

Communication in Social Insects

Sophisticated Problem Solving by Groups of Tiny-Brained Animals

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Abstract

Collective intelligence allows groups of individuals to solve problems which otherwise could not be solved by a single individual. Insect workers have tiny brains, but by functioning as part of a self-organized colony, they find sophisticated solutions to vital organizational problems (e.g., finding a suitable new home or exploiting the best food sources in a changing environment). In consensus decision making, unanimity among workers is crucial. In contrast, combined decision making requires that different groups of workers within the colony chose different options. Communication and learning are often fundamental in collective decision making. However, as workers gain experience, communication may lose importance as an information source for workers. How social insects collectively solve problems parallels decision making in other biological systems (e.g., neuronal networks), and investigation into social insect collective decision making has inspired new solutions to optimization problems in areas such as computer sciences and the organization of communication networks.

Introduction

Insect societies, like human societies, confront many organizational challenges. These include the collection and transport of resources (e.g., food or building material), the establishment and maintenance of transportation routes, the removal of waste materials, and the defense of colony resources. Over the last 100 years, an impressive number of communication signals have been identified that help organize these tasks in social insects. Most of these are chemical signals; however, tactile signals and, to a lesser degree, signals perceived

via the other sensory modalities, can also be important. The vast majority of the studied signals regulate recruitment activities, either to food sources, new nest sites, or sites of aggressive interactions with intruders (Hölldobler and Wilson 1990, 2009; Wilson 1971). During recruitment, workers communicate with other workers. Queen signals are important in regulating the reproductive division of labor (Winston 1987), whereas brood signals modulate division of labor among workers (Pankiw et al. 1998).

Work in insect societies is not centrally organized (e.g., by a leader giving orders); instead, self-organization is the process by which activities are regulated (Camazine et al. 2001). Each worker acquires and responds to information from the immediate environment, often by adhering to simple behavioral rules that have been shaped by natural selection. Individual insect workers may not have the cognitive capabilities of some of their vertebrate counterparts, but by functioning collectively in groups, they show an astonishing ability to solve organizational problems. The ability of a group to solve a problem in a way that goes beyond the capacities of individuals is often called *collective intelligence* (also referred to as collective cognition or swarm intelligence; Couzin 2009; Krause et al. 2010).

This chapter reviews recent progress in our understanding of the remarkable collective problem-solving abilities of social insects and the role of communication in decision making. In some cases, problem solving is largely based on the emission and response to a single signal, as in the case of the waggle-dance signal during nest-site selection in honeybees or trail selection in the black garden ant (*Lasius niger*). Others (e.g., the organization of a particular task) may involve multiple signals, such as the different pheromones in ant foraging (Dussutour et al. 2009; Jackson and Ratnieks 2006). Social cues (i.e., information provided inadvertently by other individuals) deliver further social information to help organize tasks (Detrain and Deneubourg 2009; O'Donnell and Bulova 2007). In honeybee foraging, at least six signals are thought to be involved in the organization of foraging (Anderson and Ratnieks 1999; Grüter and Farina 2009; Seeley 1998). However, the meaning of a signal is often not fixed but can be context dependent, and its usefulness varies with the experience of the receiver (Hölldobler 1999).

Communication and Collective Intelligence

Honeybee Nest-Site Selection

Nest-site selection in European honeybees (*Apis mellifera*) nicely illustrates how a group solves a problem that cannot be resolved by an individual worker. When a honeybee colony swarms, about 5,000–10,000 workers and a queen leave the hive and settle nearby in a cluster (Lindauer 1955; Seeley 2010). During the following hours or days, the bees explore their surroundings and

locate 10–30 potential new nest sites of varying quality (Lindauer 1955). Choosing a good nest site is important because the quality of the nest site affects the survival chances of the colony (Seeley 2010).

