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Reviews

Olfaction in Lepidoptera

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Received 14 September 1994; received after revision 16 January 1995; accepted 27 March 1995

Abstract. Odours play a very important role in the life of insects belonging to the order Lepidoptera. In the present paper, a review is given of the current knowledge of morphology, development and function of the olfactory system in larval and adult moths and butterflies. Research regarding both the antennal and accessory olfactory pathways, as well as both the pheromone and the host odour detecting systems, is reviewed.
Key words. Olfaction; olfactory receptor neuron; sensillum; antenna; antennal lobe; glomerulus; pheromone; kairomone; host odour; Lepidoptera.

Introduction

The function and morphology of the olfactory system both in vertebrates and invertebrates have attracted much attention[49,177,178,189]. Several obstacles have limited the possibility of attacking the different aspects involved, e.g. finding the relevant stimuli for investigations of olfactory function, and inaccessible neural units. In the Lepidoptera these obstacles have been overcome by the identification of very specific olfactory stimuli, i.e. semiochemicals, and by the development of methods to record neural activity from, and biochemical processes taking place in, both peripheral and central olfactory neurons, and methods to stain these neurons for morphological analysis.

Moths and butterflies depend to a great extent on olfactory cues as markers of attractive or unattractive sources. This olfactory dependence holds true for activities involved both in reproduction and food search. Conspecific mates often communicate by means of sexual pheromones[10], ovipositing females are attracted to the odour of suitable host plants[165], while larvae on a crowded host plant can emit repelling odour signals to conspecific females looking for a suitable oviposition site[6].

The function of lepidopteran olfaction did not open up to investigation until Dietrich Schneider and coworkers developed methods to record neural responses from the lepidopteran 'nose', the antenna[176,179]. Around the same time, Butenandt[29] identified the first moth sex pheromone from an extract of 500,000 females of the silk moth, *Bombyx mori*. These two events initiated a long chain of investigations on the function of the peripheral olfactory sense in Lepidoptera. When Boeckh and Boeckh[20] managed to record action potentials extracellularly, and Matsumoto and Hildebrand[136] intracellularly, from interneurons situated in the primary olfactory centres of the moth brain, the antennal lobes, they made it possible to go one step further in the investigation of the olfactory system in Lepidoptera.

During the last 30 years, a large number of investigations of both the peripheral and the central lepidopteran olfactory system has been published[135a,178]. These studies have resulted in a much greater understanding of how these systems work, and how they are connected with behaviour. In this review, I aim at compiling the knowledge regarding different aspects of lepidopteran olfaction that has been accumulated in recent years to provide a base for future work in the area and to allow researchers outside the area to obtain concise information from a single source.

Olfactory guided behaviours

Behaviourally important odour input in the Lepidoptera can be divided into two main groups; insect-produced odours and plant-produced odours. The insect-produced odours are often involved in intraspecific communication, as pheromones, while the plant-produced odours are used as cues for determining the suitability of foraging sites for oviposition and feeding. What are the problems a moth or a butterfly has to solve with its olfactory system? The larva's main problem is food, so its olfactory receptors should be devoted to this end. An adult male moth has to be able to detect the female moth, often over a great distance. He has to be able to follow the pheromone plume from the moment of first encounter with the pheromone odour molecules to the endpoint of physical contact with the female. It might also be in the male moth's interest to be able to detect odours emitted from the plant where the female is sitting, and if the male forages during adulthood, he has to be able to detect flower scents. The female moth primarily needs to detect different oviposition cues that may indicate host plant suitability and presence of potential competitors or co-habitants. In many species, the female also needs to detect the male short-distance sex pheromone, which has been proposed

to give her a means of measuring the male's quality. If the female seeks nectar, she has to be able to detect nectar-rich flowers. In some species, the sexual roles are reversed or changed, so that the female uses sensitive pheromone detectors to locate the male[119,186,229,231]. The part of the system involving plant compound and oviposition cue detection holds true also for butterflies. With regards to sex pheromone communication, butterflies use sex pheromones only for close range attraction, so the very sensitive pheromone detection system typical of male moths is not present[25].

Sex pheromone communication among moths has been intensely studied, and the behaviours elicited are well known[10]. A long distance attractant released by the female evokes a more or less stereotyped response from the male. The different phases of this behaviour have been studied in wind tunnel experiments[9,30,108,117,131] and in tethered flight experiments[161]. In brief, the male gets aroused, takes flight and orients into the pheromone plume. After entering the plume, the male often initiates a zigzagging flight pattern[9]. The male reaches the bait, lands and often performs a hair pencil display. During this display, the male releases a short distance pheromone, an aphrodisiac, aimed at attracting the female's attention for the eventual copulation[157,158]. Even if the bait consists of the synthetic pheromone blend applied to a piece of rubber, bearing no visual resemblance to a female moth, the male moth often makes copulation attempts. In butterflies, only close range orientation towards a mate has been observed to be guided by sex pheromones[25,172].

Similar behaviours as those released by sex pheromones can be evoked by plant-produced odours. Both male and female moths have been shown to fly upwind towards compounds identified from a nectar-producing flower[79]. Female moths and butterflies orient towards odours released by suitable host plants[77]. Oviposition can be stimulated or deterred by odours. Female moths have been shown to refrain from oviposition where odours identified from larval frass or conspecific eggs are present[6,15]. A lepidopteran larva can detect odours emitted by the host plant[44–46,184,185], and food-seeking and host choice can be elicited by these odours[38,65].

