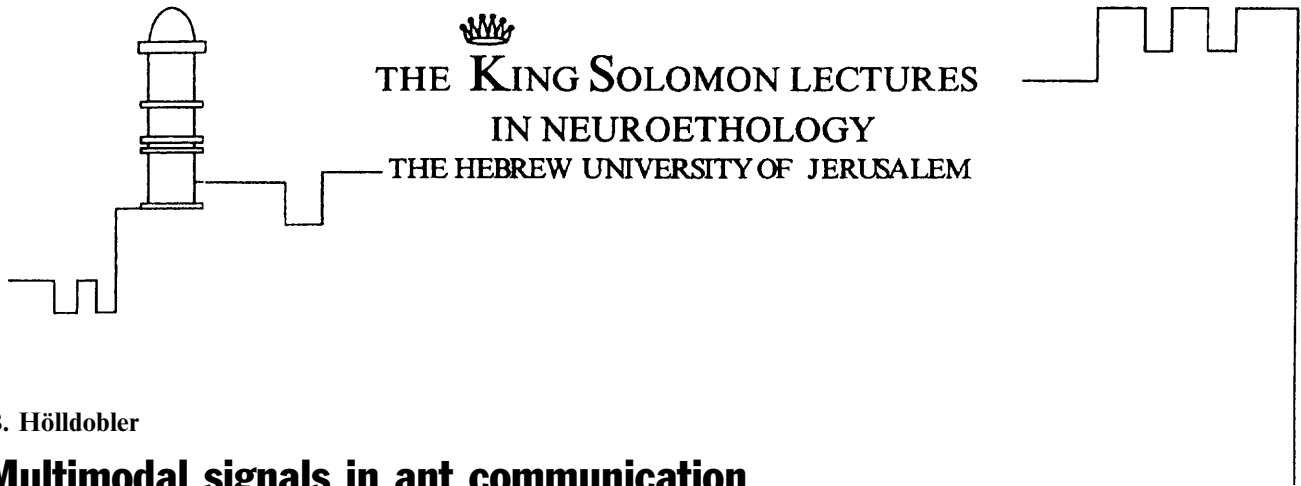


## REVIEW



B. Hölldobler

## Multimodal signals in ant communication

Accepted: 5 December 1998

### Introduction

Communication is one of the central features of life. Mutually beneficial interactions of organelles, cells, organs, organisms and societies, depend on communication. But communication does not have to be exclusively mutualistic, it can be manipulative and even exploitative, whereby the gain is skewed to the side of the signal sender or, in a few cases, to the receivers side (Markl 1985). In the social insects we find excellent examples for all these nuances of communicative interactions. Communication in the social insects, and particularly in the ants, is based mainly on chemical signals, but nevertheless the modes of communication in ants are very diverse. We have only begun to fully appreciate the complexity of the ants' communication mechanisms.

In the early stages of the study of chemical communication in animals, scientists assumed that in insects behavioral responses are released by single chemical substances, whereas in vertebrates and particularly in mammals, chemical signals are complex blends of substances, mediating inter-individual recognition and

interactions. However, most insect semiochemicals, have proven to consist of several compounds, whereby different components of a complex pheromone mixture may have different effects on the receiver (e.g. Bradshaw et al. 1979; Morgan 1984; Hölldobler and Carlin 1987; Hölldobler and Wilson 1990; Hölldobler 1995). Thus, with respect to the sophistication of their chemical communication systems, vertebrates and insects do not differ greatly.

It is also well known, and studied in several vertebrate groups, that communication can work through several sensory channels; that is, a signal can be composed of distinct physical components, transmitted simultaneously or in tightly paced sequence. Such cross-modal perception of composite signals has been investigated particularly well in humans and non-human primates and in birds (e.g. Kuhl and Meltzoff 1982; Kuhl 1983, 1989; Hauser 1996; Partan 1998), and, in fact, already was recognized by Darwin in his book *The expression of the emotions in man and animals* (1872) where he noted that the power of communication by language is much enhanced by "the expressive movements of the face and body".

Multimodal signals are less well studied in the invertebrates. The paragon example is the recruitment communication in honeybees, where the information about distance, location and quality of a food source is

B. Hölldobler  
Theodor Boveri Institut (Zoologie II), Biozentrum,  
Am Hubland, D-97074 Würzburg, Germany

transmitted through four or five sensory modalities: auditory, vibrational, tactile, olfactory and gustatory (von Frisch 1965; Michelsen 1993; Seeley 1995; Kirchner and Grasser 1998; Tautz and Rohrseitz 1998). The so-called “dance language” of the honeybees is also one of the best known cases of information transfer about the external environment; in a sense it exhibits the property of displacement, a feature attributed by some scientists only to human language (Hockett 1960). Though the dance-communication of the honeybees is clearly unique in its complexity of cross-modal integration, we find multimodal signals in many other forms of communication in social insects, and particularly in the ants (Hölldobler and Wilson 1990). In addition to the multicomponent chemical signals, there exist the knocking, stridulation, stroking, jerking, wagging, grasping, and antennations, all of which have been observed to occur during communication behavior in ants, but in the past they have been mostly considered relatively unimportant in affecting the receivers’ behavior. One of the first scientists who recognized the significance of such behavioral patterns in the context of recruitment communication in ants was the late Raja Szlep-Fessel from the Hebrew-University, who studied the role of motor-displays in *Monomorium*, *Tapinoma*, and *Pheidole* ants (Szlep and Jacobi 1967; Szlep-Fessel 1970).

I am very pleased that it is the King Solomon Lectures that occasioned this paper, in which I will report research that in part is rooted in the early discoveries by Raja Szlep-Fessel.

**Key words** Pheromone · Vibrational signals · Chemical communication · Recruitment · Social insects

---

### **Substrate-borne vibrations: modulatory signals in chemical communication**

Smith (1977) distinguishes two kinds of multimodal signals: “fixed composite signals” in which the signal components are transmitted simultaneously, and “fluid composite signals” in which the emissions of the various components are separated in time. Both types occur in ant communication. But more important than the timing of the production of the signal components is temporal pattern of their perception by the addressees. A multimodal signal can be a “fixed composite signal” on the signaler’s side and can become a “fluid composite signal” on the receiver’s side, because different components of multimodal signals are broadcast with different speeds. An excellent example of such a case is the multimodal alarm communication in carpenter ants (*Camponotus*).

Workers of *C. herculeanus*, *C. ligniperdus* and several other *Camponotus* species strike the surface of the wooden chambers and galleries in which they live with their mandibles and gasters, producing vibrations that can be perceived by nest mates for 20 cm and more.

Much of the behavior is classified as direct alarm communication; however, Markl and Fuchs (1972) and Fuchs (1976) showed that the drumming alters other behavioral responses as well. Certain behavioral categories are “tightened up”, and for others transitional probabilities are raised, and hence uncertainty reduced, if the ant is in a particular initial state when the signal is received. The vibrational signal produced by knocking thus appears to be a modulatory signal. Such signals do not always merely release behavioral responses of a particular kind, but instead often appear to adjust the behavior of nest mates toward one another in a manner appropriate to the surrounding environment (Markl 1983, 1985; Hölldobler 1984). According to this interpretation, outwardly inefficient communication systems serve different, but no less important, purposes than more direct deterministic systems. They influence the behavior of receivers, not by forcing them into narrowly defined behavioral channels but by slightly shifting the probabilities of the performance of other behavioral acts. Modulatory signals alter the probability of reactions to other stimuli by influencing the motivational state of the receiver.

Recently we have focused again on the drumming or knocking behavior in *Camponotus* and found that a majority of ants receiving the vibrational signal reacted by standing still. When we exposed ants to their alarm pheromone, undecane, a significantly larger number reacted with aggressive behavior if they have been exposed to the drumming signal shortly before (U. Raub, J. Tautz, B. Hölldobler, unpublished observations). We also found that the vibrational signal travels faster in the wooden chamber system than the chemical signal. In an alarm situation the alerting vibrational signal has a wider active space than the chemical releaser. However, when combined with the vibrational signal, the chemical signal may have a wider effective reach than when emitted alone, because the ants’ response-threshold for the pheromone is lowered. The drumming signal alone hardly elicits aggressive behavior in the recipients but obviously tunes the ants to be more responsive to the comparatively slow-traveling chemical releaser.

