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REVIEW

Pheromones in the life of insects

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Abstract Life in insect societies asks for a permanent flow of information, often carried by rather simple organic molecules. Some originate from plants as odours of blossoms or exudates from trees. Especially important are the intra- and interspecific combinations of compounds produced by the insects themselves. These are called pheromones or ecto-hormones and serve a variety of tasks. The paper deals mainly with honeybee pheromones, but takes also into consideration those of wasps and hornets. Effects of pheromones are monitored ethologically by direct observation and filming as well as in a more quantitative manner with using direct and indirect calorimetry. In all experimental set-ups alarm pheromones were used as controls. They show an up to fourfold increase of activity after a few seconds, determined for small groups of insects as well as for a whole hornet nest placed in a 25-l calorimeter. A variety of cosmetics like soaps, shampoos, lotions and perfumes are included in the investigations because of repeated reports about unwarranted insect attacks which are said to be provoked by such products. None of the applied substances provoked a significant reaction of the bees ($p > 0.05$). A short appendix discusses the still questionable existence of pheromones in man, which were confirmed under laboratory conditions, but not yet for daily life.

Keywords Calorimetry · Cosmetics · Energy metabolism · Information · Insects · Pheromones

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Introduction

Social insects like ants, termites, honeybees, bumblebees, hornets and wasps live together in colonies of several hundreds up to many thousands of individuals with a specific sharing of tasks and work. Thus, it is extremely necessary for colony members to exchange information through the population. During evolution different kinds of information transmission were developed on various levels including direct contact between individuals, optical and acoustical signals as well as chemical cues inside and outside their hives, mounds or nests. The honeybee dances on combs detected and intensively studied by Karl von Frisch (1967) became well-known even to a lay public. In this paper we will concentrate on the information exchange by chemical substances transported as scents in air, since these are an extremely important means of communication for honeybees as well as other social insects.

Pheromones

Information molecules in the sense of attractants may originate in the blossoms of flowers and especially in nectar and pollen or in exudates from trees such as propolis. But equally important are some glands in social insects that produce secretions serving communicative purposes (Schmidt

et al. 1998). In the honeybees these are the Nasonov gland, the mandibular glands, the setose sting glands and the tarsal Arnhart glands (Free 1987; Williams et al. 1982; Winston 1987). Their secretions are not only used at the hive to mark the entrance, but they are also used for finding a sexual partner, marking a territory, in orientation, swarm clustering or guidance to special flowers. The most important application for social insects is hive defence.

Typical substances secreted by the Nasanov gland are geraniol, citral, farnesol and nerol. Together with rather simple molecules like isopentyl acetate (the main odour component of ripe bananas!) or hexanone from the sting glands these compounds or specific mixtures of them are called *pheromones* in insect sciences. Referring back to *hormones* that are secreted inside the body, the term *pheromones* (or *ecto-hormones*) was coined by Karlson and Lüscher (1959) for highly volatile chemical substances which are secreted externally by one individual and induce a specific reaction in another member of the same species (Karlson and Lüscher 1959). Pheromones can be divided into *signal pheromones* which are attractants or repellents that induce short time reactions like an alarm and in *primer pheromones* that are used for the long-term organization of social groups. Meanwhile, many pheromones are known and their compositions intensively studied (Table 1). Moreover, artificial pheromones have been constructed with the same molecules but in varying blends. Many of them show the same effect as their natural counterparts. There are quite a number of odours which are used for communication among social insects and provoke special activities. Not all of them can be catalogued as pheromones. For many of these the question is still open.

Pheromone molecules have to evaporate and dissipate quickly and are often transported by air over rather large distances. They should be diluted by diffusion and mainly convective mixing in a short time down to very low concentrations making space for new scents and thus new information. Only molecules with molecular weights between 100 and 200 are suited for this purpose, and it is thus obvious that the organic compounds found in pheromones are small and simple aliphatic ones. These compounds may correspond closely to the mixture of scents produced in blossoms. It has been shown that the scent of a honeybee abdomen might be amazingly similar to that of a rose (Bertsch 1975, p. 104). Therefore, the question arose whether such scent molecules of flowers might have entered the genetic library for odours and pheromones of their pollinating insects.