Morphological characteristics of the lepidopteran olfactory system

Peripheral olfactory organs

The main olfactory organ of the Lepidoptera is the antenna (figs 1 and 2). The larval antenna is very simple, consisting of only three segments. On the larval antenna, three olfactory sensilla, together housing 16 olfactory receptor neurons, are present in the species investigated so far[48,184]. On the adult antenna, up to

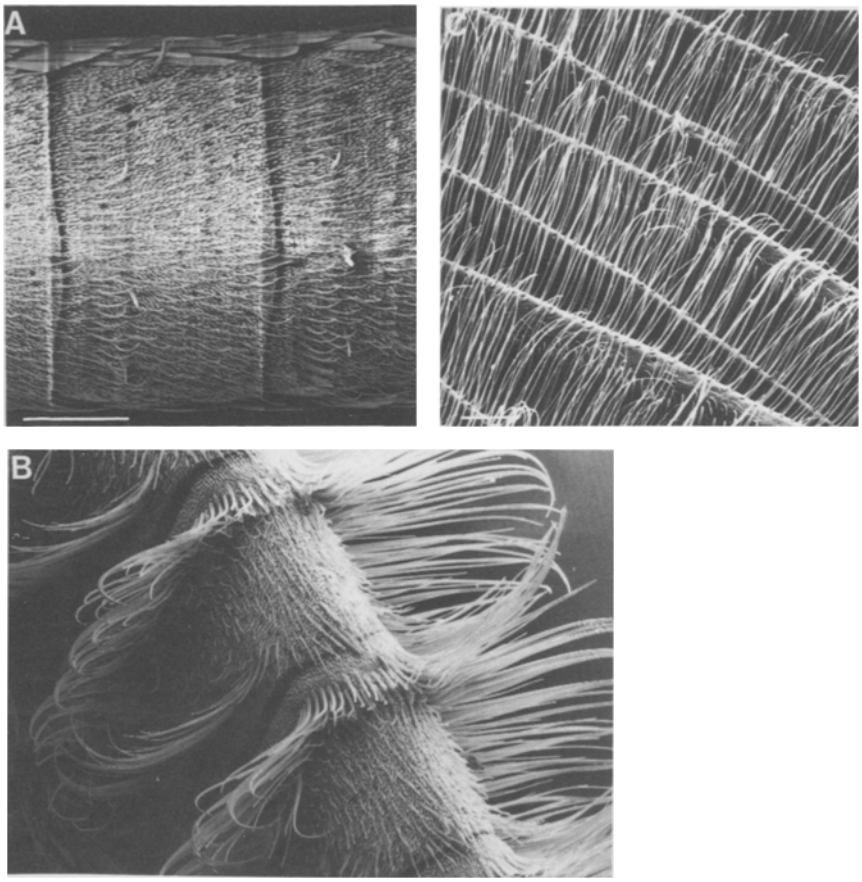

Figure 1. *A*, *B*) Antennal segments of a female and a male *Deilephila elpenor*, a sphingid moth. Note the strong sexual dimorphism. Scale bar = 100 µm. *C*) Antennal branches of the male saturniid moth *Antheraea polyphemus*. The branches and the sensilla form a veritable molecular sieve, to catch the female sex pheromone molecules. Scale bar = 100 µm. (E. Hallberg, unpubl.)

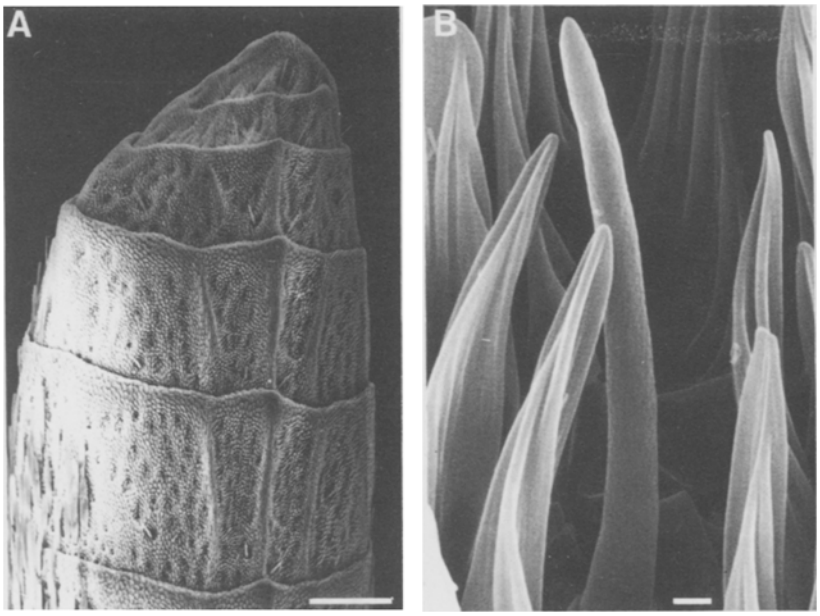

Figure 2. *A*) The distal tip of a butterfly antenna, the head of the club-shaped olfactory appendage. Scale bar = 100 μm. *B*) A sensillum basiconicum on the butterfly antenna. The sensillum is surrounded entirely by scales protruding from the antennal surface. Scale bar = 2 μm. (E. Hallberg, unpubl.)

100,000 sensilla[123], each containing a number of sensory cells, functioning as odour detectors, are present. The antenna displays different outer morphology in the different types of Lepidoptera. In the day-flying butterflies, which depend more on visual stimuli than on olfactory cues, the antenna is thin and club shaped (fig. 2)[42,58,146,153], while the other extreme is present in certain male moths, where the antenna is plumose, with a large area, adapted to detect a few odour molecules (fig. 1)[59,194].

The adult moth antenna has been intensely studied in both sexes, and the antennae often display a pronounced sexual dimorphism. In most species, the female antenna is filiform, or slightly pectinate with a moderate number of short-to-medium length sensilla, while the male antenna ranges from being filiform in some species, to being extremely developed as a molecular sieve. The sieve is accomplished by the larger number of sensilla present on the male antenna, and the greater length of these sensilla. This extreme male adaptation is found in species using female, long-distance sex pheromones (fig. 1)[194].