A very different form of modulatory communication in ants was discovered in the short-range recruitment process of *Aphaenogaster albisetosus* and *A. cockerelli* (Hölldobler et al. 1978; Markl and Hölldobler 1978). These ants of the North American southwestern deserts are adept at retrieving large prey objects, such as dead insects, within short periods of time. After discovering an object too large to be carried or dragged by a single ant, a scout worker discharges poison gland secretion into the air. The main recruitment component in the poison gland contents of *A. albisetosus* is 4-methyl-3-heptanone, and that of *A. cockerelli* is (R)-(+)-1-phenylethanol (Hölldobler et al. 1996). Nestmates as far away as 2 m are attracted by these respective pheromones and move toward the source. When a sufficient number of foragers has assembled around the prey, they jointly carry it swiftly to the nest. Time is of the essence,

because the *Aphaenogaster* must remove the food before formidable ant competitors, including fire ants (*Solenopsis*), *Monomorium* sp. and *Forelius pruinosum*, arrive in large numbers on the scene. *Aphaenogaster* workers, in addition to releasing the poison gland pheromone, also regularly stridulate. Once the foragers encounter the vibration, they remain in the vicinity for up to twice as long as when no stridulation occurs. Ants perceiving the signals also start to encircle the prey sooner, and they are likely to release the attractive poison gland pheromone earlier. Overall, both the recruitment of workers and the retrieval of the food object are advanced by 1–2 min as a consequence of stridulation. The vibration thus serves as a communication amplifier in this particular circumstance, conferring a considerable advantage on the *Aphaenogaster*, who must race to acquire food in the highly competitive desert environment.

A similar link of stridulation to the recruitment process has been noted in the European harvesting ant genus *Messor*, which employs stridulatory vibrations in conjunction with odor trails laid with secretions from the Dufour's gland (Hahn and Maschwitz 1985; Buser et al. 1987). Baroni-Urbani et al. (1988) provided experimental evidence for the enhancement of the recruitment communication by substrate-borne stridulatory vibrations in *Messor*, but neither in *Aphaenogaster* nor in *Messor* has it been shown that stridulatory signals alone elicit a recruitment response in the recipient ants. In these cases the substrate-borne vibrations are part of a multimodal signal lowering the response threshold of the receiver for the releasing component of the signal. A recruitment response appears to be elicited by only one component of the multimodal signal.

---

### Context-specific response to signals

This situation is different in the multimodal communication system of leaf cutting ants of the genus *Atta*.

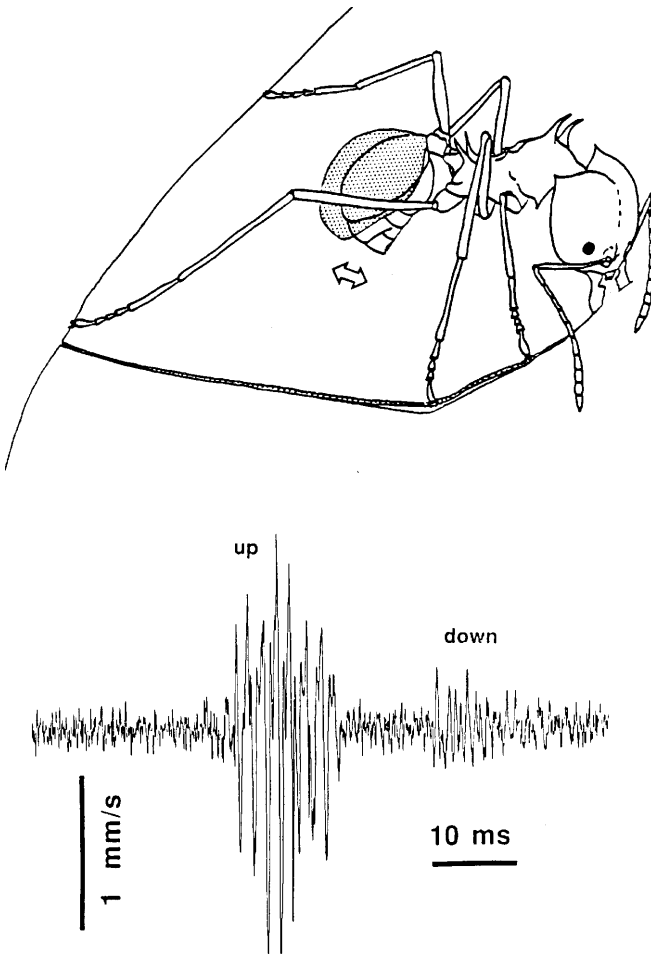
Markl (1967, 1983) discovered that in *Atta* workers substrate-borne stridulatory signals can release specific behavioral responses in the recipient nest mates, but the semantic contents, i.e., the message signaled by the sender and the meaning of the signal for the receiver (Smith 1977), can vary according to the situational context. For example, *Atta* workers produce an alarm pheromone (4-methyl-3-heptanone) in the mandibular glands (Moser et al. 1968). The effect of this chemical alarm signal can be enhanced when combined with stridulatory vibrations. Indeed, ants held by an enemy ant or by a pair of forceps release the alarm pheromone and simultaneously stridulate. *Atta* workers also stridulate when trapped under soil, for example after a partial cave-in of the nest. Markl discovered that in such situations the ants are attracted to the source of the substrate-borne vibrations alone and start digging until the stridulating nest mate has been freed. Interestingly, however, not all workers responded equally well in this rescue situation: the soldier caste exhibited very little

response, but workers that were occupied with digging and soil transport inside the nest, responded best. Although alarm and rescue signals are multimodal signals in the leaf-cutting ants, the workers respond to both components when presented separately.

The significance of context for modifying the message-meaning relationship in communication of leaf-cutting ants became particularly clear by our recent discovery that stridulatory vibrations can also function as close-range recruitment signals during foraging (Roces et al. 1993; Rocés and Hölldobler 1996). It is well known that foragers of leaf-cutting ants cut vegetation into small fragments which they transport to the nest where the material is processed by the ant colony's fungal garden (Hölldobler and Wilson 1990). In addition to the well-developed chemical communication system (Jaffé and Howse 1979), leaf-cutting ants also use mechanical signals during recruitment communication. Workers of *Atta cephalotes* stridulate during the cutting of leaf fragments. The cuticular vibrations produced by the stridulatory organ extend along the body and travel through the workers' head into the leaf being cut. We recorded the stridulation signals by means of noninvasive laser-Doppler vibrometry. The substrate-borne vibrations consisted of long series of repetitive pulse trains (chirps), each pulse resulting from the impact of the scraper on a ridge of the file of the stridulation organ. The signal repetition rate varied between 2 and 20 chirps per second. Typical wave forms recorded from the leaf being cut are presented in Fig. 1. The temporal pattern of the recorded chirps does not differ from that previously observed during alarm vibrations in the same species (Markl 1983). It has been demonstrated that nearby workers respond to these stridulatory vibrations transmitted along the twig by orienting toward the source of the vibrations, even in the absence of chemical signals, so that stridulation acts as a short-range recruitment signal (Roces et al. 1993).

