



# Chemo sense

EDITORIAL

## "Think Like an Ant"

By Graham Bell

Director, Graham Bell and Associates  
g.bell@atp.com.au

A colleague once said "to solve chemical sensing problems, *think like an ant*".

In this issue we welcome a review from one of Australia's foremost insect neuroethologists, Judith Reinhard, on how insects process chemical information, if not how they actually think. Insects are exquisite users of chemical senses. Insects have solved many problems - can we learn from them?

*New Zealand wines* are reaching new levels of excellence, assisted by programs on the sensory quality of their best styles, such as the project starting on understanding aroma and flavour of Sauvignon blanc, described in this issue of *Wine Sense*, by Wendy Parr. New Zealand's investment in sensory research on wine will leave competitor countries "eating their must".

The 7th Annual Scientific Meeting of the Australasian Association for ChemoSensory Science (AACSS) takes place at Noosa, Queensland, from 1-3 October 2004 (see <http://get-me.to/aacss>). The meeting after that will be held from 2-6 December 2005 at Heron Island. Plan your trips now ■

## Insect Chemical Communication

Judith Reinhard

Research School of Biological Sciences,  
The Australian National University,  
Canberra, ACT, Australia 2601

reinhard@rsbs.anu.edu.au

### INTRODUCTION

**Communication, signalling, and sensory perception among insects** probably invokes in most of us the image of chemical messages and chemical senses that operate through the nervous system. By various accounts, this is accurate: Whether measured by the percentage of insect species that rely on chemical messages, insect behaviours that are modulated by chemical senses, or the complexity of structures responsible for chemical signalling and perception, the chemical communication channel is a predominant feature of insects (Greenfield, 2002). The chemical channel arose quite early in the evolution of life and has been exploited for communication by many organisms from bacteria to humans. In insects it serves a variety of communicative functions, including kin and predator recognition, defence, orientation, recruitment, and mate attraction.

The small to minute body sizes of insects may be largely responsible for their general reliance on chemical senses. Typically, the opportunities for effective communication over long distances along the mechanical and visual channels are limited by the physical dimensions of insects, and their morphological and physiological constraints (Greenfield, 2002). Chemical signalling and perception, however, may not suffer such debilitating effects of scale. Considering insect body sizes and levels of structural complexity, chemical communication can offer several

## INSIDE:

Edible packaging in bad taste?

New Zealand wine study

Flavour Perception

Heron Is: 2-6 Dec 2005

cont. pg 2



TM

**E-Nose Pty Ltd**

Graham Bell and Associates Pty Ltd  
Centre for ChemoSensory Research  
ISSN 1442-9098

# Insect Chemical Communication continued

advantages over alternative modalities, not least because of its potential for very high specificity. An organism may transmit a variety of chemical signals across considerable ranges and around barriers, regulate their emission, and perceive and discriminate these compounds with a high level of sensitivity. Drawbacks are that chemical signals cannot be sent rapidly and a signaller's control over the direction in which it transmits its messages is quite limited. Additionally, it may be difficult for a receiver to localize the source of a distant chemical signal (Greenfield, 2002). Nonetheless, insects have evolved some amazingly effective mechanisms of chemical communication.

This article reviews major types of chemical communication signals with examples from the insect world. It then briefly describes the sensory mechanisms involved in insect chemoreception and concludes with some of the recent advances and progress made in the field.

## CHEMICAL COMMUNICATION SIGNALS

A broad term for chemicals involved in animal communication is semiochemical, from the Greek *semeion* sign (Law and Regnier, 1971). Semiochemicals are usually divided into two subclasses: *pheromones*, used for communication within the species (intraspecific signals), and *allelochemicals*, used for communication between species (interspecific signals).

*Pheromones* were originally defined as 'substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction, for instance a definite behaviour [releaser pheromone] or developmental process [*primer pheromone*]' (Karlson and Lüscher, 1959). While releaser pheromones, such as trail or alarm pheromones (see below), have an immediate effect on the behaviour of the receiver, primer pheromones have longer term physiological effects on the receiver, in the original definition by 'stimulating olfactory sensory neurons that send signals to the brain to release the hormones of the

endocrine system' (Wilson and Bossert, 1963). Examples of primer pheromones include caste determination in social insects such as termites, ants, bees, and wasps, and locust development rates (Wyatt, 2003). The most famous example of a primer pheromone is the honey bee queen mandibular pheromone (a mixture of two fatty acids: 9-ODA and 9-HDA) which suppresses ovary development in worker bees (Free, 1987).