Olfactory receptors are also present on the maxillae of the larva[47,65,184] and on the labial palps of adult moths and butterflies[122]. On the palp, the olfactory sensilla are present in the so-called labial palp pit.

Different morphological types of sensilla, present on the antenna, are responsible for the detection of odours in the insect's environment (figs 3 and 4). All of the olfactory sensillum types display the same basic inner morphology (fig. 5), but range from long slender sensilla trichodea to sensilla coeloconica situated in cuticular pits[102,123,192,194,230]. One to several receptor cells send dendrites into the lumen of the cuticular part of the sensillum. In the lumen, the outer dendritic segments are surrounded by sensillum lymph. The cuticle of the sensillum is perforated by a number of pores or slits, allowing the entrance of odour molecules into the sensillum lymph. The cell bodies of the receptor cells are situated below the base of the sensillum. There they lie surrounded by three types of auxiliary cells: the thecogen, the tormogen and the trichogen cell. These cells are involved in the formation of the sensillum during ontogeny, and in the regulation of the ionic composition of the sensillum lymph[50,59,102,153,195]. From the cell body, an axon projects into the ipsilateral antennal lobe[70,116].

The most well-investigated sensillum type is the s. trichodeum (figs 3B and 4A, B), which is involved in sex pheromone and in host odour detection. The external morphology of this type is, as the name implies, hair-like. The length of the hair can vary greatly. The lepidopteran s. trichodeum usually contains 1–3 sensory cells that send unbranched outer dendritic segments into the hair lumen (fig. 4A and B)[50,195]. The outer dendritic segment tapers towards the distal part[69,99]. In the silkmoth, *Antheraea polyphemus*, the dendritic outer segment has nodes moving along its length[101,227]. The surface of the sensillum is penetrated by a moderate number of pores[99]. Another hair-like sensillum type is the s. basiconicum (figs 3B and 4C). This type is shorter than the s. trichodeum, has a larger number of surface pores, and the sensory cells, which are usually in about the same number as in the s. trichodea, have dendritic outer segments that branch profusely[194]. The s. basiconica have been shown to be involved both in pheromone and in host-odour detection[54,85]. Larval olfactory sensilla are of this type[44,45,184].

Two additional olfactory sensillum types, whose functions are less well known, are the s. auricillica (figs 3C and 4E) and the s. coeloconica (figs 3D and 4D). The

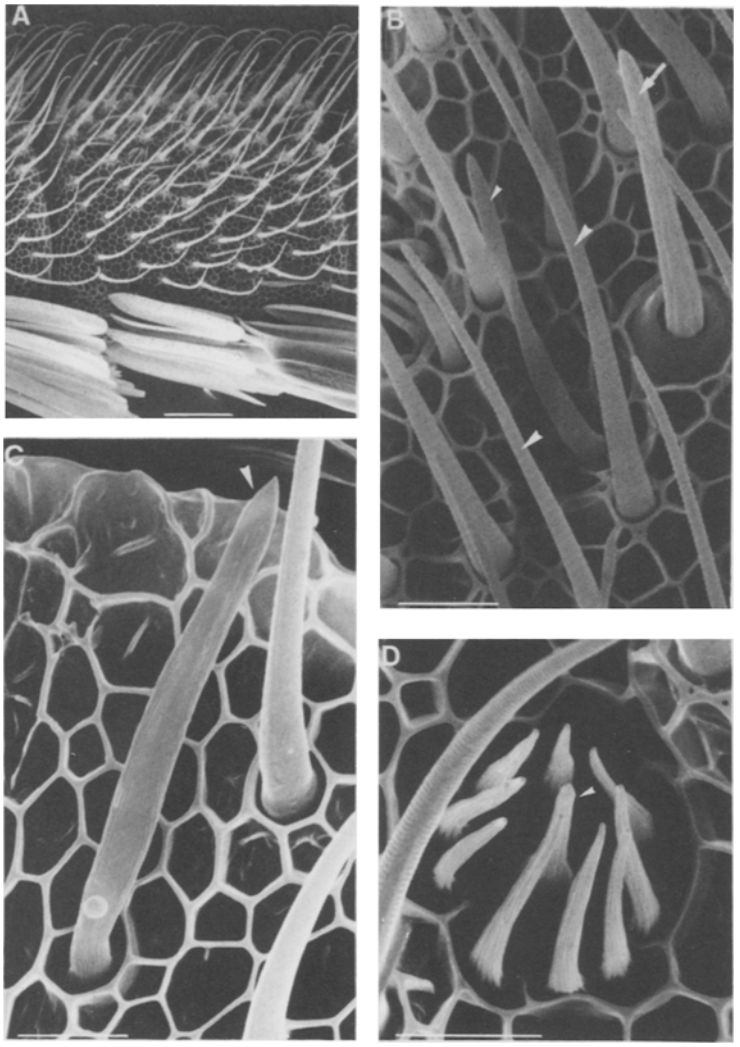

Figure 3. *A*) A segment of the male *Ostrinia nubilalis* antenna. Four types of olfactory sensillum types are present. Scale bar = 100 μm. *B*) Two types of olfactory sensilla, the sensillum trichodeum (large arrowhead) and the sensillum basiconicum (small arrowhead). A mechanosensitive sensillum chaeticum can also be seen (arrow). *C*) A sensillum auricillicum (arrowhead). *D*) A sensillum coeloconicum. The arrowhead points at the sensillum proper, which is surrounded by a 'fence' of cuticular spines [61]. Scale bar in *B*, *C* and *D* = 5 μm.