Detection and discrimination of odours and pheromones

Pheromones as well as odour molecules are detected with sensory cells located in the antennae of insects. When odour molecules hit the epicuticula of the sensillae, they are adsorbed and quickly transported by facilitated diffusion and through pores into the inner lymph-containing part of this organ, where they are bound by special proteins and brought to specific olfactory receptors. Matching of odorants with such receptors leads to an activation of the corresponding neurons (Dettmer and Peters 2003; Van der Goes van Naters and Carlson 2006). Large gene families are engaged in odour detections in all animals (Bargmann 2006) underlining the importance of olfactory cues in life. Not so in insects; they seem to have a smaller number of odour-responsible genes and types of odorant receptors. The fruit fly *Drosophila* has only 62 such receptor types encoded by 60 genes. Instead of using many different narrowly tuned receptors, it applies a few broadly tuned receptors and a combination of various strategies to differentiate between the signals (Bargmann 2006). The sensitivity is extremely high—binding of a few molecules provokes a neuronal excitation which may lead to changes in behaviour. To demonstrate this high sensitivity, just two textbook examples shall be mentioned.

Table 1 List of some pheromones of honeybees (taken from the literature)

Pheromone	Gland	Purpose
Nasonov	Nasonov (worker)	Orientation
Alarm	Mandibular (worker) Sting (worker)	Alarm and defence
Recognition		Kin or colony recognition
Queen	Mandibular (queen)	Queen recognition Drone attraction Worker attraction Swarm cluster stabilization
Scent	Nasonov (worker)	Recruital
Tergite	Tergite (queen)	Inhibition of queen rearing drone copulation
Marking	Mandibular (drone)	Marking congregation spots
Footprint	Tarsal (worker)	Orientation at flowers

It could be shown by Vareschi (1971) that a honeybee drone reacts on 9-oxo-E-2-decenic acid, an important compound produced by the queen, with a sensitivity that is 3–7 powers of ten higher than towards corresponding saturated fatty acids with four (C4) to twelve (C12) carbon atoms. That means that 10^9 molecules of this compound per ml are enough to produce about 60 nerve impulses per second (cited after Dettmer and Peters 2003). Calculating this number down to the air space around a sensilla of the antenna, one arrives at a few molecules sufficient to provoke a reaction.

The best-known example of insect communication with high sensitivity originates from the silk-worm moth *Bombyx mori*. The female produces the sexual attractant bombykol in its abdomen-situated odour glands. The *Bombyx* male discriminates this molecule with sensory cells of its antennae, even at very small amounts. One molecule of bombykol is enough to guide the male in the odour gradient of an airflow to the female (Dettmer and Peters 2003; see also Nachtigall and Blüchel 2000).

Alarm pheromones

These especially important compounds are found in honeybees, wasps, ants and termites. They are mixtures of several kinds of molecules which are highly volatile as necessary for a short-term signal. The alarm pheromone of the honeybee contains about 20 compounds, among which isopentyl acetate and 2-heptanone are the most important ones. A few of them are listed in Table 2. Alarm pheromone composition varies between bee species and shows even differences between neighbouring hives in a bee yard. They may provoke intra- as well as interspecific reactions. A bee sting injures the victim, marks him, recruits nest mates for defence of the colony, which also sting the victim and thus induce an aggressive mass attack, well-known from disturbed wasp or hornet nests (Edwards 1980). As honeybees are social insects, the response of an isolated individual is considerably less aggressive than when in contact with a larger bee group.

Alarm pheromones became known to a broad audience by the so-called killer bees of South America. African honeybees are normally more aggressive than the European bees which have been bred by humans for hundreds of years to become calm and easy to handle. When the African bees were imported into South America in 1956 to be crossed with the already imported European bees for obtaining a honeybee race with a higher honey production, the South African bees escaped by accident and spread rapidly to most parts of the continent and further up to the north. Lethal accidents due to mass attacks by the aggressive Africans were frequently reported (Winston 1992). Up to now, about 1,000 fatalities due to excessive stinging have been recorded. The composition of the African alarm pheromone is rather similar to the European one, isopentyl acetate and 2-heptanone being also the main components. It seems that the higher amount of pheromone produced in the African bees is important for the attacks rather than the mixture of substances.