The swarm is able to solve this problem despite the fact that none of the few hundred scout bees involved in the decision-making process knows more than one or two of all the options (Seeley and Buhrman 1999). If a scout discovers a cavity that fulfils her innate preferences, she advertises her find through a waggle dance (Lindauer 1955). Originally studied in the context of foraging communication, the waggle dance (Figure 11.1) is a highly stereotyped dance-like behavior (von Frisch 1967). Karl von Frisch discovered that by means of dancing, foragers advertise the existence, odor, and location of a profitable food source to nest mates inside the hive (von Frisch 1967). Scouts perform waggle dances on the swarm cluster to (a) tell their nest mates the location of the nest site and (b) provide their opinion about the quality of the nest site. The better the quality, the longer a scout dances (Lindauer 1955; Seeley and Buhrman 2001; Seeley and Visscher 2008). Because scouts dance longer after finding a good nest site, they recruit additional bees, some of which will also perform waggle dances on the swarm after inspecting the cavity. As a consequence of this positive feedback, the amount of dancing for a very good cavity increases. At the same time, the number of dances for suboptimal cavities decreases (Seeley and Buhrman 1999) because individual scouts have an intrinsic tendency to cease dancing gradually (Seeley and Visscher 2008; Visscher 2007) and because the number of new recruits advertising the site is lower than the number of bees which discontinue dancing. In this way, groups of scouts advertise different locations until the number of scouts favoring one

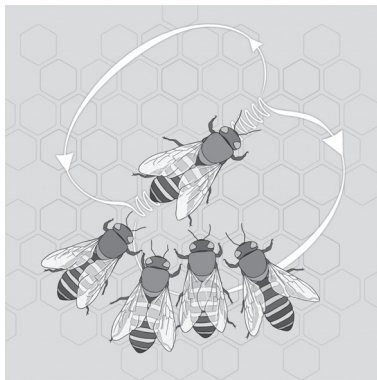


Figure 11.1 Depiction of a honeybee performing a waggle dance and four follower bees. The dancer performs a waggle run, then turns to one side, circles back to the starting point of the waggle run, then starts another waggle run and usually turns to the other side and so on. Some bees perform more than 100 waggle runs during one single dance. Dancers produce airborne sounds, create airflows, cause vibrations in the comb, and releases chemicals into the air. Followers often touch the dancer with their antennae. Illustration by N. Stadelmann; reprinted with permission from Grüter and Farina (2009).

particular site reaches a threshold or quorum. Once scouts sense that the critical number of scouts at the nest site has been reached, they initiate the next stage of house hunting (Seeley and Visscher 2004). These scouts start producing a piping sound which stimulates other bees on the swarm to warm up their flight muscles and prepare for lift-off (Seeley and Tautz 2001). Shortly before lift-off, scouts excitedly run on top of and between other bees on the swarm to announce that lift-off is imminent (Seeley 2010).

Foraging Trail Selection in Ants

Ant foragers provide another example of how groups of insects solve complicated problems. In a complex environment, such as the forest floor, it is usually impossible to locate a straight path between the nest and the food source. An ant colony (e.g., aphid-tending species like *Formica spp.* or *Lasius spp.*) will often visit the same food location for weeks or even months (Quinet and Pasteels 1996; Rosengren and Fortelius 1986; Salo and Rosengren 2001). Hence, to save energy and reduce exposure to predators, it is important to find the shortest of a large number of possible paths (Beckers et al. 1992), a challenge similar to a problem known in mathematics as the “traveling salesman problem.” Here, a salesman has to find the shortest path to visit N cities exactly one time. So, how do ants do it?

After discovering a sugar food source, foragers of the black garden ant (*L. niger*), like many other ants, lay a pheromone trail back to the nest to guide other foragers to the food source. A recruit following a pheromone trail has a tendency to choose a stronger trail if she has to choose between two paths at a bifurcation (Aron et al. 1993; Beckers et al. 1993; Deneubourg et al. 1990; Detrain and Deneubourg 2008). This trail asymmetry, where there is a stronger and a weaker pheromone trail option at a bifurcation, develops as follows: two foragers might start on the same path but by chance use two different paths of unequal length around an obstacle to get to the food source (Beckers et al. 1992; Camazine et al. 2001) (Figure 11.2a). The ant using the shorter path will make more trips to the food source per unit time and thus more pheromone will accumulate on the shorter section of the path around the obstacle (Figure 11.2b). Recruited ants walking toward the food source are likely to choose the path with more pheromone when they reach the bifurcation caused by the obstacle. This positive feedback mechanism will amplify small initial differences between options and lead to a collective choice of the shorter branch (Beckers et al. 1992; Couzin 2009; Camazine et al. 2001). Again, the ability of the colony to select the best option does not depend on individuals knowing all the options and making direct comparisons between them. The choice in this type of experiment is never unanimous, as in nest-site selection, but it often leads to >80% of all ants converging on the best option. How ants solve the problem of finding the shortest path has inspired a new solution to the traveling salesman problem: the ant colony optimization algorithm (Dorigo and Stützle 2004).