*Releaser pheromones* are often divided by function. The most commonly known are *sex pheromones*, which are highly species-specific and serve to attract mates for reproduction. The first sex pheromone was identified in 1959 from the silk moth *Bombyx mori* (Butenandt et al., 1959). Many further insect sex pheromones have been identified to date and a number are commercially used in pheromone traps for pest control (Bell, 2004). Another important group are *trail pheromones*, employed by social insects for orientation and to recruit nest mates to a suitable food source. They are produced by a variety of glands and can be composed of numerous different, mostly

volatile compounds. When navigating their territory, ants and termites deposit these pheromones on the ground thus developing an extensive net of chemical routes (Hölldobler and Wilson, 1990; Pasteels and Bordereau, 1998; Kaib, 1999). Other social insects use airborne *orientation pheromones*. For example, the honeybee releases a mixture of geraniol, citral, farnesol and other minor compounds from her Nasonov gland into the air in a number of orienting situations, including nest entrance finding, forage marking, and swarming (Free, 1987; Winston, 1987).

*Alarm pheromones* are another type of pheromone most highly developed in social insects. They are often multi-component, usually composed of small and highly volatile compounds, such as mono- and sesquiterpenes or acetates, and many of them also have a defensive function (Winston, 1987; Hölldobler and Wilson, 1990; Schmidt, 1998; Quintana et al., 2003). Depending on species, alarm pheromones can trigger a panic and escape response, or simultaneously alert, attract and evoke aggression. The most famous

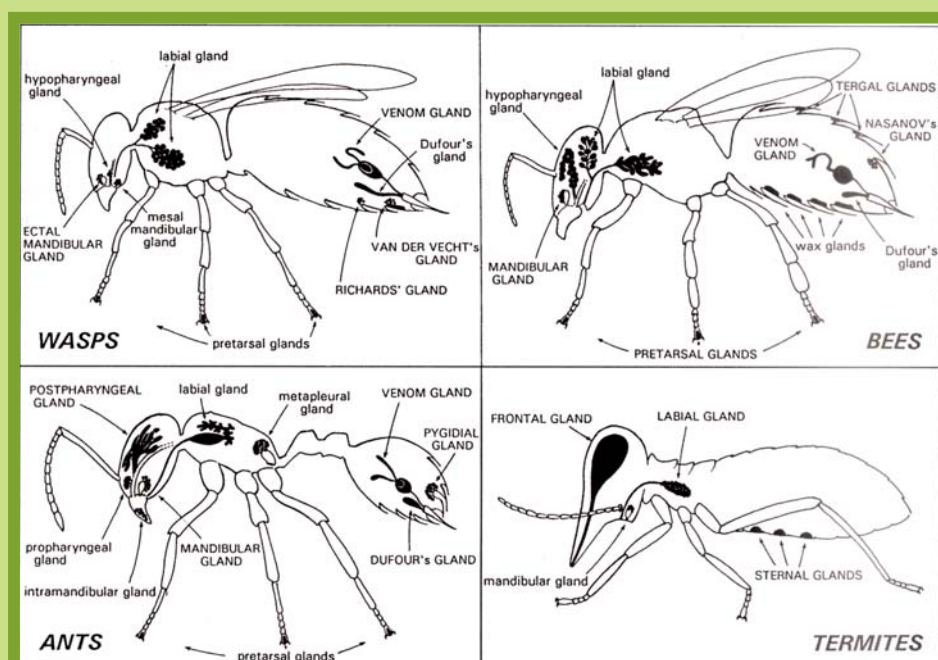


Fig. 1: Schematic profile drawings of the commonly found exocrine glands in wasps, bees, ants, and termites. Glands with a pheromonal function are given capital lettering. Figure reproduced with acknowledgement to Wyatt, 2003; original figure from Billen and Morgan, 1998.

# Insect Chemical Communication continued

example is the so-called killer bee, where the alarm pheromone from a single bee can within seconds alert the entire hive to attack and kill a potential predator (Winston, 1992). *Kin recognition pheromones*, as used for social recognition in social insects do not fit the original pheromone criterion of a 'defined chemical mixture eliciting particular behaviour or other response'. The cues used for social recognition of kin, clans, colony members and the like are complex, greatly varied mixtures of many compounds, mostly long chain hydrocarbons on the insect cuticle (Vander Meer et al., 1998). The differences between the odour mixtures in quantity and quality of compound composition are the actual message.

The best example for *aggregation pheromones* are bark beetles. The first beetles arriving on a suitable tree start to bore into the bark and release a long-range aggregation pheromone, a mixture of terpenoids some of which are synthesized de novo, others produced by symbiotic bacteria in the beetle gut or sequestered from host tree compounds (Greenfield, 2002; Wyatt, 2003). The pheromone attracts conspecifics of both sexes in great numbers, leading to a mass attack and often killing of the host tree.