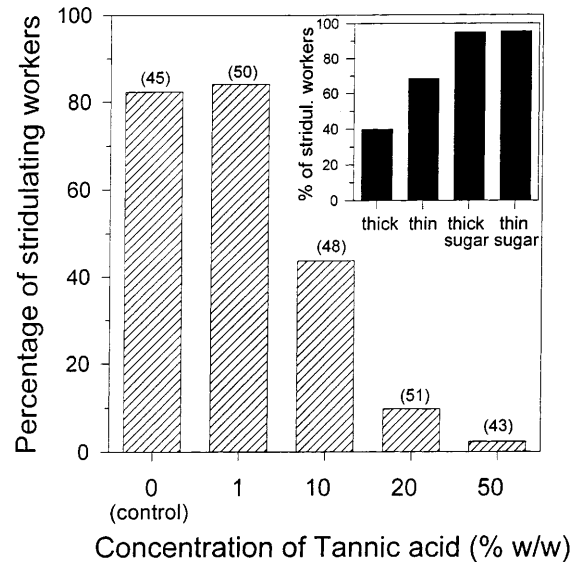
How does the stridulatory signal component interact with the chemical recruitment component? The ants respond to both components when presented to them separately. When the stridulatory and the chemical components were tested against each other in a choice experiment, the chemical component was always significantly preferred. However, in another set of experiments, where the ants could choose between the multimodal signal (chemical plus vibrational components) and chemical component alone, the ants significantly chose the multimodal signal (F. Rocés and B. Hölldobler, unpublished observations). In the natural situation at the foraging site, the vibrational component appears to be superimposed on the global (wide-range) chemical recruitment signal and thus fine-tunes the ants' close-range recruitment response.

Next we investigated how far these vibrational recruitments can be graded, as known from chemical signals. In leaf-cutting ants, for instance, the individual chemical recruitment behavior of workers changes in relation to food quality (Roces and Nuñez 1993). We



**Fig. 1** Schematical illustration of an *Atta* worker cutting a leaf and simultaneously stridulating by moving the gaster up and down (courtesy F. Rocés). Stridulation signals produced by an *Atta cephalotes* worker, recorded by laser-Doppler vibrometry on the leaf being cut (as velocity of the leaf's vibration). Measurements performed 20 mm away from the cutting site (from Rocés et al. 1993)

therefore asked whether the probability of stridulation is related to the quality of the leaf being cut. To answer this question, we presented ants with leaves of different qualities, and recorded the proportion of workers that stridulated during the cutting activity. We compared tender leaves with tough leaves of *Ligustrum vulgaris*, or we made tough leaves attractive by coating them with sugar solution, or we offered increasingly less palatable leaves by coating them with different concentrations of an aqueous solution of tannic acid. The results were very clear: the percentage of *A. cephalotes* workers that stridulated strongly depended on the quality or attractiveness of the leaf. Significantly more ants stridulated when cutting tender or sugar-coated leaves in comparison to tough leaves. While most workers stridulated when cutting untreated tender leaves, or leaves coated with 1% solution of tannic acid, only 2% of the foragers stridulated when cutting leaves coated with 50% tannic acid solution (Fig. 2; Rocés et al. 1993; Rocés and Hölldobler 1996).



**Fig. 2** Percentage of *Atta cephalotes* workers that stridulated while cutting tender leaves of *Ligustrum vulgaris* previously coated with different concentrations of an aqueous solution of tannic acid. In parenthesis: total number of ants observed. Inset: percentage of *A. cephalotes* workers that stridulated while cutting leaves of different toughness, and the same kind of leaves coated with 20% sugar solution (from Rocés et al. 1993 and Rocés and Hölldobler 1996)

The message-meaning relationship of stridulatory vibrations in *A. cephalotes* can be still different in yet another context. In foraging columns of the leaf-cutting ants, minim workers (the smallest worker subcaste) “hitchhike” on leaf fragments being carried by larger workers (Fig. 3). It has been demonstrated that they defend leaf carriers against parasitic phorid flies (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990). We investigated the cues used by the potential hitchhikers to locate leaf carriers and found evidence that stridulatory vibrations transmitted by the leaf carrier attracts the minim workers (Rocés and Hölldobler 1995). What is our evidence?

Firstly, we noted a significant increase in the repetition rate of stridulations produced by workers engaged in cutting as they maneuvered the leaf fragment into a carrying position and returned laden to the nest. Even workers which did not stridulate during cutting were observed to stridulate as they loaded up the fragment. This is the moment when hitchhiking usually commences, even though it is a dynamic process that is also observed along foraging trails (Feener and Moss 1990). The leaf-borne vibrations, transmitted through the workers' legs, were considerably attenuated. Their amplitude, ca.  $2 \times 10^{-6}$  cm, lies near the sensitivity threshold measured electrophysiologically in leg nerves of *Atta* workers ( $1.3 \times 10^{-7}$  cm in forelegs of minor workers, Markl 1970), which make possible the detection of the signals up to a maximum distance of 2–3 cm. For comparison, stridulatory vibrations transmitted through the mandibles during cutting are much more intense and can be perceived at 10–20 cm or more from

**Fig. 3** Minim workers of *A. cephalotes* hitchhiking on a fragment carried by a forager along a foraging column (from Rocés and Hölldobler 1995)



the source (Rocés et al. 1993). Although minims are on average three to four times more sensitive to substrate-borne vibrations than large workers (Markl 1970), vibrations transmitted through the leaf carrier's legs can be effective only in the immediate vicinity of the stridulating ant.

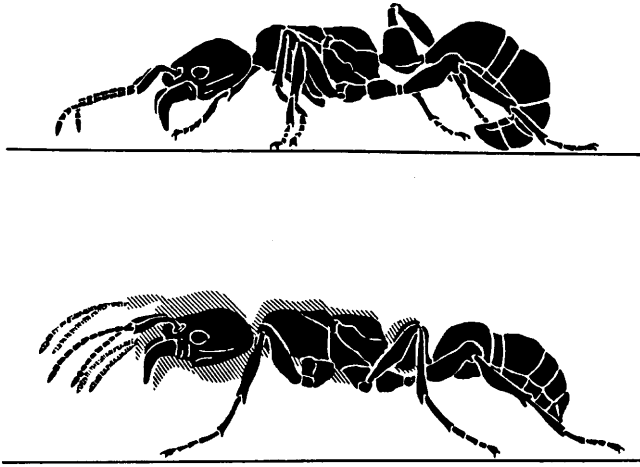
Secondly, we observed that minims, roaming around, are attracted to leaf-borne stridulatory vibrations. In an experimental situation they spent a significantly longer time on an artificially "stridulating" than on the "silent" leaf, even in the absence of cutting workers.

Thirdly, the occurrence of hitchhikers was significantly higher in leaf carriers foraging on leaves that were experimentally made to vibrate continuously, even though the number of workers engaged in cutting was roughly similar for both the "stridulating" and the "silent" leaves. Thus, the increased occurrence of hitchhiking is not the result of a higher number of loaded workers being contacted by the minims. It is important to note that in our experiments, the non-vibrating leaf was not always completely "silent", because approx. 50% of workers cutting fragments actually stridulated. Hitchhiking also occurred on these "silent" leaves, but less frequently. Since the number of available leaf carriers was similar for both kinds of leaves, we suggest that the more frequent perception of stridulatory vibrations increased the readiness of the minims to respond by climbing on a leaf carrier.