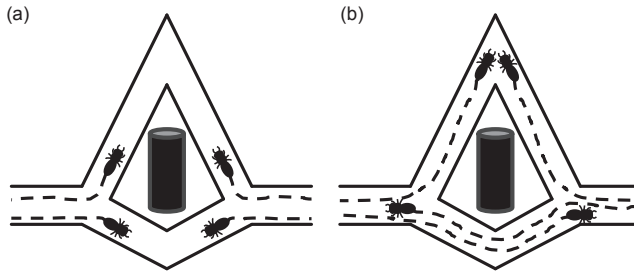


Figure 11.2 Selection of the shorter path by ants. (a) Ants laying pheromone trails to and from the food source walk on two paths of different lengths around an obstacle. (b) The shorter distance of one branch leads to a faster accumulation of pheromone on the branch. As a consequence, more ants choose the shorter branch when reaching the decision point (after Beckers et al. 1992).

Integration of Multiple Information Sources

Multiple Information Sources Used in Territorial Tournaments

Consensus decision making can involve rather complex communication processes. Perhaps the most spectacular example of how groups of insects integrate multiple information sources comes from territorial tournaments of the honey ant *Myrmecocystus mimicus*. Here, mutualistic intra-colony and manipulative inter-colony communication leads to a group decision (Hölldobler 1976b; Hölldobler and Wilson 2009).

Colonies of *M. mimicus* defend their territories aggressively against conspecific intruders. If conflicts between two colonies occur, a few hundred ants are recruited by chemical signals to the tournament site where they display their fighting abilities to the opponent side through stereotyped aggressive displays (Hölldobler 1976a; Hölldobler and Wilson 2009). During the display, an ant tries to appear as big as possible to “impress” its opponent. Usually the smaller ant yields and walks away. To appear bigger, ants walk on stilted legs and raise their head and abdomen. Ants also inflate their abdomen to make it bigger. Some of the ants use an additional bluff and mount small stones to appear larger (Hölldobler and Wilson 2009). During the display, ants drum their opponent with their antennae and kick their legs against the opponent. The function of this behavior is not known. A contest lasts only a few seconds, after which the ants search for a new opponent and the procedure is repeated.

Two methods appear to be involved in reaching a group decision about which side wins: head counting and caste polling (Hölldobler and Wilson 2009). Small colonies seem to rely mostly on caste polling, in which by some unknown mechanism the ants are able to estimate the proportion of majors (large workers, sometimes called soldiers) among the ants in the tournament. The proportion of majors provides information about colony size, and combatants from smaller colonies usually retreat quickly into the nest when facing a

side with a large proportion of majors (Hölldobler and Wilson 2009). If both colonies are large, head counting provides additional information. Here, a specialized group of smaller ants, the “reconnaissance ants,” gathers information about the number of ants on the opposing side. They move through the tournament site and experience many short contacts with both nest mates and opponents. If necessary, these ants also recruit more combatants to the tournament site by laying pheromone trails.

The options for each side are either a collective retreat, a continuation of the tournament, or an escalated attack which can lead to the enslavement of the weaker colony. Many aspects of the group decision process are not yet understood; for example, how reconnaissance ants estimate the relative strength of both sides and how they induce a collective response. However, it seems clear that different types of information are involved in the consensus decision-making process.