Table 2 Main components of the honeybee alarm pheromone (Schmolz et al. 1999a)

Isopentyl acetate	Highly active	$C_7H_{14}O_2$
2-Heptanone	Highly active	$C_7H_{14}O$
2-Heptanol	Highly active	$C_7H_{16}O$
1-Hexanol	Highly active	$C_6H_{14}O$
1-Octanol	Less active	$C_8H_{18}O$
1-Butanol	Less active	$C_4H_{10}O$

Behavioural observations

Earlier pheromone investigations were carried out with ethological assays. They are cumbersome and time consuming and have to be performed in the field under sometimes adverse conditions. In any case, investigators have to keep a distance from the test site because alarmed social insects might be a real hazard to them (MacLean and Schmolz 2004).

In parallel with the physiological experiments reported below, ethological studies were performed on the same bee hives. After a pre-period to monitor the frequency of in- and out-flying bees, isopentyl acetate, hexanone and some cosmetics were exposed to the insects for 1 min and then removed for a post-period. During these three periods video clips were taken with a digital camera and later on evaluated in a 1-s time frame for the number of bees present on the landing board directly in front of the hive entrance. Isopentyl acetate causes a significant increase in the bee number and their locomotor activity, the other compounds non-significant effects and the cosmetics no effect at all (von der Heydt, unpublished results). For the moment, the pleasant take-home-message is that no actions are provoked by cosmetics whatsoever one applies to feel better or more attractive.

Simultaneous ethological and physiological investigations of pheromone actions of honeybees were monitored by means of oxygen concentration measurements (indirect calorimetry, see "Calorimetric observations") and visual observation in hermetically closed 750-ml vessels. For estimating the effects these vessels—equipped with an electrolytic oxygen sensor and an inlet for the pheromone—were theoretically divided into three equal volumes (upper, middle, lower) and the bottom. Pre-period, pheromone period and post-period were filmed as video-clips with a digital camera, and the distribution of bees in the vessel was evaluated from still pictures every second. The results for the

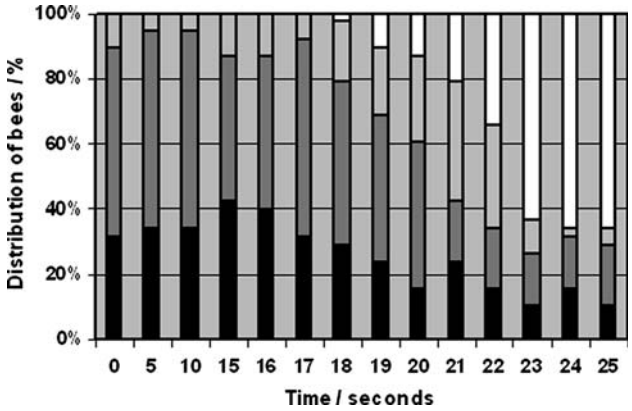

Fig. 1 Distribution of worker bees in a 750-ml vessel before and during the application of isopentyl acetate. The independent axis shows the experimental time in seconds (not to scale), the dependent axis the percent distribution. The *bars* represent from the bottom to the top: the bottom of the vessel; the lower third of the volume; the middle third; the upper third (see text)

pheromone period are depicted in Fig. 1 and a typical distribution of bees in all three periods in Fig. 2.

The pheromone was injected after a short pre-period of 10 s (Fig. 1). During this time about 35% of the bees were sitting on the bottom (black bar), 60% occupied the lower volume (dark grey bar) and only 5% the middle one (light grey bar). No bee was seen in the upper part. This was typical for all experiments with this setup. The picture changed considerably after 8 s. The first bees appeared in the upper volume (white bar), a number that increased to 65% at the end of the 25-s observation period. The middle part became nearly empty. The next video-clip 30 s later showed a mean of 51% of bees in the upper part with a decreasing tendency from 58 to 40%, only 9% in the centre, 28% in the lower part and 12% on the bottom. One minute later the distribution returned to values of 0 (0), 34 (6), 17 (58) and 49 (36)%, respectively (the values in brackets are those of a video-clip 5 min before the start of the experiment proper).