---

#### **Motor displays in recruitment communication: modulatory and graded signals**

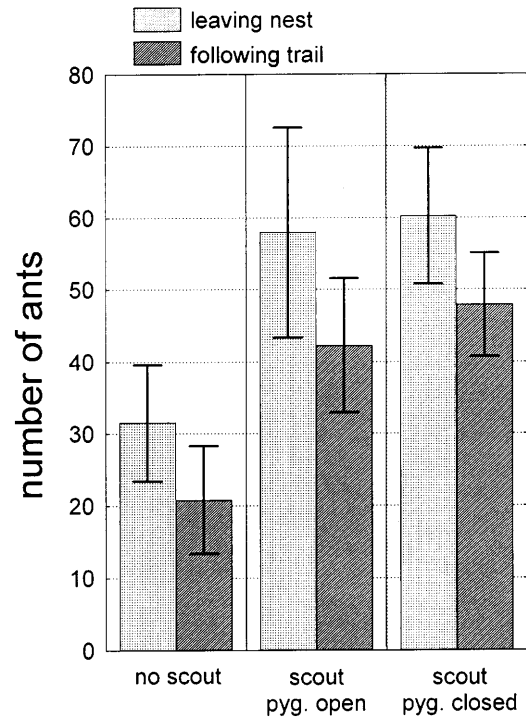
The cumulative studies during the past 25 years have made it clear that motor displays and tactile signaling play an important role during recruitment communication in many ant species, where they usually interact with chemical signals. They have been studied in several species of the Formicinae (reviewed in Hölldobler and Wilson 1990), but they have been observed in species of other subfamilies as well (Wilson 1962; Szlep and Jacobi 1967; Leuthold 1968; Szlep-Fessel 1970) including the phylogenetically less advanced ponerine species of the genus *Amblyopone australis* (Hölldobler and Palmer 1989), *Myrmiom rgeri* (Hölldobler et al. 1998) or *Pachycondyla marginata* (Hölldobler et al. 1996). A more detailed study was conducted with the latter species, a neotropical ant that specializes on hunting termites. Colonies of this species occupy ephemeral nests and frequently emigrate to new nest sites and hunting grounds (Leal and Oliveira 1995). We studied the emigration behavior in the laboratory and found that a scout ant that has discovered a new suitable nest site returns to the nest with the gaster bent down and slightly forward, so that the last tergum was dragged over the ground (Fig. 4). This is the trail-laying behavior during which the trail pheromones from the pygidial gland (located between the 6<sup>th</sup> and 7<sup>th</sup> abdominal tergites) is



**Fig. 4** Schematic illustration showing typical behavioral pattern of a *Pachycondyla marginata* worker laying a trail with secretions from the pygidial gland (above), and exhibiting a shaking display inside the nest (below)

deposited. When the scout entered the old nest, some nestmates reacted by increasing their locomotory activity, leaving the nest and some followed the trail laid by the scout ant. These ants moved to the new nest, inspected it and also returned to the old nest exhibiting typical trail laying behavior. Finally, one or several of those ants performed a striking motor display: a rapid, light, vertical shaking of the body, each bout lasting about 0.5–2 s (Fig. 4). Once nestmates encountered such shaking ants, some individuals reacted by shaking too, others started running towards the exit and soon many ants formed columns and moved along the trail of the scout ants toward the new nest site.

Pygidial gland contents alone not only releases trail-following behavior, it also elicits a recruitment response; that is, the number of ants leaving the nest is much higher than that recorded when other glandular secretions were presented at the nest entrance (Hölldobler et al. 1996). We noted, however, that a recruiting ant that performed the shaking display inside the nest elicited a considerably better recruitment response than the experimental trails laid with pygidial gland secretions. To investigate whether this is due to the shaking display, we performed an experimental series in which we compared the recruitment response to artificial pygidial gland trails (each trail was drawn with secretions of one-gland-equivalent along a 40-cm-long trail) under different conditions. (1) The artificial trail was presented at the nest entrance without the stimulation of a scout inside the nest. (2) The artificial trail was presented after a scout had entered the nest, and the paper on which the scout had laid a trail was removed. (3) Identical experiment as (2), except the pygidial gland of the scout was sealed with wax. The response of the ants to artificial trails in experiments 2 and 3 were not significantly different, but in both cases the responses were significantly better than in experiment 1 (Fig. 5) (B. Hölldobler,

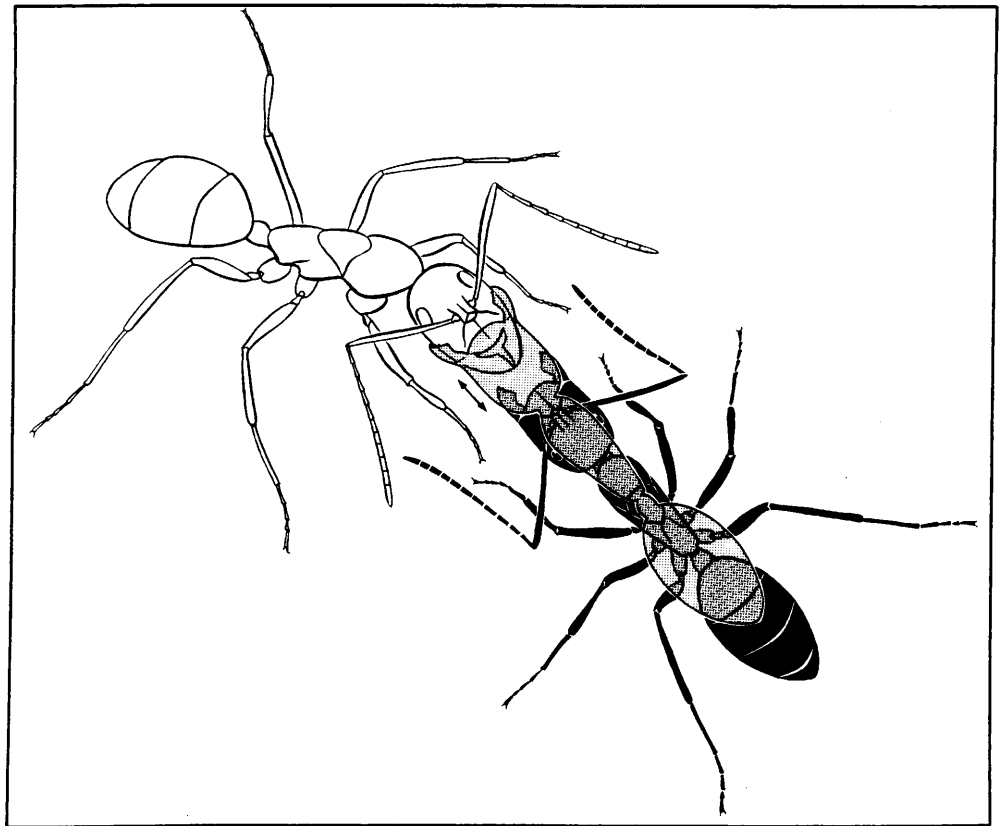
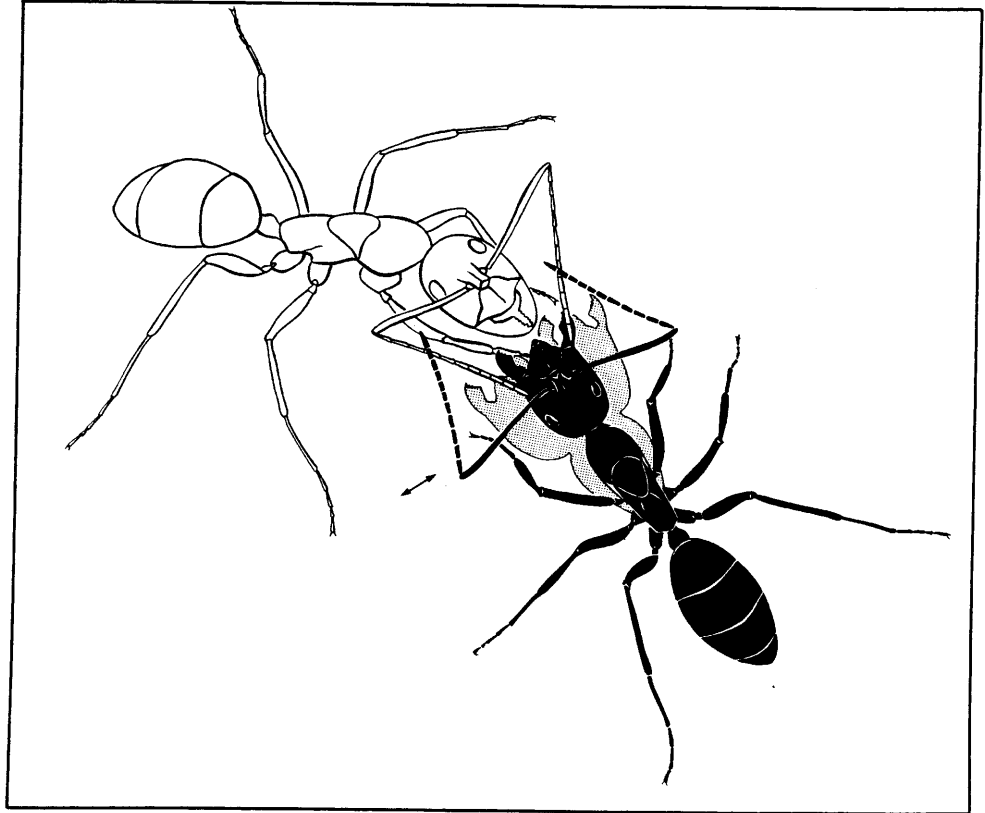


**Fig. 5** Mean number ( $\pm$  standard deviation) of *Pachycondyla marginata* workers following artificial trails laid with pygidial gland secretions. The responses of workers being not exposed (ten tests) or being exposed to shaking scouts (with pygidial gland open or closed, nine tests each) were compared

unpublished results). These results strongly support the hypothesis that the shaking display inside the nest is an effective additional stimulus enticing the ants to move out and follow the pygidial gland trail. Though in this case the trail pheromone alone elicits trail following behavior, the motor display quite obviously enhances the response, and can therefore be considered a modulatory signal.