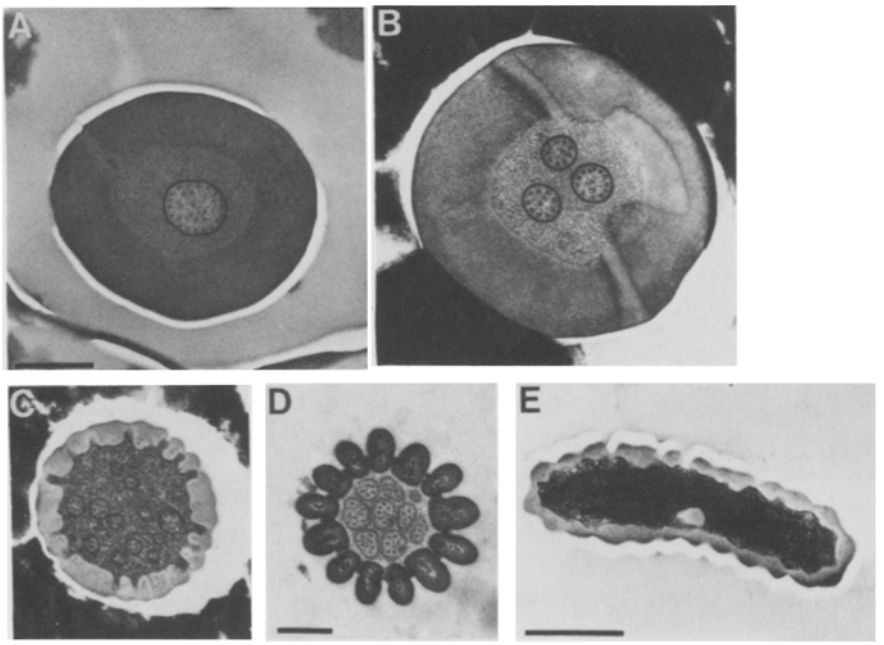

Figure 4. Transmission electron micrographs of sections through the different types of olfactory sensilla present on lepidopteran antennae. *A*) A sensillum trichodeum containing one receptor neuron. Scale bar = 500 nm. *B*) Sensillum trichodeum containing three receptor neurons. Scale the same as in *A*. *C*) A sensillum basiconicum. The receptor neurons have branched at this level, giving rise to multiple arbours. Scale the same as in *A*. *D*) A sensillum coeloconicum. Scale bar = 500 nm. *E*) A sensillum auricillicum. Scale bar = 500 nm [61].

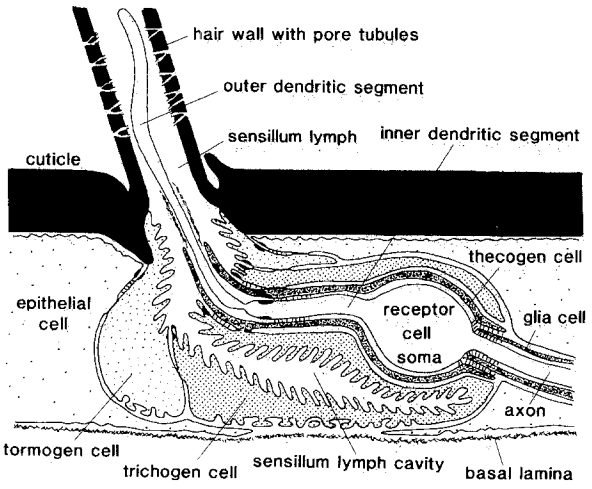

Figure 5. Schematic drawing of a lepidopteran olfactory sensillum. The receptor neuron cell body lies surrounded by the three supporting cells, the thecogen, the trichogen and the tormogen cell. These cells also form the borders for the outer and inner sensillum lymph cavities. The outer dendritic segment constitutes the receptor neuron's sensory part. The signal is propagated to the central nervous system, i.e. the antennal lobe, via the receptor neuron axon. (Redrawn after an original by T. A. Keil[87].)

s. auricillica can have a very varied appearance, from raisin-shaped to ear-shaped[59–61,102,230]. Functionally, these sensilla are involved in plant odour detection[43,142]. The s. coeloconica consist of a peg-shaped sensillum situated in a pit. The pit is often surrounded by a fence of cuticular protrusions[59–61,102,230]. Nothing is known about the function of sensilla coeloconica.

All or most of these sensillum types are present on the antenna in different moth species. The butterfly antenna is less developed for extreme sensitivity. In *Pieris brassicae*, a groove along the flagellum, facing forward during flight, houses the sensilla. Some sensilla are also found scattered over the forward facing surface of the antenna.[42]. A similar arrangement is seen in other butterflies (fig. 2)[58,146,153]. In *P. brassicae*, trichoid, basiconic and coeloconic sensilla have been observed[42]. In three other butterfly species investigated, other names were assigned to the sensilla, but the morphological characteristics reported also put these sensilla into the three categories reported in *P. brassicae*. No clear sexual dimorphism has been reported in the antennal morphology or sensillar setup in butterflies[42]. Some subtle differences between the sexes were, however, demonstrated in *Euphydras editha*[153].

The sensilla present in the labial palp pit display morphological characteristics typical of olfactory sensilla. Numerous pores penetrate a grooved sensillum surface. A single dendrite lies surrounded by the sensillum lymph. The dendrite is more or less cylindrical in its proximal part, but towards the tip of the sensillum, the dendrite becomes lamellated and folded[24,122]. The receptor neurons present in the labial palp pit sensilla have been demonstrated to respond to CO_2 in the moth *Heliothis armigera* and in *Rhodogastria* moths[24,191].

In the larva, olfactory sensilla basiconica are present on the galeal maxillae[44]. These sensilla are multiply innervated, and respond to a broad spectrum of plant odours[111,185].