Multiple Pheromones on Foraging Trail Systems

The previous examples demonstrate how consensus decision making results in a group converging on one solution. Unanimity, for example when choosing a new home, is crucial for the survival success of the group (Visscher 2007; Seeley 2010). However, there is no single optimal solution when it comes to sending foragers to different food sources because colonies need to exploit many food sources at the same time, and because the quality and location of the food source changes with time (Seeley 1995). Often, individuals must integrate more than one information source to make adaptive decisions in such a dynamic environment. In recent years, research has uncovered multiple pheromones on foraging trails. Pharaoh’s ants (*Monomorium pharaonis*) use at least three different trail pheromones to organize their foraging activities (Jackson and Ratnieks 2006; Robinson et al. 2008; Robinson et al. 2005). While two attractive pheromones guide foragers along the entire trail, one repellent pheromone directs foragers away from unprofitable trails at bifurcations (Ratnieks 2008; Robinson et al. 2008; Robinson et al. 2005). Having such a “no entry” signal for unrewarding branches is likely to increase foraging efficiency (Stickland et al. 1999), but why have two different attractive pheromones? These two pheromones operate at different timescales: one is short-lived (minutes), the other lasts longer (days) (Jackson et al. 2006; Robinson et al. 2008). These different timescales provide foragers, who might otherwise not rely strongly on route memories, a kind of long- and short-term “memory” of good food sources (Dussutour et al. 2009; Ratnieks 2008). The short-lived pheromone helps colonies to respond quickly to changes, such as the sudden appearance of a food source, whereas the long-lived pheromone increases the chances of rediscovering food sources that were rewarding in the past after temporal unavailability (Dussutour et al. 2009; Ratnieks 2008).

Multicomponent Signals

The availability of multiple information sources may be separated in time and space, as in the case of trail pheromones in Pharaoh's ants, or they may be provided during the production of a single signal. Multicomponent signals simultaneously provide more than one type of information (Bradbury and Vehrencamp 1998; Partan and Marler 1999, 2005; Rowe 1999). Here, the term *multicomponent signal* refers to all communicative components of the animal's behavior that occur simultaneously (Partan and Marler 2005). The honey ant walking on stilted legs and simultaneously drumming her opponent with her antenna is a good candidate. Pheromone blends consisting of different chemical compounds, each having an effect on receiver behavior, are another example (Hölldobler 1995, 1999). Perhaps the best-known example, and one of the most complex communication behaviors in the animal world, is the honeybee waggle dance (Grüter and Farina 2009; von Frisch 1967) (Figure 11.1).

A dancing bee provides various types of information to surrounding bees. First, a dancer attracts and excites other bees and primes them to receive more information. This is probably best described as a modulatory component, increasing the motivation of surrounding bees to receive more information. Some bees will start following the movements of the dancer (Figure 11.1). A dancer also provides olfactory information: odor cues that cling to the dancer's body and are released into the air during dance maneuvers as well as odor cues present in regurgitated nectar samples, which are offered to a follower. Olfactory cues can affect the behavior of surrounding bees even if they do not physically come into contact with the dancer (Grüter and Farina 2009; Thom et al. 2007; von Frisch 1923). Food odors present on the nectar and on the forager's body indicate the type of food source the dancer has visited. Dance followers learn these odors and use this olfactory information to locate the advertised food source in the field (Farina et al. 2005; von Frisch 1967; Wenner et al. 1969). In addition, dancers also release hydrocarbons (*Z*-(9)-tricosene, tricosane, *Z*-(9)-pentacosene, and pentacosane). These chemicals seem to induce foraging behavior in bees that perceive them inside the hive (Thom et al. 2007). Two other components of the waggle-dance signal provide information about the location of the visited food source: distance and direction. Distance is encoded in the duration of the waggle phase (von Frisch 1967). The body orientation relative to gravity provides dance followers with information about the direction of the food source relative to the position of the sun (von Frisch 1967). It is still not clear which sensory modalities are involved in the decoding of the location components (Dyer 2002; Michelsen 2003). Candidates include airborne sounds, air flows produced by the wings, vibrations of the substrate, or tactile signals detected when the antennae touch the body of the dancer (for a discussion, see Dyer 2002; Michelsen 2003).

Communication and Social Learning

Learning by copying or interacting with other individuals (i.e., social learning) is common in social insects (Leadbeater and Chittka 2007, 2009). The close proximity of many workers in the nest or during the performance of collective tasks leads to many opportunities for social learning. Communication between workers, however, often does not require learning by the animals that respond to the signal. For example, there is no evidence that Pharaoh's ants learn about food locations when they follow pheromone trails (Ratnieks 2008). Similarly, the responses of insect workers to alarm pheromones of nest mates in the presence of intruders, or the response of workers to queen or brood pheromones does not seem to involve any learning.