Let me now focus on a case where the motor display can function as a graded signal component in multimodal recruitment communication. But first I have to briefly describe a recruitment technique which we call group-recruitment. It is quite common in the formicine genera *Camponotus* and *Polyrhachis*. The recruiting ant summons 2–30 nestmates at a time, which follow closely behind the leader ant to the target area. This behavior has been studied in greater detail in *C. socius* from the southern United States (Hölldobler 1971). We found that scouts use chemical signposts around newly discovered food sources and lay a trail with hindgut contents from the food source to the nest. The trail pheromone alone does not induce recruitment to any significant extent. Inside the nest the recruiting ant performs a waggle display when facing nestmates head-on (Fig. 6). The vibrations last 0.5–1.5 s and comprise 6–12 lateral strokes per second. Nestmates are alerted by this behavior and subsequently follow the recruiting ant to the food source. We demonstrated the significance of

**Fig. 6** Schematic illustration of the motor-displays of *Camponotus socius* during recruitment to food source (above) and to new nest sites (below). (From Hölldobler 1971)



the motor display inside the nest by closing the rectal opening of the recruiting ants with wax plugs. With the waggle display thus separated from the chemical signals, it was proved that significantly more workers follow the pheromone trail when they first have been exposed to the waggle display. We could also show that the intensity of the waggle display performed by individual scouts and the response of the nestmates is positively correlated with the colony's need of food. A successful scout from a starved colony exhibits a more vigorous waggle display, contacting more nestmates, and is followed by more ants. In an experimental situation, where only the scouts were starved and the colony was well fed, the scout returning from a food source performed a vigorous waggle display, but significantly fewer ants responded.

On the other hand, scouts that were well fed and were allowed to return after 5 days from a food source to the starved colony, exhibited no or only very weak motor displays, but extensive regurgitation. Some scouts moved back to the food source, usually not followed by nestmates. When they returned again to the nest, they often performed a vigorous waggle display and were subsequently followed by a good number of nestmates (Hölldobler 1971; B. Hölldobler, unpublished results). These observations suggest that the waggle display can be employed as a graded signal and its intensity depends on the motivational state of the recruiter individual as well as the responsiveness of the colony. This is not the case with the chemical component of the recruitment signal: higher concentrations of the trail pheromone do not elicit a stronger following response. In other species, such as the fire ant (*Solenopsis invicta*) that employ chemical mass communication, motor displays are quite unimportant and the response is almost entirely regulated by the amount of pheromone released (Wilson 1962; Hangartner 1969).

---

### Motor displays as specifiers in multimodal communication

We have already discussed the significance of the waggle display performed by scouts as part of their recruitment behavior in *C. socius*. During the waggle display the recruiting ant usually holds its mandibles open and its labium extended. The behavioral pattern resembles that of an ant offering food to a nestmate, and indeed, frequently the scout appears to present food samples to the surrounding ants. Thus, the waggle display can be interpreted as having derived from an intention movement that precedes the social food exchange. This intention movement has become ritualized, emerging as a communicative signal, that informs nestmates about the discovery of food. Typically for ritualized signals, the waggle display is highly repetitive and stereotyped, in comparison to its precursor (the intention movement). A different motor display is employed by *C. socius* workers when they recruit nest mates to a new nest site. It is more of a jerking movement, which can be applied from all

sides toward the encountered ant. More frequently, however, it is performed when the recruiter faces a nestmate. Usually the recruiter has a higher position than the recruitee and in jerking backwards it often pulls the passive nestmate on its head (Fig. 6). From a slow-motion picture analysis of the movement patterns it became obvious that this particular motor display specifying recruitment to nest emigration, is derived from an intention movement initiating adult transport which is frequently also employed in nest emigrations (Hölldobler et al. 1974). In conclusion, we can state that during recruitment both to food sources and to new nest sites *C. socius* workers employ the same trail pheromone originating from the rectal bladder, but specify the recruitment context by specific motor displays inside the nest. Whereas only foragers respond to the waggle-display, a much larger worker cohort (including nurse-ants and even males) respond to the jerking display.

Thus the multimodal signals of *C. socius* seem to convey information about the external environment. Marler (1978), who investigated whether animal vocal signals might inform others about the external environment, called such signals "symbolic", and later "referential" or better "functionally referential" (Marler et al. 1992; see Discussion in Hauser 1996). According to Hauser (1996) a signal is referential "if it is reliably associated with objects and events in the world. As a result of this association, listeners can accurately assess the range of potential contexts for signal emission. The breadth of this range depends, in part, on the specificity of the signal with regard to target objects and events." This statements concerns exclusively vocalization in vertebrates, but can be easily applied to the waggle-dance communication in honeybees and the recruitment communication in *C. socius*, and in other ant species.

Additional evidence for functionally referential communication and ritualization in ants can be found, for example, in the multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Hölldobler and Wilson 1978). Workers of this species utilize several recruitment systems to draw nestmates from the nests to the remainder of the nest tree and foraging areas beyond. These include (1) recruitment to new food sources, under the stimulus of odor trails produced by the scout with secretions from her rectal gland, together with tactile stimuli presented while the scout engages in mandible gaping, presenting its extruded labium (similar to food offering), antennation and head waving; (2) recruitment to new terrain, employing pheromones from the rectal gland and tactile stimulation by antennal play; (3) short-range recruitment to territorial intruders or prey, during which the terminal abdominal sternite is exposed and dragged for short distances over the ground to release an attractant from the sternal gland. Presumably also alarm pheromones from the mandibular glands are released in this context (Bradshaw et al. 1979); (4) long-range recruitment to intruders, mediated by odor trails from the rectal gland and by antennation



and intense body jerking. The latter motor display, used during recruitment to enemies, closely resembles behavioral patterns during the actual attack maneuvers themselves. In the latter situation, the ants move elevated on stilt-legs, raise the gaster into a vertical position, and with their mandibles aggressively opened (labium intruded) they jerk toward each other until they grasp the opponent. Exactly the same display is performed by a recruiter to summon nestmates for colony defense, except the recruiting ant stops short of seizing the encountered nestmate, and the motor pattern is more repetitive and exaggerated. We have therefore interpreted the signals to be a ritualized version, “liberated” during evolution to serve as a signal when a nestmate is encountered in the context of colony defense. The nestmates react to these stimuli by moving along the odor trail laid by the recruiting scout toward the invasion site.

Can we still call this mutualistic communication, or should we follow Dawkins and Krebs (1978) and speak in this case of manipulative communication? Do the recruiting individuals employ exaggerated “attack-symbols” in order to manipulate nestmates to rush into battle? One could argue fighting among colonies often leads to fatalities, thus those ants involved in the battles obviously risk their lives. However, it is mostly the older individuals, the “disposable” worker group, that respond to the “battle cry”. Those ants have degenerated ovaries and the best they can do is fighting “for the good of the family” (Hölldobler 1979).