Calorimetric observations

Physiological investigations represent an alternative to the time consuming ethological assays. For it has often been shown that the metabolic rate of an animal is a sensitive measure of its activity and gives comprehensive information about its energetic status (Schmolz and Lamprecht 1999, 2004). There are two ways of monitoring the locomotor activities of living objects and their metabolism calorimetrically: direct and indirect calorimetry. Both techniques are non-invasive and non-specific so that unexpected effects can be monitored also. While direct calorimetry measures the heat flow from a living specimen to its (constant temperature) environment (Schmolz and Lamprecht 1999, 2004), indirect calorimetry determines oxygen consumption or carbon dioxide production rates which can be transferred into energy units. This latter is the more common way to obtain information about the metabolic levels (Moritz and Bürgin 1987; Moritz and Southwick 1992). Southwick and Moritz (1985) performed intensive indirect investigations on alarm pheromones with bee groups from 1 up to 6,700 individuals. They found short-term elevated oxygen consumption rates, an increase with the number in smaller groups and clear dose–effect relationships at a specific concentration level, and recommended this approach as a means to determine quantitatively the temperament of honeybee species.

A Calvet type twin calorimeter with 100-ml vessels was applied in the direct approach. Twenty to thirty honeybees were placed in the reaction vessel which was continuously flushed with thermally equilibrated air. After a pre-period to get the calorimetric base-line, the air stream was led for 1 min through a washing bottle with a pheromone saturated atmosphere and afterwards switched back to the foregoing conditions. Figure 3 shows the experimental setup including calorimeter, air pump, washing bottle and chart recorder. Figure 4 shows the calorimetric results. The pre-period, stimulation phase and post-period of the thermal power as function of time are clearly indicated. The response of the insects to the pheromone seems to be slow, but this is due to the thermal inertia of the instrument; it appears within a few seconds using direct observations (see Fig. 7). The excitation of the bees decreases after a short time, the signal usually drops below the level of the pre-period, showing an exhaustion effect of the animals and a compensation for the additional energy spent during the *attack*. Similar curves were obtained calorimetrically for hornets, for whom only four pheromone components could be determined as active compounds in their venom up to now, among them 2-methyl-3-butene-2-ol.

MacLean and Schmolz (2004) used the same setup for the hornet *Vespa crabro* in groups of five individuals in the calorimetric vessel. They investigated nine different alarm pheromone components; just not only the known intraspecific ones, but also six interspecific ones like isopentyl acetate. Both kinds produced significant increases in the heat production rate after their application. The authors showed that the vapour pressure of the compounds (boiling points between 69 and 176°C; mean 106°C) had no influence on the results; and they speculated that the compounds develop their action subsequently. In this picture, highly volatile components induce a rapid response of the hornets, while the other substances demonstrate an enduring effect.

In another series of experiments alarm pheromones were tested for complete colonies of the hornet *V. crabro* (Schmolz et al. 1999a). Their nests were kept during a summer season in 25-l cool-camping boxes transformed