If, however, the appropriate response to a signal is unpredictable because of environmental changes, social learning can help colonies respond adaptively to these changes. Accordingly, studies have shown that certain levels of environmental instability favor social learning versus innate responses or asocial learning (Laland et al. 1996; Rendell et al. 2010). The foraging environment of social insect colonies, for example, often changes, and social learning of currently rewarding food locations or food types is common (Leadbeater and Chittka 2007, 2009). Honeybee foragers learn about good food sources by following waggle dancers. Ants of many species follow pheromone trails while walking to a food source (Hölldobler and Wilson 1990). While pheromones guide the initial trips, ants learn about the features of the food location and the route to and from it and use these memories during later foraging trips (Collet and Collet 2002; Rosengren and Fortelius 1986; Salo and Rosengren 2001).

Another example of social learning, tandem running (Figure 11.3a), has been considered an example of teaching (Franks and Richardson 2006; cf. Leadbeater et al. 2006). During tandem running, an ant that has found a food

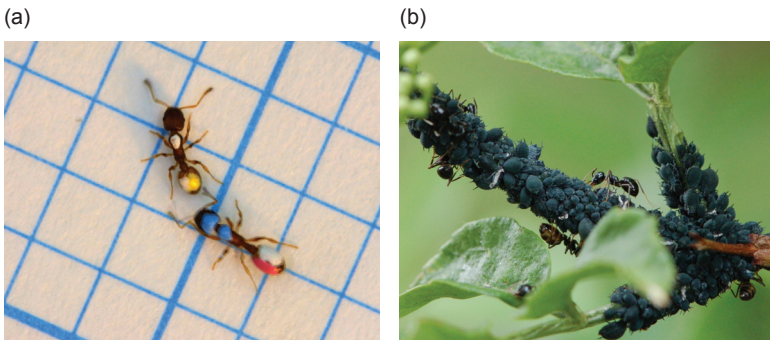


Figure 11.3 (a) Tandem running in the ant species *Temnothorax albipennis*. The ant with the blue paint marks, the pupil, closely follows the recruiting ant, the teacher, to a resource (photo by Tom Richardson). (b) Foragers of the ant *Lasius fuliginosus* collecting honeydew secreted by aphids. Foragers visit the same foraging locations for several months (photos by Christoph Grüter).

source guides one recruit from the nest to the food. The recruit follows by keeping antennal contact with the leader (Hölldobler and Wilson 1990). The leading ant is considered the “teacher” because she (a) modifies her behavior in the presence of the follower, (b) incurs time costs while doing so, and (c) helps the “pupil” to learn more quickly (Caro and Hauser 1992; Franks and Richardson 2006). The honeybee waggle dance is another candidate behavior which may fulfill these criteria. However, although there is clear evidence that the latter two criteria are fulfilled, the first criterion has not yet been experimentally demonstrated.

Traditions in Social Insects

Behavioral traditions are thought to be one of the foundations of culture, and it is thus understandable that research has not paid much attention to social insects when looking for examples of traditions. However, some behaviors warrant closer inspection.

Traditions can be defined as group-specific behavioral patterns that are socially transmitted from one generation to the next (Laland and Janik 2006; Leadbeater and Chittka 2007). Many social insects forage at the same food locations for weeks, months, or even years (Quinet and Pasteels 1996; Salo and Rosengren 2001) (Figure 11.3b). The ant *F. uralensis* visits very stable aphid clusters for long periods of time (Salo and Rosengren 2001). During winter, when foraging is impossible, foragers retain information about these locations, revisit them in spring, and recruit new foragers to the location. Hence, older foragers of a colony socially transmit the information about good food locations to new foragers from one year to the next (Salo and Rosengren 2001).

Another example, discussed in Leadbeater and Chittka (2007), is the social transmission of temporal foraging activities in honeybees. There is evidence that honeybee brood in cells learn about the time of peak foraging, possibly via vibrations on the comb caused by dancing, and later prefer to forage at the same time when they become foragers some 3–4 weeks later. Both examples show that one can find socially transmitted behaviors, performed beyond individual life spans, in groups of tiny-brained animals.