*Allelochemicals*, the second subclass of semiochemicals, deal with interspecific communication. They are further divided depending on the costs and benefits to signaller and receiver (Nordlund, 1981). Chemical signals can be eavesdropped ('overheard') by unintended recipients: for example, specialist predatory beetles use the pheromones of their bark beetle prey as *kairomones* to locate them (Wyatt, 2003). Other signals are emitted in order to benefit the signaller at the cost of the receiving species. Chemical signals used in such deceit are termed *allomones*: for example, bolas spiders synthesise particular moth pheromones to lure male moths of those species into range for capture. (Wyatt, 2003). Semiochemicals benefiting both signaller and receiver in mutualisms are termed *synomones*. An example of such mutual but unintended benefit is hydroquinone, a phagostimulant secreted by many different

termite species from their labial glands (Reinhard et al., 2002). This chemical signal acts as pheromone when perceived by nest mates (=same species), however could be used as synomone when perceived by a different termite species which happens to share the same foraging territory.

The independent and multiple evolution of semiochemicals is illustrated not only by the diversity of compounds produced but also by the enormous variety of specialised secretory glands (Fig. 1). Importantly, most semiochemicals are multi-component blends, where not only the qualitative composition but also the ratio of compounds is crucial, contributing to the high specificity of chemical communication signals. Specificity can also be gained by using different stereoisomers or enantiomers of the same compound; for example, among sympatric scarab beetles in Japan (Leal, 1999), one uses (S)-japonilure as its female sex pheromone, whereas the other uses (R)-japonilure.

As this brief overview demonstrates, classification of semiochemicals rapidly becomes complicated, not least because the same chemical may be used as a pheromone within a species but may be exploited as kairomone or synomone by another. The

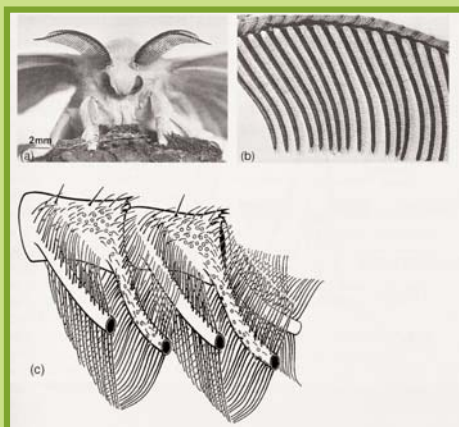


Fig. 2: (a) Male silk moth (*Bombyx mori*) showing the numerous side branches and sensillary hairs of the antennae which form an effective olfactory sieve. (b) Scanning electron micrograph close-up of the antennae. (c) Two segments of a moth antennae drawn in schematic detail. Figure reproduced and modified with acknowledgement to Wyatt, 2003, original figures from Kaissling, 1987, Steinbrecht, 1999, photo/micrographs (a), (b) by R.A. Steinbrecht.

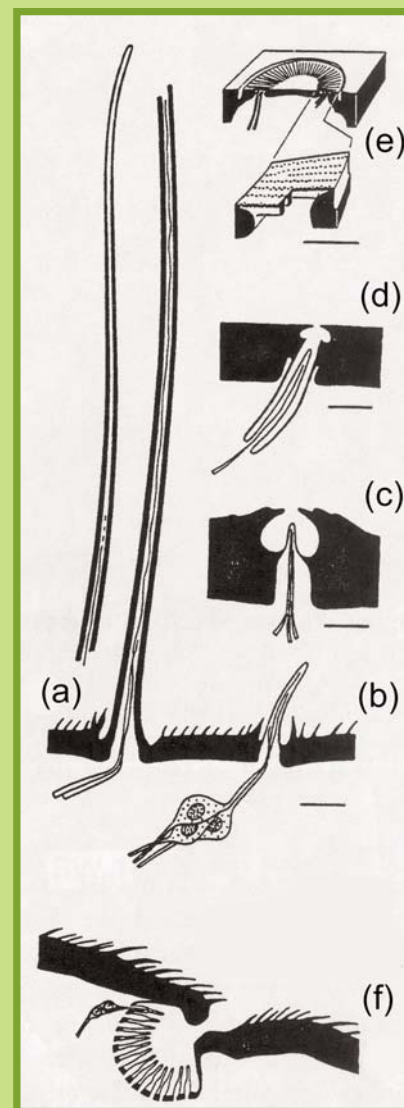


Fig. 3: Schematic outline of the different types of olfactory sensilla. All cells except chemosensory neurons omitted for clarity. (a) Sensilla trichoidea, (b) *S. basiconica*, (c) *S. coeloconica*, (d) *S. ampullacea*, (e) *S. placodea*, (f) sensilla field on antenna of the fly *Sarcophaga argyrostoma*. Scale in (a) - (d): 10  $\mu\text{m}$ , in (e): 1  $\mu\text{m}$ . Figure reproduced and modified with acknowledgement to Kaib, 1999; original figure from Kaissling, 1971.

above definitions should therefore be used with caution, always keeping in mind that the insect chemical world is much more complex and intertwined than we might be aware of.