Antennal development

The development of the antenna and its sensilla has been studied in detail in the male silkmoth, *A. polyphemus*[100]. In the pupa, it is known that the antenna develops from a flattened epidermal sack[103]. This epithelium differentiates and gives rise to sensillar and to non-sensillar regions. Each sensillum springs from a congregation of 6–7 cells, giving rise to the sensory and the supporting cells[104]. The sensilla develop into their final shape during the first 10 days of the pupal phase[105]. During the final 10 days, the antenna develops its adult shape, including the cuticular layer. In the sphinx moth *Manduca sexta*, all the neurons on the flagellum develop in synchrony[173]. In *A. polyphemus* some differences have been observed in the time of appearance of different sensillar types[105].

Neural structures start appearing shortly after pupal ecdysis, but the functional properties of the peripheral olfactory system do not appear until later. In an electroantennographic investigation of excised antennae from *M. sexta* pupae and adults, it was shown that the antennae start responding to pheromone stimuli a few days before eclosion, but the EAG response continues to increase until the moth has reached an age of three days[187]. One to three days of age has also been shown to be the maturation point for the peripheral olfactory system in other moths[41,170,188]

The antennal lobe

From the antenna, the receptor neuron (RN) axons project through the antennal nerve (AN) into the ipsilateral antennal lobe (AL) in the adult (fig. 6)[70,116] and to the antennal centre (LAC) in the larva[83,111]. The LACs are paired, deutocerebral neuropil displaying a glomerular structure. The AL develops from the LAC, making up the main part of the adult lepidopteran deutocerebrum[109]. The adult AN reaches the ipsilateral AL from a frontal-dorsal direction. When the AN has entered the AL, it splits into two tracts. One, carrying mechanosensory fibres, originating in antennal mechano-receptive cells, projects past the AL and into other brain centres. The other tract, which carries all the olfactory axons from the antenna, terminates in the AL[70,116].

The AL consists of a large number of spheroidal neuropil called glomeruli and of cell bodies belonging to different types of AL interneurons (fig. 6)[27,80]. The glomeruli are areas of intense synaptic interactions between antennal RNs and AL interneurons, and are surrounded by an incomplete layer of glial processes. These processes cover the surface of the glomerulus,

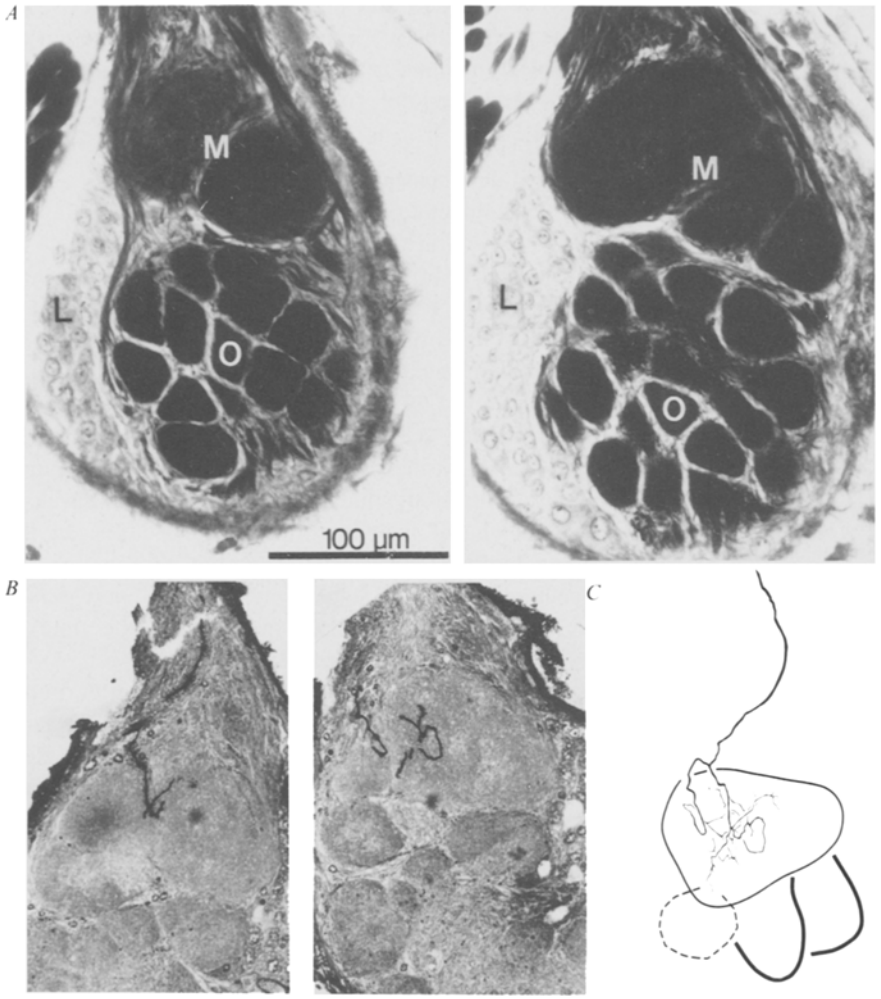

Figure 6. *A*) Two sections through the antennal lobe of the male *Agrotis segetum*. The antennal nerve enters from the top of the photographs. The male-specific macroglomerular complex (M) is situated just at the entrance of the antennal nerve into the antennal lobe. The ordinary, sexually isomorphic glomeruli (O) are situated below the macroglomerular complex. The lateral cluster of antennal lobe cell bodies (L) is visible. *B*) Cobalt staining of a single, physiologically identified, receptor neuron from the male *A. segetum* antenna into the largest glomerulus of the macroglomerular complex. The orientation of the lobe is the same as in *A*. *C*) Reconstruction of the receptor neuron seen in *B*.

and form its outline[208]. The glomerulus consists of axonal branches of the antennal RNs and of AL neuron neurites. The synapses in the AL glomeruli are usually dyads, where one output synapse contacts two postsynaptic elements. Synapses with three or four postsynaptic elements also occur. The glomerular synapses are chemical[21,208].