Communication and Memory

As workers perform a task, they often acquire information that affects the way they subsequently perform that task. Foragers, for example, can acquire route memories during foraging. On the way to the food source and back, they learn landmarks, colors and odors of food sources, how to handle them, and the timing of food abundance (von Frisch 1967). After only three visits, honeybee foragers remember the features of a food source for the rest of their life (Giurfa 2007; R. Menzel 1999). Hence, an experienced forager leaving the

nest can either use communicated information from nest mates (social information) to find a food source or rely on memory (private information) about known food source locations. Experienced foragers frequently pay attention to dances (Biesmeijer and Seeley 2005; Grüter et al. 2008) and may, therefore, even encounter situations where social information and private information are in conflict. Sometimes these dances indicate an unknown location but carry an odor that the follower bee knows from past foraging trips to a different food location. Here, the follower experiences a conflict between the indicated vector and the memorized route linked to this odor (Grüter et al. 2008). This can be a common situation when a colony exploits multiple patches of the same plant species. In this situation, honeybees seem overwhelmingly to prefer their memory over the communicated information, if the food sources are close to the nest and of high quality (Grüter et al. 2008; Grüter and Farina 2009).

Ant foragers face similar choices between social information, such as a chemical trail and private information. In many ant species, the foraging trail network of a colony has a binary tree structure (Stickland et al. 1999). Ants that found food at the end of a branch with little or no pheromone face a conflict between the pheromone information and their route memory at bifurcations when the alternative branch is marked with more pheromone. As with the honeybee, memories seem to override the pheromone trail in a number of species (Grüter et al. 2011; Harrison et al. 1989; Klotz 1987; Salo and Rosengren 2001; Traniello 1989; but see Aron et al. 1993; Hölldobler 1976a). In the ant *L. niger*, memory overrides social information at bifurcations after one single foraging trip (Grüter et al. 2011). Relying on memory as an information source during foraging makes sense if foragers learn and retrieve information depending on the quality of the food source. Indeed, there is good evidence that the use of memory to locate food depends on the quality of the reward. In both wasps and bees, foragers are more attached to their food source if the quality of the experienced reward was high (Greggers and Menzel 1993; Jeanne and Taylor 2009; Ribbands 1949). However, it is likely that other circumstances favor the use of communicated information. If private information is outdated, unreliable, or associated with high costs (e.g., due to the distance between the food source and the nest), then communicated information might become more important (Kendal et al. 2005; Laland 2004).

Similarities between Insect Colonies and Neuronal Systems

Research in recent years has uncovered similarities in consensus decision-making processes of very different biological systems, such as insect colonies and neuronal systems (Couzin 2009; Marshall et al. 2009; Seeley 2010; Visscher 2007). Both social insects and brains face the problem of choosing among various options based on information that is distributed across many subpopulations, each with only limited information. In both types of systems,

separate populations (workers in insect colonies or neurons in brains) accumulate evidence for alternative choices. In visual information processing in monkey brains, for example, different groups of neurons report information about a visual stimulus present in a small part of the visual field (Marshall et al. 2009): the stronger the stimulus, the more active the neurons. As soon as one population reaches a threshold, a decision is made for the corresponding option (e.g., moving the eye in a certain direction). In both systems, these neuron populations may be arranged in a way that leads to cross-inhibition, where the activation of one population suppresses the activity of the others (Marshall et al. 2009; Visscher 2007). In honeybee swarms, the inhibition is the removal of recruits from the recruit pool by recruitment in another group. In both honeybee swarms and neuronal systems, cross-inhibition between populations helps to sharpen the differences in signal strength between the different options (Seeley 2010; Visscher 2007).

Conclusions

By functioning in self-organized groups, insect workers are capable of solving complex problems. Communication is one of the key tools that enable colonies to solve organizational problems. In some situations, unanimity is crucial. House-hunting insects have to reach a consensus; otherwise, the colony may be unable to move to a safe home. In other situations, a colony needs to choose numerous different options simultaneously, such as the successful allocation of foragers to various food patches in foraging. This is an ongoing challenge because the foraging environment can change on a daily basis. Hence, collective decision making occurs between two extremes: consensus decision making leads to all animals of a group doing the same thing, whereas combined decision making means that each individual chooses its own option. Indeed, some decision-making processes result in a mix of consensus and combined decision making, all resulting in the creation of adaptive solutions for complex problems.