## INSECT CHEMORECEPTION

The insect antennae are the major organs for

cont. pg 4

# Insect Chemical Communication continued

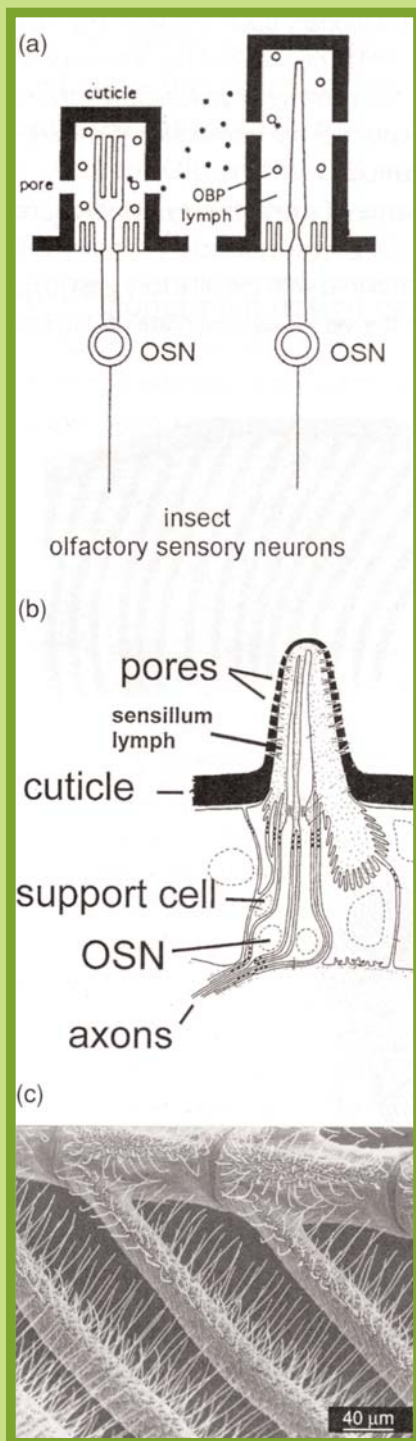


Fig. 4: (a) Schematic diagram and (b) drawing of chemosensory sensilla showing odour molecules diffusing through pores in the cuticle of the sensillum, and carried by odorant binding proteins (OBP) through the sensillum lymph to the olfactory sensory neuron (OSN). (c) Scanning electron micrograph of silk moth antenna, showing long trichoideal sensilla. Figure reproduced and modified with acknowledgement to Wyatt, 2003; original figures from Hildebrand and Shepherd, 1997, Kaissling 1998, Steinbrecht 1999, photo/micrograph by R.A. Steinbrecht.

perception of chemical signals (Fig. 2). They carry chemosensory sensilla in great numbers and of various types (Fig. 3). However, the key sense insects use to detect the chemical cues in their environment is olfaction rather than what we know as taste from vertebrates. Taste in insects refers to contact chemoreceptors, i.e. sensilla that need to come into direct contact with a cue that is non-volatile or of very low volatility. As in the case of an ant tapping its antennae on a fellow ant to detect the complex mixtures of long-chain hydrocarbons on its cuticle that allow distinction of nest mates from strangers. If considering invertebrates it is often difficult to make a clear distinction between olfaction and taste, as some cues can be perceived by both olfactory and gustatory sensilla depending on the physical phase a cue occurs in at a specific moment. Therefore, it may be better to use 'chemoreception' as a more conclusive term for insects covering both olfaction and taste (Wyatt, 2003).

Across the animal kingdom, chemoreceptive systems are remarkably similar. All have chemosensory neurons with one end exposed to the outside world, in case of insects sheathed by a sensillum, the other end extending into the processing centres of the nervous system (Fig. 4). In insects, a chemical signal enters the sensillum lymph through a pore, where it first binds to pheromone- or odorant-binding proteins (BPs: PBPs and OBPs, respectively), the former often highly specific (Wyatt, 2003) (Fig. 4, 5). It is believed that the signal-PBP/OBP-complex is then transported to the chemosensory neuron, where it binds to a specific olfactory receptor protein (OR or R) in the neuron membrane (Fig. 5). In insects, the first of these receptor proteins were only identified in 1999 (Clyne et al., 1999; Vossahl et al., 1999). They all belong to the same 'seven-transmembrane-domain' protein family, however they differ between taxa a great deal (Pilpel and Lancet, 1999).