The cell bodies of the AL interneurons are situated in three different clusters along the rim of the AL. The largest cluster is the lateral cluster (LC), situated along the side of the AL facing the optic lobe. This cluster can be divided into two main parts, LC1 and LC2, with LC1 dorsal to LC2 (fig. 6). Along the side of the AL facing the midline of the brain, the medial group of cell bodies can be observed, and in the part of the antennal lobe facing forward, the anterior cell body group is present. In these cell soma clusters, there is a sexual dimorphism in number of somas only in the MC, where the male has some[30] somas more than the female in *M. sexta*[80]. The cell bodies in the Lepidoptera are insulated from each other by finger-like glial processes[208].

Most of the glomeruli present in the AL, the ordinary glomeruli, are of a similar size and usually number around 50. This character is sexually isomorphic, and the number and location of glomeruli are very constant within both moth and butterfly species[168,169]. In males of species utilising female long-distance sex pheromones, a part of the glomerular setup has been transformed into the macroglomerular complex (MGC) (fig. 6)[27,33,116,136], a characteristic array of glomeruli situated just at the entrance of the AN into the AL. The MGC is significantly larger than the ordinary glomeruli, and the most well-studied element of the AL. The MGC consists of 2–6 glomeruli, situated close together[20,68,70,116]. Typically, a large, cumulus cloud-shaped glomerulus is situated just at the entrance of the AN. Generally, the cumulus displays a complicated structure of folds and invaginations[68]. The cumulus is surrounded by a number of satellite glomeruli of varying shape and size. In the noctuid moths studied, the cumulus often has smaller spheroid satellites situated on each side of it[36,70]. In the sphingid *M. sexta*, the cumulus lies on a toroid-shaped glomerulus, allowing neural processes to pass through a central opening to the cumulus[68]. Toroid-shaped satellites have been reported also from the silk moth, *Bombyx mori*[116].

Antennal lobe development

The AL develops from the LAC. Early in pupal development, the AL displays small clusters of AL neuron cell bodies along the rim, and a homogeneous neuropil surrounded by a glial sheath[208]. The AL neurons send neurites into this neuropil. During development, antennal RN axons enter the AL, where they trigger a dramatic change. The RN axons pass the glial sheath and enter the homogeneous neuropil. There they initiate the formation of protoglomeruli, consisting of densely packed axonal RN branches. When the protoglomeruli have been formed, glial processes grow in from the AL perimeter and form a sheath around each protoglomerulus[154,209]. To form a final glomerulus, neurites from AL neurons enter the protoglomeruli, and form synapses with the RN axonal branches and with each other. This process takes place during the first half of pupal development[21,154,209]. The importance of axonal ingrowth from antennal RNs has been demonstrated in ablation experiments. Without antennal input during development, no glomeruli are formed[173,210]. The importance of the antennal input for the formation of AL structures was also demonstrated in grafting experiments performed on the sphinx moth, *M. sexta*. When a male antennal imaginal disc was transferred to a female at the larval stage, the female developed a normal male antenna, as well as a male-specific MGC in the AL[182,183].

Receptor neuron projections

Receptor neuron axons of both adults and larvae project into single glomeruli of the ipsilateral AL or LAC, respectively (fig. 6B)[70,111,116]. No multiglomerular RN projection patterns have been observed in adults, and they have not been studied in the larva. The projection pattern of male pheromone-specific RNs into the MGC has been studied in detail. By utilising a technique allowing staining of physiologically identified RNs it has been possible to investigate the functional significance of the MGC glomeruli (fig. 6B and C)[70].

In some species, like the noctuid *A. segetum*[70] and the sphingid *M. sexta* (Christensen et al., unpubl.), a strong separation between the input from RNs with different specificities is evident. In other species, like *Heliothis*

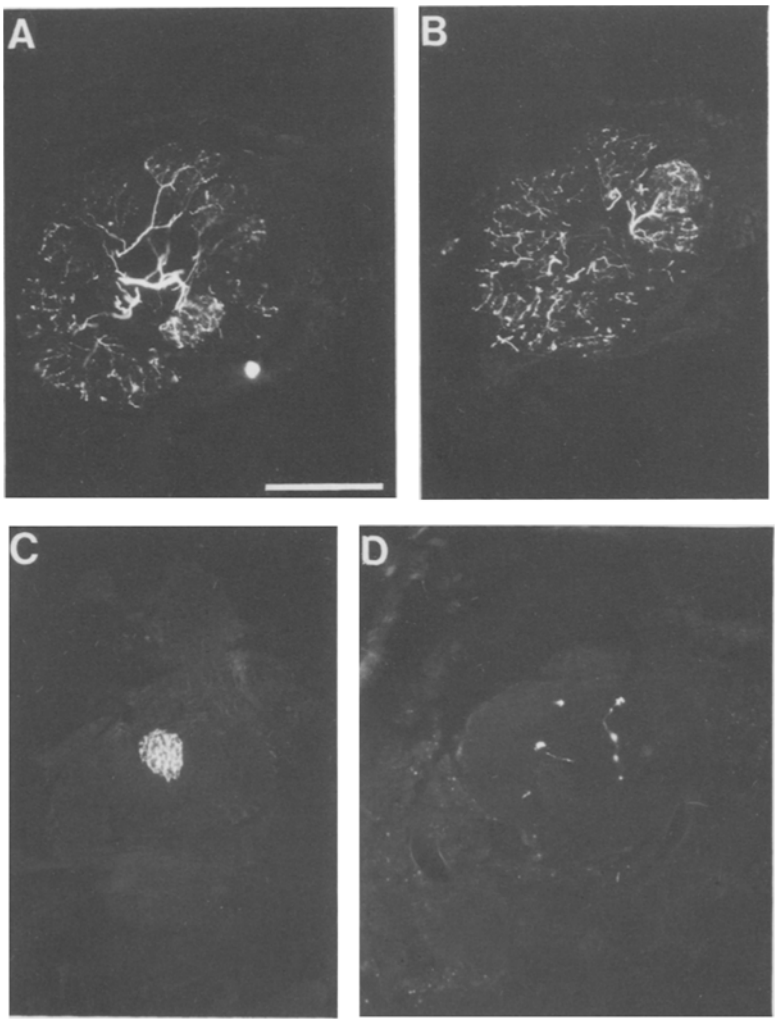

Figure 7. *A*, *B*) Sections through a female *Spodoptera littoralis* antennal lobe showing arborizations of a local interneuron. *C*) Dendritic branches of a projection interneuron invading a single glomerulus. *D*) Section through the calyces of the mushroom body showing axonal terminations of a projection interneuron. Scale bar = 100 µm.