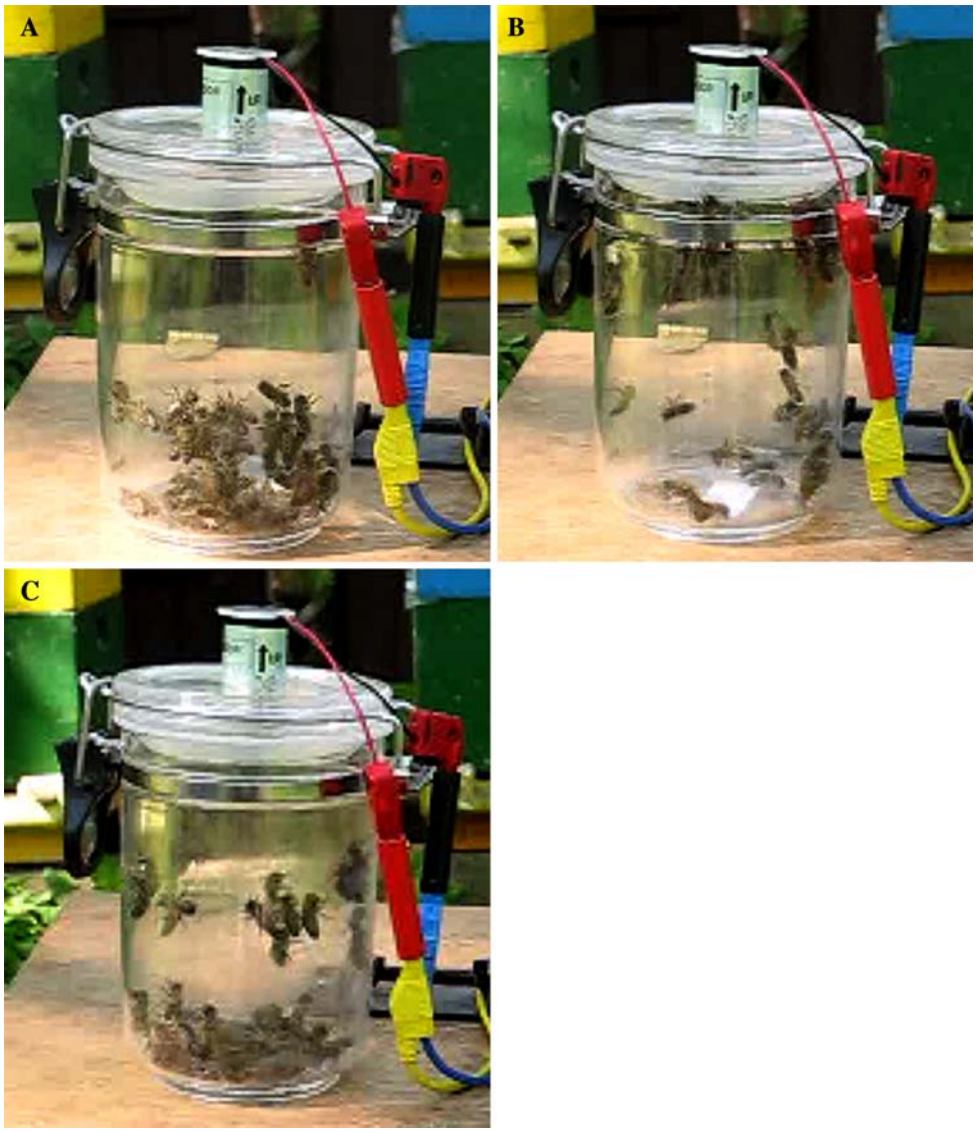

Fig. 2 Photos taken from the video clips. **a** a few minutes before the start of the experiment; **b** at the maximum of the pheromone effect; **c** a few minutes after the maximum (please notice the condensed water at the lower wall as sign for a highly increased metabolic rate and loss of water by locomotor activity). The full video clip can be seen under Supplementary data

into very simple and inexpensive calorimeters (Fig. 5). The specifically active venom compound 2-methyl-3-butene-2-ol was injected through a hole in the calorimeter wall directly on the paper wall of the nest where it provoked an immediate, strong and longer lasting effect (Fig. 6): the heat production rate nearly doubled to values that were calorimetrically obtained from flying hornets earlier (Schmolz et al. 1999b). Such values are in agreement with results of Veith et al. (1984). Astonishingly enough, the hornets also reacted interspecifically on the bee components 2-heptanone and isopentyl acetate, although these two compounds were already shown not to be present in the hornet pheromone.