From a molecular perspective, binding to the OR activates so-called G-proteins, which are also located in the neuron membrane and part of a phosphorylation dependant energy exchange, triggering a cascade of

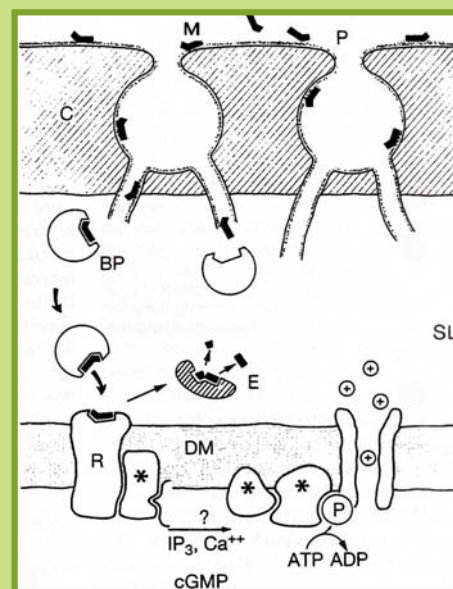


Fig 5: Simplified schematic concept of perireceptor events in insect chemosensory sensilla. Absorbed stimulus molecules (M) diffuse from the hair surface through pores (P) in the cuticle (C) into the sensillum lymph (SL). There, they are taken up by odorant- or pheromone-binding proteins (BP) and are transported through the aqueous lymph until they reach a specific receptor molecule (R) on the outer dendritic membrane (DM). This activates dendritic ion channels via membrane bound proteins (\*) and intracellular second messenger cascades. The stimulus molecule is degraded by specific enzymes (E) into inactive metabolites so that it can no longer activate the receptor. Figure reproduced and modified with acknowledgement to Kaib, 1999; original figure from Boeckh, 1995.

signalling reactions (Fig. 5). These eventually lead to electrical impulses being sent down the axon of the neuron to the antennal lobe (AL) (Fig. 6). The AL is structured into a number of neuron groups (glomeruli) that are innervated separately and only in response to specific, individual odours or classes of chemically similar ones (Hansson, 1999). From the AL the processed signal is then sent on to higher integrative centres of the brain, such as the mushroom bodies (MB, Fig. 6), which are believed to be involved in the control of complex behaviours.

As an insect moves through its environment, it is constantly bombarded by a large number of chemicals and it has the ability to detect, discriminate and distinguish innumerable different molecules as different odours. However, not all chemicals are detected and perceived as