Thus, up till now we have mainly discussed so-called mutualistic communication, during which information is shared within the colony to the benefit of all members of the entire society. The cooperative functioning and collective fitness of the colony depend on such mutualistic communication. The social interactions mediated by such communication can be considered an important part of the “extended phenotype” of the colony and we can expect colonies in a population to show variations with respect to their extended phenotypes (Dawkins 1982). Colonies compete with one another for resources; those colonies that establish and maintain territories in the most economic way, or employ the most effective recruitment system to retrieve food, exhibit the most powerful colony defense against enemies and predators, will be able to raise the largest number of reproductive females and males every year, and thus will have the greatest fitness within the population of colonies.

We should not ignore, however, that there exist various conflicts among individuals or groups of individuals within the society in the context of reproductive competition, some of which involve complex manipulative communication (Heinze et al. 1994; Bourke and Franks 1995). Nevertheless, the inclusive fitness of all individuals of a colony depends on the effectiveness of the colony as a whole. In fact, in many ant species the competition among colonies of a population by far outweighs the competition among individuals within a colony.

### Communicating “resource holding potential” among colonies

Animals engaged in aggressive competition communicate to their opponents information about their fighting ability, also called “resource holding potential” (RHP). Such information includes body size, strength of teeth, horns or antlers. As behavioral ecologists have frequently noted, if the RHP of opponents are very unequal, the contest is quickly decided; the weaker individual yields. However, if the opponents are similar in their exhibited RHP, the contestants engage in an elaborate communication behavior, the signals of which do not provide reliable information about the intent to escalate the aggression or to flee. In such situations, “the outcome of a competitive interaction must be decided by a volley of signals, with each individual attempting to extract the most useful information with regard to the relative probability of winning or losing a fight” (Hauser 1996).

We will continue to apply Dawkin’s “extended phenotype concept” and look at competitive contests in ants. Territories of ant societies are part of the extended phenotype. They are defended cooperatively by the usually sterile worker castes, and because of the division of labor between reproductive individuals and the workers, fatalities caused by territorial defense have a different qualitative significance for social insects as compared to solitary animals. The death of a sterile worker represents an energy and labor debit, rather than the destruction of a reproductive agent. In fact, worker death might more than offset its costs by bringing or maintaining resources and colony security (Hölldobler and Lumsden 1980).

Nevertheless, ritualized combat is also known to exist in a few ant species (Hölldobler and Wilson 1990). Its ecological significance has been analyzed in greater depth in the honey ant *Myrmecocystus mimicus* (Hölldobler 1976, 1981; Hölldobler and Lumsden 1980; Lumsden and Hölldobler 1983; B. Hölldobler, unpublished results). These ants conduct tournaments in which tens to hundreds of ants can be involved, but almost no physical fights occur. Instead, individual ants engage each other in highly stereotyped aggressive displays (Fig. 7). During these tournaments spatiotemporal territories are defended, and simultaneously opposing colonies seem to assess each others’ strength. Depending on the outcome of this mutual assessment, the opponents either continue to fight a ritualized combat whereby the tournament site can be shifted toward the nest of the weaker colony and thus interfering with the foraging activity of that colony; or, if one colony is considerably stronger the contest will quickly escalate into the raiding and possibly enslavement of the weaker colony.

We postulated that numerous threat displays between individual workers at the tournament site are integrated into a massive group display between opposing colonies. In parallel to the procedure followed by solitary animals, the groups’ “strategic decision” whether to retreat, to



**Fig. 7** The tournament of the honey ants, *Myrmecocystus mimicus*. Lateral display between two opponents vigorously antennating each others' bodies

recruit reinforcements in order to continue to fight by display, or to launch an escalated attack, depends on information about strength of the opposing colony, and this information is obtained during ritualized combats at the tournament site. The behavioral patterns involved suggest it is based on complex multimodal communication.

During the tournament contest the ants walk on stilt-like legs while raising head and gaster. When two hostile workers meet, they initially turn to confront each other head-on. Subsequently they engage in more prolonged lateral display during which they raise the gaster even higher and point it toward the opponent (Fig. 7). Simultaneously, they drum intensively with their antennae

on and around each other's abdomen, and frequently kick their legs against the opponent. This is almost the only physical contact, although each ant seems to push sideways as if she were trying to dislodge the other. After several seconds one of the ants usually yields and the encounter ends. The ants continue to move on stilt-like legs. They soon meet other opponents, and the whole procedure is repeated. When they meet nestmates the encounters last only 1–2 s and are terminated by a brief jerking movement of the body. They seem to be able instantly to discriminate foreign ants from nestmates once they touch each other with their antennae. Presumably colony specific, little volatile chemical signals, such as blends of cuticular hydrocarbons, are responsible for nestmate recognition. One of the features that appears to be important during the displays is size of individual ants. If a large and a small ant are matched in a displaying encounter, usually the smaller ant yields.

Displaying ants not only walk in a stilt-like manner while raising the gaster and head, but sometimes also appear to inflate the gaster, so that the tergites are raised and the whole gaster appears considerably larger. There is also a tendency of the tournament ants to mount little stones and pebbles and display down to their opponents. In fact, the behavioral analysis of the display suggests that during encounters the contestants gauge each other's size, and that there is a tendency among the ants to bluff, i.e., pretend to be larger than they really are.

From these observations we developed two models of ways in which *M. mimicus* may assess one another's strength during the tournaments. Individual workers may use the rate of encounters with nestmates and opponents ("head-counting model") to gain a rough measure of the enemy's strength. Alternatively, individuals may determine whether a low or high percentage of the opponents are major workers and use this information to estimate the opposing colony's strength, since a high percentage is a reliable index of large colony size. Indeed, our investigations showed that majors are more frequently represented among tournamenting ants than among groups of foragers. Among colonies reared in the laboratory from founding queens, those younger than 4 years have a disproportionately small group of majors in the worker population.

Field experiments indicate that both assessment mechanisms are involved in intercolony communication, and the data suggest that in particular small immature colonies rely on the "caste polling" technique, which enables them quickly to assess whether or not the opponent is a mature colony. When confronted with large workers, small colonies immediately retreat into the nest and close the nest entrance. This tactic enables small colonies to prevent larger ones from mounting a raid.

Concerning the head-counting method, our investigations revealed that it is not the entire tournamenting worker force that does the "counting". A small group of "reconnaissance-ants" move through the tournament and gather the information. These ants are of smaller body size, and their encounter times with opponents and nestmates are not significantly different and last only 1–3 seconds. Their trajectories in the tournament are considerably larger than those of the display ants. Individuals of this "reconnaissance-group" recruit reinforcements from the home nest, by laying chemical trails with secretions from the rectal bladder and by performing a rapid jerking display at the nest, which apparently excites nestmates which follow the recruiting ant to the tournament site. Inspections of the condition of the fat-bodies, ovaries, and external wear and tear of the responding workers suggest that most of them are older individuals and especially ants of larger body-size remain at the tournament as display ants. Thus, the *Myrmecocystus* colonies communicate to neighboring colonies their resource-holding potential by summoning cohorts of large display ants to tournament sites. Colonies that are unable to match the challenge retreat and forage into other directions or wait inside the nest

until the dominant neighboring colony is inactive. Indeed, I often observed in the field that foragers of large colonies stay inside the nest for days, for example when the foraging conditions are not good because it is too dry and termites, a main food source for *M. mimicus*, are not on the surface of the desert soil. In this "activity shadow" foragers of smaller colonies swarm out, scavenging for and hunting whatever they can find and retrieve.