Indirect calorimetric determinations were run in glass or Plexiglas containers from about 50 up to 750 ml with 1 to about 30 honeybees. It was important to vary the number, since bees are social insects that react differently depending upon the group size (Fahrenholz et al. 1989, 1992). Single honeybees are inert against alarm pheromones, groups of six or more are still easy to handle but already quite responsive towards pheromones. The containers were equipped with electrolytic oxygen sensors at the top that gave electric signals of about 50 mV proportional to the oxygen concentration in the container. Moreover, in- and outlets for air were incorporated at the top allowing for the addition of pheromones; otherwise they were hermetically sealed. After a pre-period with a constant drop of the oxygen concentration (due to the respiration of the animals) 10 ml of scent-saturated air were added to the container, and the further drop of oxygen was registered. Because it was difficult to switch back to pheromone-free air, the evaluation was limited to the first 60 s after the addition and no true post-periods were observed. Figure 1 depicts the behaviour described above. Figure 7 shows the influence of isopentyl acetate on the oxygen consumption rate of 149 honeybees (19.0 g fresh weight) at 23°C in a 750-ml vessel as shown

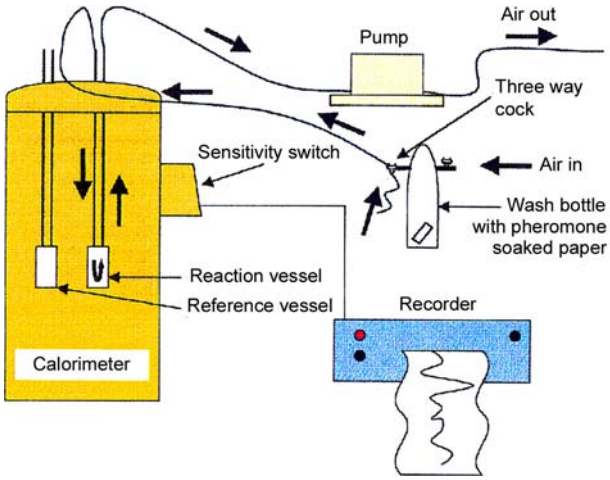

Fig. 3 Sketch of the applied Calvet-type twin calorimeter showing the flow of air through the reaction vessel either directly or via a wash bottle containing a piece of filter paper soaked with a pheromone solution (adapted from Schmolz et al. 1999a)

in Fig. 2. The pheromone component was added around 120 s; the effect is seen a few moments later. The rate increase is nearly fourfold under these experimental conditions with water condensation at the wall due to the high metabolic turnover.

Cosmetics

Investigations on alarm pheromones of social insects are not only of scientific interest, but also of practical importance. From time to time there is news in the media that special people in a group were attacked by bees or wasps without any preceding provocation; and it is often supposed that this is due to a specific body odour, a meal they had before or cosmetics these people used. These last may be perfumes as well as soaps, shampoos, lotions, crèmes, hair sprays or gels. Such *attacks* may be friendly in the sense that the insects were attracted by a special well-known smell (flower scent, e.g.) and that they only turned to aggression by the hectic behaviour of the person. When one examines carefully the sometimes-indicated ingredients of food and cosmetics, one finds several components that are also contained in pheromones (such as geraniol or citral from the Nasonov gland or *linolenic acid* and *coniferyl alcohol* of the queen retinue pheromone, e.g.) but also in forager pheromones guiding to special blossoms.

Ono and colleagues reported on alarm pheromone components of the Japanese giant hornet *Vespa mandarina* and about the fact that about 80 persons die in Japan each year after stings by Hymenopteran insects (Ono et al. 2003). They speculated whether these victims "provoked a seemingly unwarranted attack" because the venom from all seven known Japanese hornet species contains components that are also used in manufactured food and cosmetic products. Moreover, the appearance of allergies induced by wasps and honeybee stings increases worldwide and with them the fear to be stung by insects.

Therefore, it seemed worthwhile to use established experimental protocols to have a look at the actions of a broad spectrum of cosmetics (von der Heydt, unpublished results). In all experiments these were tested against isopentyl acetate as a control. Groups of 8–12 honeybees in glass vessels of about 200 ml were tested for their normal respiration rates by the previously mentioned electrolytic sensor. Then 10 ml of air, saturated with the cosmetic scent, were added, and the rate change monitored. In none of the chosen cosmetics (perfumes, after-shaves, shampoos, lotions) could a statistically significant reaction be detected on the 5% level (non-parametric Friedman test), while the reactions on isopentyl acetate were always highly significant. Thus one may generalize and conclude that there is normally no danger in using cosmetics. However, it cannot be excluded that body scent and food may have something to do with the reported effects.