# Insect Chemical Communication continued

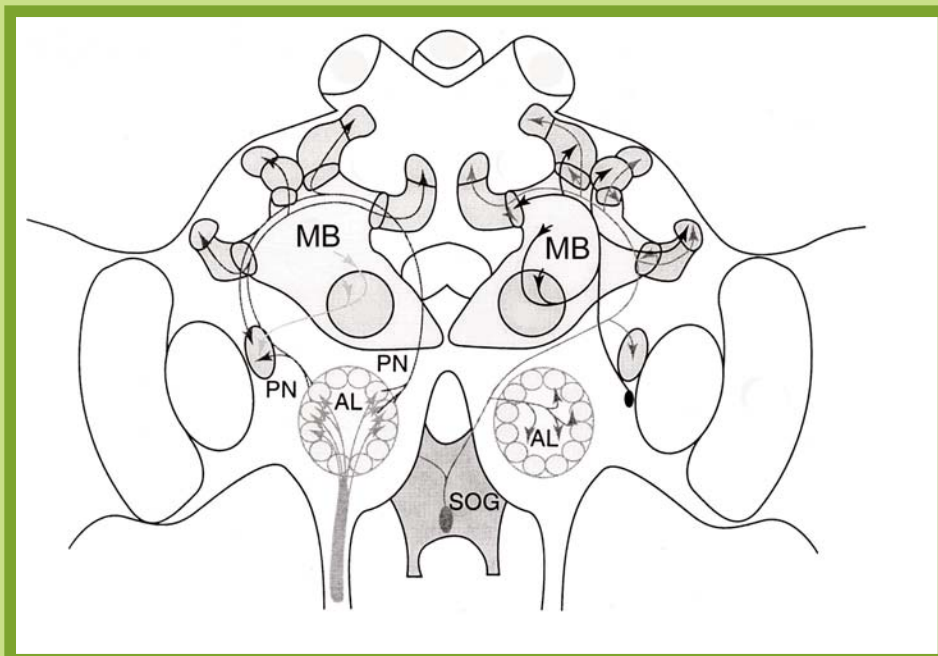


Fig. 6: Schematic view of the central brain area of the honeybee showing the antennal lobes (AL) with their specific glomeruli (small circles). From the AL projection neurons (PN) send olfactory information into the mushroom bodies (MB). The MBs are higher order integration centres of olfactory, visual, and mechanosensory information and are believed to play a role in control of complex behaviours as well as learning and memory. SOG: sub-oesophageal ganglion. Figure modified and reprinted from Trends in Cognitive Sciences, 5, Menzel, R. and Giurfa, M., Cognitive architecture of a mini-brain: the honeybee, pp. 62-71, Copyright (2001), with permission from Elsevier.

described above. Only the molecules for which evolutionary pressures have led to the development of specific binding proteins and specific receptor sites present on individual chemosensory neurons will be recognised. This selectivity bestowed upon chemosensory neurons by the receptor types expressed represents one level of signal filtering in the insect olfactory system. Further levels of filtering are accomplished after these signals reach the AL glomeruli. It is within the glomeruli that each of the different features of the olfactory signals - their quality, quantity, and temporal and spatial characteristics - are filtered out and represented as specific patterns of neural activity to higher brain centres (Hansson, 1999).

## RECENT ADVANCES

Classical methods for the study of insect chemical communication include behavioural assays using extracts of whole insects, their glands or synthetic compounds to modulate insect behaviour.

Chemical signals are characterised and isolated using methods of chemical analysis specific to the signal's molecular characteristics. The most common ones are High Performance Liquid Chromatography (HPLC), Gas Chromatography (GC) coupled with Mass Spectrometry (GC-MS) or an ElectroAntennographic Detector (GC-EAD). The latter uses insect antennae as biological detectors greatly facilitating identification of the active compounds from complex mixtures (Rostelien et al., 2000) (Fig. 7). Biosynthetic pathways of signal production are studied using radioactive labelling of precursors in the insect itself or in potential food sources.

On a neurophysiological level, insect chemoreception has been studied for decades recording activity from whole insect antennae (electroantennograms, EAG) or from single neurons (single cell recordings, SCR). In the last couple of years the development of sophisticated imaging techniques for insects has led to the discovery of the olfactory code, i.e. how different molecules are represented in the higher brain centres (Joerges et al., 1997; Sachse et al., 1999; Galizia and Menzel, 2000). As these studies are carried out in

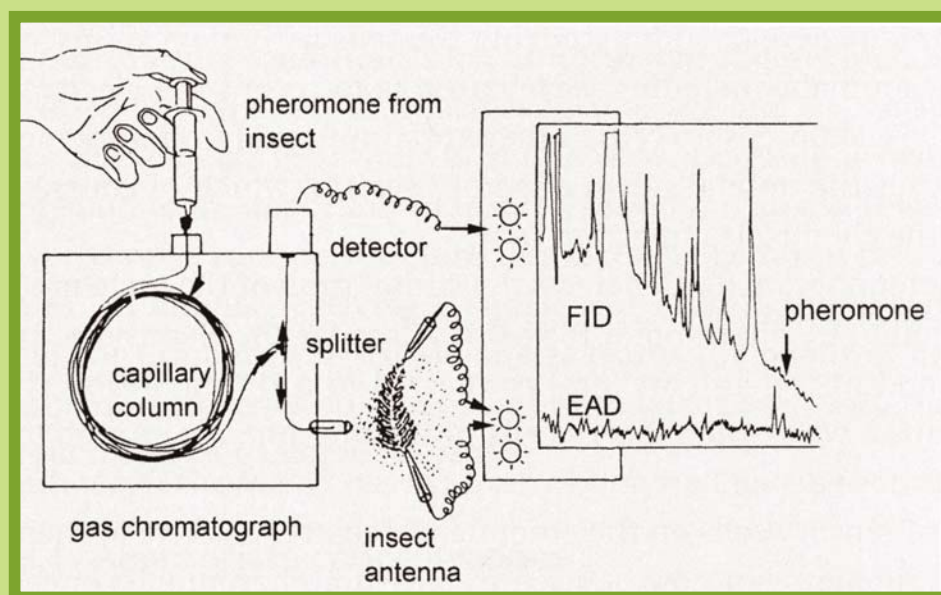


Fig. 7: GC-EAD, a powerful way of identifying possible semiochemical components. The gas chromatograph (GC) separates the mixture of compounds into a series of peaks, which are detected by the FID. Part of the GC output is diverted over the electroantennographic detector (EAD, an insect antenna), which reacts only to certain biologically active components of the mixture. The FID and EAD traces are lined up so that the positive EAD responses can be matched up with the GC peaks. Figure reproduced and modified with acknowledgement to Wyatt, 2003; original figure from Löfstedt, 1986; artist J. van der Pers.