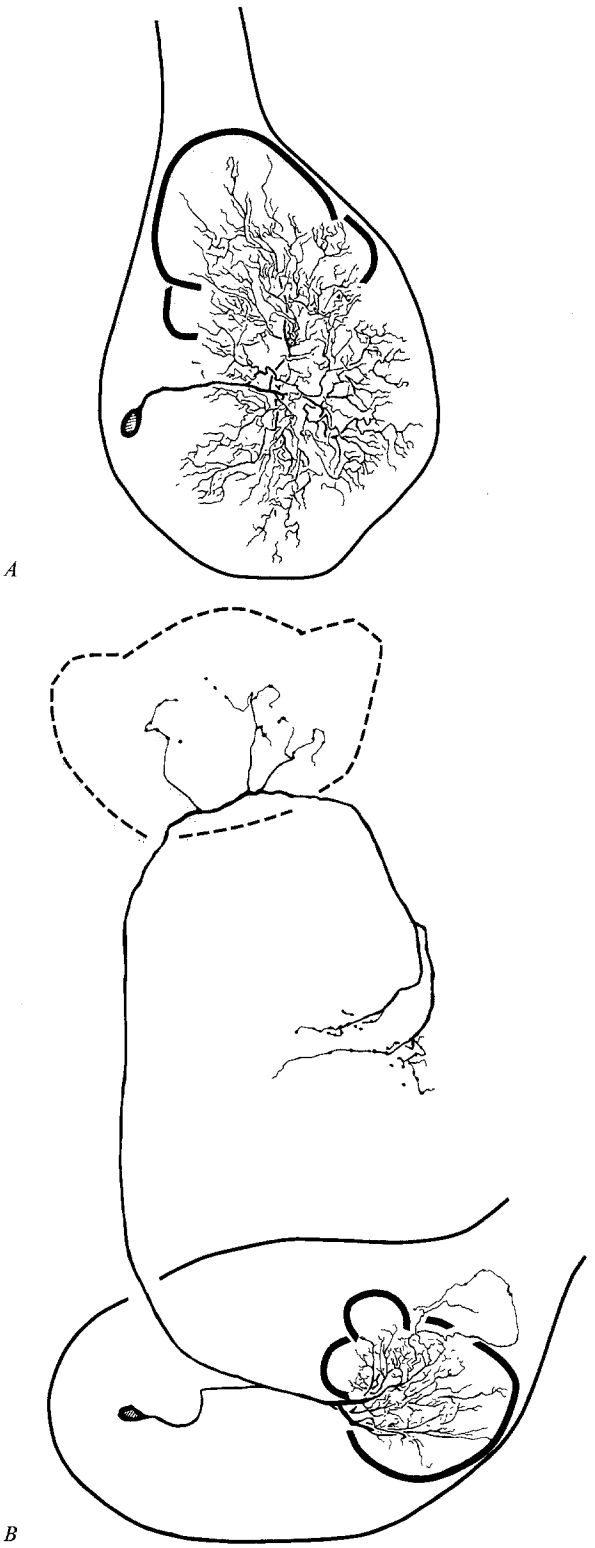

Figure 8. *A*) Reconstruction of a local interneuron from the male *Agrotis segetum* antennal lobe (thin outline) in a frontal view. The neuron innervates both the ordinary glomeruli and the macroglomerular complex (thick outline). *B*) Reconstruction of a projection interneuron in a dorsal view from the antennal lobe (thin outline) of the same species. The neuron has dendritic branches in all MGC glomeruli (thick outline) and projects its axon through the inner antennocerebral tract to the calyces of the mushroom body (dashed outline) and to the inferior lateral protocerebrum.

virescens, all pheromone component-detecting RNs, irrespective of specificity, project to the cumulus glomerulus, while RNs specifically tuned to behavioural inhibitors project to MGC satellites (Hansson et al., unpubl.). In the silkmoth, *A. polyphemus*, three types of RNs detect the three behaviourally relevant components. Two types project to the cumulus, while one satellite receives input from all three types, and another satellite is targeted by only one RN type (Williams and Hansson, unpubl.). The patterns are clearly different between species. In *M. sexta*, the functional properties of the MGC glomeruli were evident also in recordings from AL projection interneurons[68].

The female has no MGC, but in a species where the female has been shown to detect her own major pheromone component with specific sensilla[128], the RNs detecting the pheromone component were seen to project to an ordinary glomerulus situated just at the entrance of the AN into the AL, i.e., where the male MGC is located[149a]. Ordinary glomeruli receive input from non-pheromone specific RNs in both males and females[70] (Christensen et al., unpubl.).

The only bilateral projection into the AL comes from the labial palp pit organs. One distinct glomerulus, situated near the LC2 soma cluster and far down in a posteroventral location in the AL, receives bilateral input from the labial palp pit organs. This glomerulus is present in both sexes and in both moths and butterflies[110,121]. From the larval maxillae, the olfactory receptors send their axons to the suboesophageal ganglion[111].