The territorial tournaments may be considered one of the pinnacles in ant multimodal communication. They involve mutualistic intra-colony and manipulative inter-colony communication. By means of chemical trails and motor displays, nestmates are summoned to the tournament site and during encounters and confrontations with other ants they use colony-specific chemical cues for recognition of nestmates and opponents. Though it is said that the use of visual signals in ants is at least minor, and in fact not a single example has yet been solidly documented (Hölldobler and Wilson 1990), *M. mimicus* workers have relatively large eyes and are very good at detecting moving objects when hunting. It is therefore quite likely that vision also plays a role during tournament interaction. Certainly tactile signals appear to be very important, because the ants continuously antennate the opponent's whole body, but especially the gaster. A great deal of such antennation might serve, however, to receive information rather than send it. Nevertheless, it is entirely possible that multimodal communication during tournament-interaction in *M. mimicus* involves chemical, mechanical and visual sensory channels.

---

## Outlook

Martin Lindauer (1985), in remembering his great teacher Karl von Frisch, writes, "'Nature never lies' he said and he always impressed on his students: 'auch kleine Dinge muß man in der Biologie ernst nehmen' (in biology you also have to consider little things seriously)." Indeed, the "little things", such as a jerking movement, a hardly noticeable waggle display, or an up and down motion of the gaster may seem incidental behaviors of little significance in social interactions among ants, but a careful analysis of such behavioral patterns reveals that they often play an important role in the subtle regulation of ant communication. I think we have underestimated the complexity of communication signals in ants, having focused our analyses on one or the other sensory channel through which the signals are perceived and processed. The lesson we have learned from studies of chemical signals, namely that insect semiochemicals have proven to be complex mixtures, and single-compound pheromones are actually quite rare (Silverstein and Young 1976; Hölldobler and Carlin 1987) have now to be extended to other modalities, and greater attention has to be paid to multimodal combinations of signal components. Certain components function as straight-forward releasers, others as subtle modulators of motivational states of the receivers.

We have relatively little problem when considering motivational or emotional states in mammals affecting the individual's readiness to send or perceive communication signals, but we are still quite hesitant to investigate the role of motivation in social insect communication. Yet those of us studying communication in social insects are fully aware of the fact that the behavior of the signal sender, as well as that of the signal receiver, depend strongly on the motivational states of the individuals (Roces 1993; Roces and Nuñez 1993), although we cannot precisely measure motivational states. What is the physiological basis of motivational states? What is different in the hemolymph chemistry of a "hungry" ant performing a much more vigorous recruitment display than a well-fed forager? How are such physiological differences relayed to the endocrine and central nervous systems that drive the behavior? How do scouts gauge their colony's food condition when adjusting their recruitment behavior? What role do modulating signals play in fine tuning the society's response to external stimuli, and what role does "individuality" play in ant communication, and thus in the social organization of the ant colony? After all, workers of some ant species can live for several years, and most likely can gather experiences. Does this cause variation in signal senders and receivers? Does it affect the message-meaning relationship? What goes on inside the body of a young nurse ant that, when perceiving an alarm signal, quickly retreats to more secure sections of the nest, or in an older worker that responds by rushing out with aggressively gaping mandibles?

We recently discovered that the brain volume of *Camponotus floridanus* workers increases by approx. 20%, while the antennal lobes and the mushroom body neuropile almost double their volume in the first 10 months of adult life. In addition to the age-dependent changes the mushroom body neuropile may further increase due to particular activities outside the nest, such as foraging (Gronenberg et al. 1996). Presumably greater sensory stimulation is responsible for that brain volume increase. Thus, it is quite possible that the changes in signaling competency and responsiveness during adult life may be related to brain plasticity. We need to understand better the processing of communication signals in the brain of the receiver individual. Although considerable progress has been made in the analysis of the neural processing of chemical signals (Hildebrand 1996; Galizia et al. 1998), almost no attention has been paid to the processing and effects of multimodal signals in the insect brain. Here I see a vast domain for fruitful collaborations of sociobiologists, behavioral physiologists and neuroethologists.

**Acknowledgements** I thank Professor Jeffrey Camhi for inviting me to deliver the King Solomon Lectures 1997, and for his very generous hospitality. I am grateful to my coworkers who have contributed to many different aspects of the research on which this paper is based, especially to Dr. Flavio Roces, who also critically read the manuscript. Research reported in this paper was supported by grants from NSF (USA) and DFG (Germany).

I wish to dedicate this paper to Professor Hubert Markl, on the occasion of his 60th birthday, and in recognition of his pioneering discoveries and influential concepts that have advanced our understanding of animal communication.

## References

- Baroni-Urbani C, Buser MW, Schilliger E (1988) Substrate vibration during recruitment in ant social organization. *Insectes Soc* 35: 241–250
- Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton, N.J., USA
- Bradshaw JWS (1981) The physicochemical transmission of two components of a multiple chemical signal in the African weaver ant (*Oecophylla longinoda*). *Anim Behav* 29: 581–585
- Bradshaw JWS, Baker R, Howse PE (1979) Multicomponent alarm pheromones in the mandibular glands of major workers of the African weaver ant, *Oecophylla longinoda*. *Physiol Entomol* 4: 15–25
- Buser MW, Baroni Urbani C, Schilliger E (1987) Quantitative aspects of recruitment to new food by a seed-harvesting ant (*Messor capitatus* Latreille). In: Pasteels JM, Deneubourg JL (eds) From individual to collective behavior in social insects. Birkhäuser, Basel, pp 139–154
- Darwin C (1872) The Expression of the emotions in man and animals. Murray, London, England
- Dawkins R (1982) The extended phenotype. Freeman, Oxford
- Dawkins R, Krebs JR (1978) Animal signals: information or manipulation. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 2282–2309
- Eibl-Eibesfeldt I, Eibl-Eibesfeldt E (1967) Das Parasitenabwehren der Minima-Arbeiterinnen der Blattschneider-Ameise (*Atta cephalotes*). *Z Tierpsychol* 24: 278–281
- Feener DH Jr, Moss KAG (1990) Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. *Behav Ecol Sociobiol* 26: 17–29
- Frisch K von (1965) Tanzsprache und Orientierung der Bienen. Springer, Berlin Heidelberg New York
- Fuchs S (1976) An informational analysis of the alarm communication by drumming behavior in nests of carpenter ants (*Camponotus*, Formicidae, Hymenoptera). *Behav Ecol Sociobiol* 1: 315–336
- Galizia CG, Nägler K, Hölldobler B, Menzel R (1998) Odour coding is bilaterally symmetrical in the antennal lobes of honeybees *Apis mellifera*. *Eur J Neurosci* 10: 2964–2974
- Gronenberg W, Heeren S, Hölldobler B (1996) Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Camponotus floridanus*. *J Exp Biol* 199: 2011–2019
- Hahn M, Maschwitz U (1985) Foraging strategies and recruitment behaviour in the European harvester ant *Messor rufitarsis* (F.). *Oecologia* 68: 45–51
- Hangartner W (1969) Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). *Z Vergl Physiol* 62: 111–120
- Hauser MD (1996) The evolution of communication. MIT Press, Cambridge, Mass., USA
- Heinze J, Hölldobler B, Peeters C (1994) Conflict and cooperation in ant societies. *Naturwissenschaften* 81: 489–497
- Hildebrand JG (1996) Olfactory control of behavior in moths: central processing of odor information and the functional significance of olfactory glomeruli. *J Comp Physiol A* 178: 5–19
- Hockett CF (1960) Logical considerations in the study of animal communication. In: Lanyon WE, Tavolga WN (eds) Animal sounds and communication. American Institute of Biological Sciences, Washington DC, pp 392–430
- Hölldobler B (1971) Recruitment behavior in *Camponotus socius* (Hymenoptera, Formicidae). *Z Vergl Physiol* 75: 123–142
- Hölldobler B (1976) Tournaments and slavery in a desert ant. *Science* 192: 912–914