cont. pg 6

# Insect Chemical Communication continued

vivo on an insect brain, they also shed light on synaptic plasticity, that is how the odour representation in the brain changes over time, covering phenomena such as adaptation, habituation and memory formation. Combined with the brand new neuroanatomical method of micro tomography - currently only in use in Switzerland - imaging studies might help us unravel the mystery of learning and memory.

With the completion of the *Drosophila melanogaster* genome project and more recently the sequencing of the mosquito, honeybee, and silk moth genomes, a new era of research in insect chemical communication has begun. Numerous studies on odorant- and pheromone binding proteins have been published and the discovery of the first olfactory receptor proteins in *Drosophila* (Clyne et al, 1999; Vosshall et al, 1999) has led to many new studies on ORs and the chemical signal transduction pathways in insects. The discoveries from molecular genetics are likely to greatly expand our knowledge concerning the role and evolution of these receptor proteins in chemical communication systems. The recent rapid progress in understanding chemoreception will continue as powerful new technologies in genomics, molecular genetics, neuroanatomy and imaging are combined with classical methods from chemistry and animal behaviour. For perhaps the first time, we can now investigate questions of chemical causality at every level: molecular, neurobiological, behavioural, ecological, and evolutionary.

## ACKNOWLEDGEMENTS

Charles Claudianos, RSBS, ANU provided comments on an earlier draft of the manuscript. I especially thank the authors M. D. Greenfield (2002) and T. D. Wyatt (2003) for their excellent and informative books, which were of great help in preparing this review.

