverse range of sophisticated and flexible strategies in how they produce and use signals. The information individuals gain while interacting with their world strongly affects their motivation to communicate and to respond to communicated information, and indeed what information they attend to. Learning plays a major role in modulating many aspects of communication in social insects: signaler's learn what resources are worth advertising, when it is worthwhile to signal, and even learn to signal more accurately. Receivers use acquired information to decide when and whether to follow signals at all, and what type of signaller provided information to attend to.

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