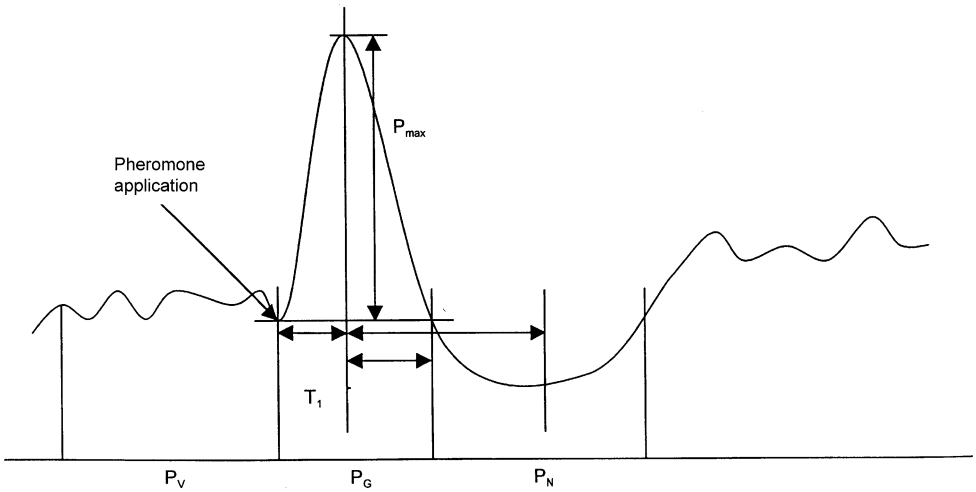

Fig. 4 Calorimetric response of a honeybee group to the application of an alarm pheromone component. The *horizontal line* gives the experimental time in arbitrary units; the *curve* represents the changing heat production rate of the group. P_V: pre-period; P_G: maximum rate; P_N: post-period. The action of the pheromone can be described by the maximum rate increase P_{max} and the time T_1 till to this point (adapted from Schmolz et al. 1999a)

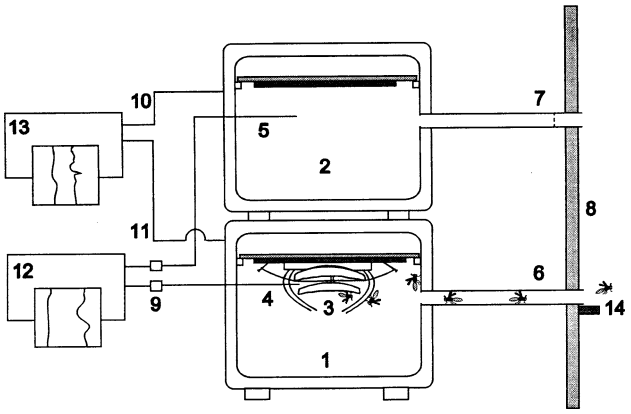

Fig. 5 Twenty-five litre twin calorimeter. 1: Reaction chamber with the hornet nest and with tube (6) to the environment; 2: reference chamber; 4,5: temperature sensors connected to a flatbed recorder (12); 8: wall of the laboratory; 10,11: connection to the heat flow sensors (Peltier elements) connected to a flatbed recorder (13)

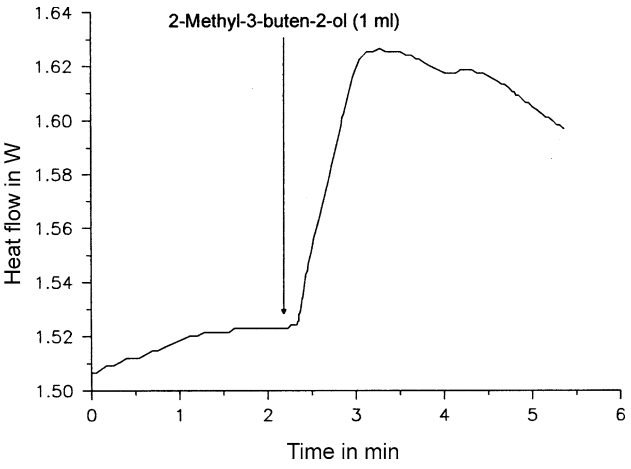

Fig. 6 Change in the heat flow of a hornet nest after the addition of an alarm pheromone component (adapted from Schmolz 1997)