## REFERENCES

- Bell, R. 2004. Pheromone traps. *ChemoSense* **6**: 5-6.
- Billen, J., and Morgan, E.D. 1998. Pheromone communication in social insects: sources and secretions. In *Pheromone communication in social insects: ants, wasps, bees, and termites*. R.K. Vander Meer, M.D. Breed, K.E. Espelie and M.L. Winston (eds.), Westview Press, Colorado, USA: 3-33.
- Boeckh, J. 1995. Chemische Sinne. In *Physiologie der Insekten*. M. Gewecke (ed.), Fischer Verlag, Stuttgart, Germany: 313-351.
- Butenandt, A., Beckmann, R., Stamm, D. and Hecker, E. 1959. Über den Sexuallockstoff des Seidenspinners *Bombyx mori*: Reindarstellung und Konstitution. *Z. Natforsch. B* **14**: 283-284.
- Clyne, P.J., Warr, C.G., Freeman, M.R., Lessing, D., Kim, J.H. and Carlson, J.R. 1999. A novel family of divergent seven-transmembrane proteins: candidate odorant receptors in *Drosophila*. *Neuron* **22**: 327-338.
- Free, J.B. 1987. *Pheromones of social bees*. Cornell University Press, Ithaca, USA.
- Galizia, C.G. and Menzel, R. 2000. Odour perception in honeybees: coding information in glomerular patterns. *Curr. Opin. Neurobiol.* **10**: 504-510.
- Greenfield, M.D. 2002. *Signalers and receivers: mechanisms and evolution of arthropod communication*. Oxford University Press, Oxford, UK.
- Hansson, B.S. 1999. *Insect olfaction*. Springer Verlag, Berlin, Germany.
- Hildebrand, J.G. and Shepherd, G.M. 1997. Mechanisms of olfactory discrimination: converging evidence for common principles across phyla. *Ann. Rev. Neurosci.* **20**: 595-631.
- Hölldobler, B. and Wilson, E.O. 1990. *The ants*. Harvard University Press, Cambridge, USA.
- Joerges, J., Küttner, A., Galizia, C.G. and Menzel, R. 1997. Representation of odours and odour mixtures visualized in the honeybee brain. *Nature* **387**: 285-288.
- Kaib, M. 1999. Chemorezeption. In *Lehrbuch der Entomologie*. K. Dettner and W. Peters (eds.), Gustav Fischer Verlag, Stuttgart, Germany: 302-320.
- Kaissling, K.E. 1971. Insect olfaction. In *Handbook of sensory physiology*, Vol. IV. L.M. Beidler (ed.), Springer Verlag, Berlin, Germany: 351-431.
- Kaissling, K. E. 1987. *R.H. Wright lectures on insect olfaction*. K. Colbow (ed.), Burnaby, BC, Simon Fraser University.
- Kaissling, K. E. 1998. Olfactory transduction in moths: I. Generation of receptor potentials and nerve impulses. In *From structure to information in sensory systems*. C. Taddei-Ferretti and C. Musio (eds.), World Scientific, Singapore: 93-112.
- Karlson, P. and Lüscher, M. 1959. 'Pheromones': a new term for a class of biologically active substances. *Nature* **183**: 155-156.
- Law, R.H. and Regnier, F.E. 1971. Pheromones. *Ann. Rev. Biochem.* **40**: 533-548.
- Leal, W.S. 1999. Scarab beetles. In *Pheromones of non-lepidopteran insects associated with agricultural plants*. J. Hardie and A.K. Minks (eds.), CAB International, Wallingford, UK: 51-68.
- Löfstedt, C. 1986. Sexual feromoner och reproductiv isolering hos natfjärilar. *Entomologisk Tidskrift* **107**: 125-137.
- Menzel, R. and Giurfa, M. 2001. Cognitive architecture of a mini-brain: the honeybee. *Trends Cogn. Sci.* **5**: 62-71.
- Nordlund, D.A. 1981. Semiochemicals: a review of the terminology. In *Semiochemicals: their role in pest control*. D.A. Nordlund, R.L. Jones and W.J. Lewis (eds.), John Wiley, New York, USA: 13-28.
- Pasteels, J.M. and Bordereau, C. 1998. Releaser pheromones in termites. In *Pheromone communication in social insects: ants, wasps, bees, and termites*. R.K. Vander Meer, M.D. Breed, K.E. Espelie and M.L. Winston (eds.), Westview Press, Colorado, USA: 193-215.
- Pilpel, Y. and Lancet, D. 1999. Good reception in fruitfly antennae. *Nature* **398**: 285-287.
- Quintana, A., Reinhard, J., Faure, R., Uva, P., Bagnères, A.G., Massiot, G. and Clement, J.L. 2003. Interspecific variation in terpenoid composition of defensive secretions of European *Reticulitermes* termites. *J. Chem. Ecol.* **29**: 639-652.
- Reinhard, J., Lacey, M.J., Ibarra, F., Schroeder, F.C., Kaib, M. and Lenz, M. 2002. Hydroquinone: a general phagostimulating pheromone in termites. *J. Chem. Ecol.* **28**: 1-14.
- Rostelien T., Borg-Karlson A.K. and Mustaparta, H. 2000. Selective receptor neuron responses to E-beta-ocimene, beta-myrcene, E,E-alpha-farnesene and homo-farnesene in the moth *Heliothis virescens*, identified by gas chromatography linked to electrophysiology. *J. Comp. Physiol. A* **186**: 833-847.
- Sachse, S., Rappert, A. and Galizia, C.G. 1999. The spatial representation of chemical structures in the antennal lobe of honeybees; steps towards the olfactory code. *Eur. J. Neurosci.* **11**: 3970-3982.
- Schmidt, J.O. 1998. Mass action in honey bees: alarm, swarming and the role of releaser pheromones. In *Pheromone communication in social insects: ants, wasps, bees, and termites*. R.K. Vander Meer, M.D. Breed, K.E. Espelie and M.L. Winston (eds.), Westview Press, Colorado, USA: 257-290.
- Steinbrecht, R.A. 1999. Olfactory receptors. In *Atlas of arthropod sensory receptors. Dynamic morphology in relation to function*. E. Eguchi, Y. Tominaga and H. Ogawa (eds.), Springer Verlag, Tokyo, Japan: 155-176.
- Vander Meer, R.K., Breed, M.D., Espelie, K.E., and Winston, M.L. 1998. *Pheromone communication in social insects: ants, wasps, bees, and termites*. Westview Press, Colorado, USA.
- Vosshall, L.B., Amrein, H., Morozov, P.S., Rzhetsky, A. and Axel, R. 1999. A spatial map of olfactory receptor expression in the *Drosophila* antenna. *Cell* **96**: 725-736.
- Wilson, E.O. and Bossert, W.H. 1963. Chemical communication among animals. *Rec. Progr. Hormone Res.* **19**: 673-716.
- Winston, M.L. 1987. *The biology of the honey bee*. Harvard University Press, Cambridge, USA.
- Winston, M.L. 1992. *Killer bees: the Africanized honey bee in the Americas*. Harvard University Press, Cambridge, USA.
- Wyatt, T.D. 2003. *Pheromones and animal behaviour: communication by smell and taste*. Cambridge University Press, Cambridge, UK ■