- Hölldobler B (1979) Territories of the African weaver ant (*Oecophylla longinoda*): a field study. *Z Tierpsychol* 51: 201–213
- Hölldobler B (1981) Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera, Formicidae). *Behav Ecol Sociobiol* 9: 301–314
- Hölldobler B (1984) Evolution of insect communication. In: Lewis T (ed) *Insect communication*. Academic Press, London, pp 349–377
- Hölldobler B (1995) The chemistry of social regulation: multicomponent signals in ant societies. *Proc Natl Acad Sci USA* 92: 19–22
- Hölldobler B, Carlin NF (1987) Anonymity and specificity in the chemical communication signals of social insects. *J Comp Physiol A* 161: 567–581
- Hölldobler B, Lumsden C (1980) Territorial strategies in ants. *Science* 210: 732–739
- Hölldobler B, Palmer JM (1989) Footprint glands in *Amblyopone australis* (Formicidae, Ponerinae). *Psyche* (Cambridge) 96: 111–121
- Hölldobler B, Wilson EO (1978) The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera, Formicidae). *Behav Ecol Sociobiol* 3: 19–60
- Hölldobler B, Wilson EO (1990) *The ants*. Belknap Press of Harvard University Press, Cambridge, Mass., USA
- Hölldobler B, Stanton RC, Markl H (1978) Recruitment and food retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). I: Chemical signals. *Behav Ecol Sociobiol* 4: 163–181
- Hölldobler B, Möglich M, Maschwitz U (1974) Communication by tandem running in the ant *Camponotus sericeus*. *J Comp Physiol* 90: 105–127
- Hölldobler B, Janssen E, Bestmann HJ, Leal IR, Oliveira PS, Kern F, König WA (1996) Communication in the migratory termite-hunting ant *Pachycondyla* (= *Termitopone*) *marginata* (Formicidae, Ponerinae). *J Comp Physiol A* 178: 47–53
- Hölldobler B, Oldham NJ, Morgan ED, König WA (1996) Recruitment pheromones in the ants *Aphaenogaster albisetosus* and *A. cockerelli* (Hymenoptera, Formicidae). *J Insect Physiol* 41: 739–744
- Hölldobler B, Obermayer M, Alpert G (1998) Chemical trail communication in the amblyoponine species *Myrmiarium rogeri* Forel (Hymenoptera, Formicidae, Ponerinae). *Chemoecology* (in press)
- Jaffé K, Howse PE (1979) The mass recruitment system of the leaf cutting ant, *Atta cephalotes*. *Anim Behav* 27: 930–939
- Kirchner WH, Grasser A (1998) The significance of odor cues and dance language information for the food search behavior of honeybees (Hymenoptera: Apidae). *J Insect Behav* 11: 169–178
- Kuhl PK (1983) Perception of auditory equivalence classes for speech in early infancy. *Infant Behav Dev* 6: 263–285
- Kuhl PK (1989) On babies, birds, modules, and mechanisms: a comparative approach to the acquisition of vocal communication. In: Dooling RJ, Hulse SH (eds) *The comparative psychology of audition*. Erlbaum, Hillsdale, N.J., USA, pp 379–422
- Kuhl PK, Meltzoff AN (1982) The bimodal perception of speech in infancy. *Science* 218: 1138–1141
- Lindauer M (1985) Personal recollections of Karl von Frisch. In: Hölldobler B, Lindauer M (eds) *Experimental behavioral ecology and sociobiology*. Fischer, Stuttgart, pp 5–7
- Leal JR, Oliveira PS (1995) Behavioral ecology of the neotropical termite-hunting ant *Pachycondyle* (= *Termitopone*) *marginata*: group-raiding and migratory patterns. *Behav Ecol Sociobiol* 37: 373–384
- Leuthold RH (1968) Recruitment to food in the ant *Crematogaster ashmei*. *Psyche* (Cambridge) 75: 334–350
- Lumsden C, Hölldobler B (1983) Ritualized combat and intercolony communication in ants. *J Theor Biol* 100: 81–88
- Markl H (1967) Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. I: Die biologische Bedeutung der Stridulation. *Z Vergl Physiol* 57: 299–330
- Markl H (1970) Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. III. Die Empfindlichkeit für Substratvibrationen. *Z Vergl Physiol* 69: 6–37
- Markl H (1983) Vibrational communication. In: Huber F, Markl H (eds) *Neuroethology and behavioral physiology*. Springer, Berlin Heidelberg New York, pp 332–353
- Markl H (1985) Manipulation, modulation, information, cognition: some of the riddles of communication. In: Hölldobler B, Lindauer M, (eds) *Experimental behavioral ecology and sociobiology*. (Fortschritte der Zoologie, no 31, pp 163–194). Fischer, Stuttgart
- Markl H, Fuchs S (1972) Klopfsignale mit Alarmfunktion bei Roßameisen (*Camponotus*, Formicidae, Hymenoptera). *Z Vergl Physiol* 76: 204–225
- Markl H, Hölldobler B (1978) Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). II. Vibration signals. *Behav Ecol Sociobiol* 4: 183–216
- Marler P (1978) Primate vocalization: affective or symbolic? In: Bourne G (ed) *Progress in ape research*. Academic Press, New York, pp 85–96
- Marler P, Evans CS, Hauser MD (1992) Animal signals? Reference, motivational or both? In: Papoušek H, Jürgens U, Papoušek M (eds) *Nonverbal vocal communication: Comparative and developmental approaches*. Cambridge University Press, Cambridge, England, pp 66–86
- Michelsen A (1993) The transfer of information in the dance language of honeybees: progress and problems. *J Comp Physiol A* 173: 135–141
- Morgan ED (1984) Chemical words and phrases in the language of pheromones for foraging and recruitment. In: Lewis T (ed) *Insect communication*. Academic Press, London pp 169–194
- Moser JC, Brownlee RC, Silverstein R (1968) Alarm pheromones of the ant *Atta texana*. *J Insect Physiol* 14: 529–535
- Partan SR (1998) Multimodal communication: the integration of visual and acoustic signals by macaques. Ph.D. Thesis, University of California, Davis
- Roces F (1993) Both evaluation of resource quality and speed of recruited leaf-cutting ants (*Acromyrmex lundii*) depend on their motivational state. *Behav Ecol Sociobiol* 33: 183–189
- Roces F, Hölldobler B (1995) Vibrational communication between hitchhikers and foragers in leaf-cutting ants (*Atta cephalotes*). *Behav Ecol Sociobiol* 37: 297–302
- Roces F, Hölldobler B (1996) Use of stridulation in foraging leaf-cutting ants: mechanical support during cutting or short-range recruitment? *Behav Ecol Sociobiol* 39: 293–299
- Roces F, Nuñez JA (1993) Information about food quality influences load-size selection in recruited leaf-cutting ants. *Anim Behav* 45: 135–143
- Roces F, Tautz J, Hölldobler B (1993) Stridulation in leaf-cutting ants: short-range recruitment through plant-borne vibrations. *Naturwissenschaften* 89: 521–524
- Seeley TD (1992) The tremble dance of the honey bee: message and meaning. *Behav Ecol Sociobiol* 31: 375–383
- Seeley TD (1995) *The wisdom of the hive*. Harvard University Press, Cambridge, Mass., USA
- Silverstein RM, Young JC (1976) Insects generally use multicomponent pheromones. In: Gould RF (ed) *Pest management with insect sex attractants*. American Chemical Society, Washington DC, pp 1–29
- Smith WJ (1977) *The behavior of communicating*. Harvard University Press, Cambridge, Mass., USA
- Szlep R, Jacobi T (1967) The mechanisms of recruitment to mass foraging in colonies of *Monomorium venustum* Smith, *M. subopacum* ssp. *phoenicium* Em., *Tapinoma israelis* For. and *T. simrothi* v. *phoenicium* Em. *Insectes Soc* 14: 25–40
- Szlep-Fessel R (1970) The regulatory mechanism in mass foraging and recruitment in soldier of *Pheidole*. *Insectes Soc* 17: 233–244
- Tautz J, Rohrseitz K (1998) What attracts honeybees to a waggle dancer? *J Comp Physiol* 183: 661–667
- Wilson EO (1962) Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). I: The organization of mass-foraging; 2: An information analysis of the odour trail; 3: The experimental induction of social responses. *Am Behav* 10: 134–147; 148–158; 159–164

Reproduced with permission of copyright owner. Further reproduction prohibited without permission.