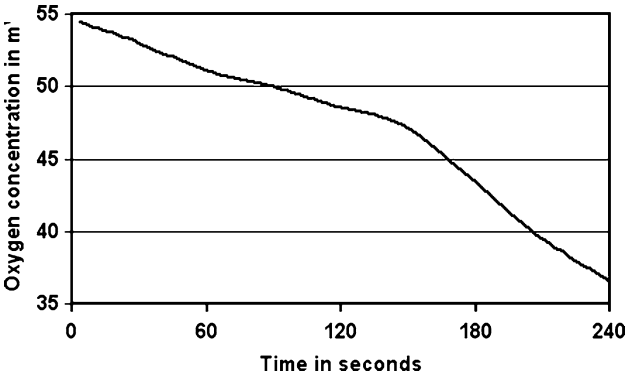

Fig. 7 Oxygen concentration in a 750 ml vessel with 149 honeybees (19.0 g fresh weight) before and after the addition of isopentyl acetate added at about 120 s. The oxygen concentration is given as the proportional electric signal in mV; 55 mV correspond to oxygen saturation. The stimulation amounts to a factor of 3.7

Conclusion

Pheromones—and odours in general—are fascinating fields for biological and biochemical investigation. They may originate from insects, other animals and even humans. Their structure is rather simple: small aliphatic and sometimes aromatic compounds with molecular weights between 100 and 200. Their composition in a pheromone with respect to number, kind and concentration makes the specific bouquet and provokes the wanted action. The evolution of the interplay between molecule and receptor was pushed forward to its absolute limit by nature (Nachtigall and Blüchel 2000): only a few or even single molecules are required for an identifiable signal in an enormous variety of other scents. A few different types of olfactory receptors and a sophisticated cooperation between them comprise the HiFi receiver of the insects. Perhaps, the perfect, chemically governed organization of social life in a bee hive or an ant nest of 10,000 of members is even more astonishing than the one odour molecule docking to the receptor of the sensilla.

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Appendix 1

With respect to pheromones, the question often arises if pheromones—which are known from unicellular yeast cells up to all classes of animals—do exist for humans too. This question is still under discussion with many hints that pheromones are important for humans also, mainly in a sociosexual context (Hatt 2004; Wysocki and Preti 2004; Shepherd 2006). After an early rather vague discussion in the book of Agosta (1992) more recent reviews (Kohl et al. 2001; Grammer et al. 2005; Fink and Sövegjarto 2006) present different aspects of their origin, detection and effects. Human apocrine glands are supposed to be the main producer of pheromones. They are located in the axillae pits and the pubic region. The fact that a functional vomeronasal organ directly connected with the limbic system exists in humans also supports the idea of pheromone activities (Monti-Bloch et al. 1998).

Axons of the receptor cells in the vomeronasal organ directly lead to the bulbus olfactorius which projects into the limbic system. Thus, the information may be received unnoticed by us. Whether the pheromones may act along this line is still discussed (Fink and Sövegjarto 2006). Nevertheless, Grammer and colleagues wrote that "human sociosexual interactions are influenced by pheromones,

even if they cannot be detected consciously" (Grammer et al. 2005).

The androstenol-androstenone-signalling system is a special focus of research. It was concluded that "… the model of humans being primarily visual creatures may require some reconsideration. Human life and interactions are influenced by pheromones whether or not affect or effect is part of our consciousness." and "Human pheromones have more potential than any other social environmental sensory stimuli to influence physiology and, therefore, behaviour." (Kohl et al. 2001). Nevertheless, doubts still exist because convincing results were only obtained under laboratory conditions until now, but not in real life. It needs carefully chosen experimental conditions to detect a—presumably weak—influence of human pheromones and body odour on the sociosexual behaviour and to prove efficacy of the commercial so-called *sexual attractants* (Fink and Sövegjarto 2006).

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