Antennal lobe neurons

Besides the RN axons, the AL contains three main groups of neural elements: local interneurons (LN), projection interneurons (PN) and axons of centrifugal neurons (CN). LNs and PNs have also been observed in the larva of *M. sexta*. The LNs are amacrine cells, with their arborizations restricted to the AL. The cell body is situated in LC1 or LC2. Often these neurons send branches into all glomeruli in the AL in a symmetrical manner. These LNs are consequently called symmetrical (figs 7A, B and 8A). The asymmetrical LNs have branches only in a few glomeruli, or have a bias towards part of their branching area, even if the arborizations cover most glomeruli. Some LNs arborize in ordinary and MGC glomeruli, while some restrain their arbours to the ordinary glomeruli[37,136].

The CNs are the least investigated of the AL neuron types. The CNs provide input to the AL from other areas of the brain, and are thought to regulate the function of other AL interneurons. The only CN that has been identified, and investigated in detail morphologically, is the single serotonergic neuron present in the AL of the sphinx moth, *M. sexta*. This neuron has its cell body located in the lateral cell body cluster of the AL, but sends an axon contralaterally to the other AL.

There it invades most, if not all, the AL glomeruli, with a very prolific branching pattern. Ipsilateral to the cell body, the neuron has smooth branches invading the calyces of the mushroom body, the lateral horn of the protocerebrum and parts of the central complex[112]. Recent investigations show that many of the synapses on the serotonergic CN in the AL contralateral to the cell body are indeed output synapses. Input synapses were, however, also found[204]. The same kind of neuron has been observed in other Lepidoptera, in both moths and butterflies, and seems to be a highly conserved feature (Hallberg and Hansson, unpubl.).

The PNs are the signal pathways to higher, protocerebral centres in the olfactory pathway. In *M. sexta*, these neurons have been classified by Homberg et al.[80], and further investigations of other moths show that the *M. sexta* typing of PNs is also applicable to other species[7,66]. The PNs are defined by three main characters: the dendritic branching pattern in the AL, the tract that the axon projects through, and the target area(s) in the protocerebrum (figs 7C, D and 8B). The PN axons leave the AL through three main tracts: the inner, the medial and the outer antennocerebral tracts (IACT, MACT and OACT). The largest sexual dimorphism in number of axons in the tracts is found in the IACT, which makes it a good candidate for the leading signal path conveying information about female pheromone odours in the male brain[80].

Protocerebral olfactory centres

A larval PN has been observed to project into the ipsilateral protocerebrum, but the exact identity of the target area is unclear[83]. The main protocerebral targets of the adult PNs are the calyces of the mushroom bodies (figs 7D and 8B) and, in the case of PNs with dendritic trees in sexually isomorphic glomeruli, the lateral horn of the protocerebrum (LH)[7,33,80]. The PNs with dendritic arborizations in the male MGC also often project to the mushroom bodies, but instead of targeting the lateral horn, these PNs have terminations in the inferior lateral protocerebrum (ILPC)[33,66,68,80]. The pathways for information regarding sex pheromone presence are thus separated from other olfactory pathways even at the protocerebral level. Interestingly, in female *S. littoralis*, where a pheromone detection system similar to that of males has been found, no difference was observed between the protocerebral branching areas of pheromone- and non-pheromone-specific PNs[7].

The main target areas in the protocerebrum for AL PNs are thus the mushroom bodies and the lateral protocerebrum. In an investigation of protocerebral, olfactory-stimulated neurons in *M. sexta*, it was shown that a very common branching area for these neurons was the lateral accessory lobes (LAL)[93]. The LALs are situated just laterally of the central body. Few neurons displayed arborizations in the mushroom bodies. The LAL branching neurons often had a bilateral branching pattern, connecting the LAL ipsilateral to the cell soma, to the contralateral protocerebrum. The fibre morphology suggested that the ipsilateral side of the bilateral LAL neurons was the input side, and that the contralateral arborizations were output fibres. These arborized in an area containing branches of descending neurons[94]. Approximately half of the investigated neurons displayed unilateral arborizations. Some of these neurons sent fibres into the areas targeted by AL PNs (i.e., the mushroom body and the lateral protocerebrum).

From the purely protocerebral neurons, signals elicited by odour stimuli are transferred to descending neurons (DN). The DNs display protocerebral branches in the LALs. Some DNs have branches in areas of the ventral protocerebrum[94]. From the protocerebrum, the DNs send an axon through the ventral nerve cord to various effector organs. The DNs carrying flight-eliciting signals will most probably have axonal arborizations in the thoracic ganglion, while neurons mediating cues involved in oviposition behaviour or pheromone production might send the signal all the way to the terminal ganglion of the ventral nerve cord (fig. 9).

Functional characteristics of the lepidopteran olfactory system

Techniques to investigate olfactory functions

The first type of measurements that were performed to study the function of the lepidopteran antenna were electroantennograms (EAG)[176]. To measure this change in DC potential, which occurs over the whole antenna when it is stimulated, the antenna's base and tip are connected to ground and a high impedance amplifier, respectively. It is then possible to record a slow, graded DC potential when the antenna is stimulated with a relevant odour. The amplitude of the EAG, which usually ranges between 0.1 and 10 mV, reflects how strongly the antenna reacts to the presented stimulus.

The EAG is thought to be the sum of all the receptor potentials elicited in all the sensilla present on the antenna[19,140]. When part of the antenna has been disconnected, a clear decrease in response has been observed[140,147,150], and when DC responses from single sensilla were compared to simultaneously recorded EAGs the correspondence was complete[148]. An arrangement of serially connected antennae was also shown to increase the overall sensitivity of the preparation[143,144]. These findings will not, however, explain all the properties of the EAG[40], and although the EAG technique has been used for over 30 years as a standard method in investigations of the insect olfactory system, its functional base has not been fully explained.

As EAGs are relatively simple to perform, and require a minimum of equipment, the technique has become a routine tool used in investigations of semiochemicals,

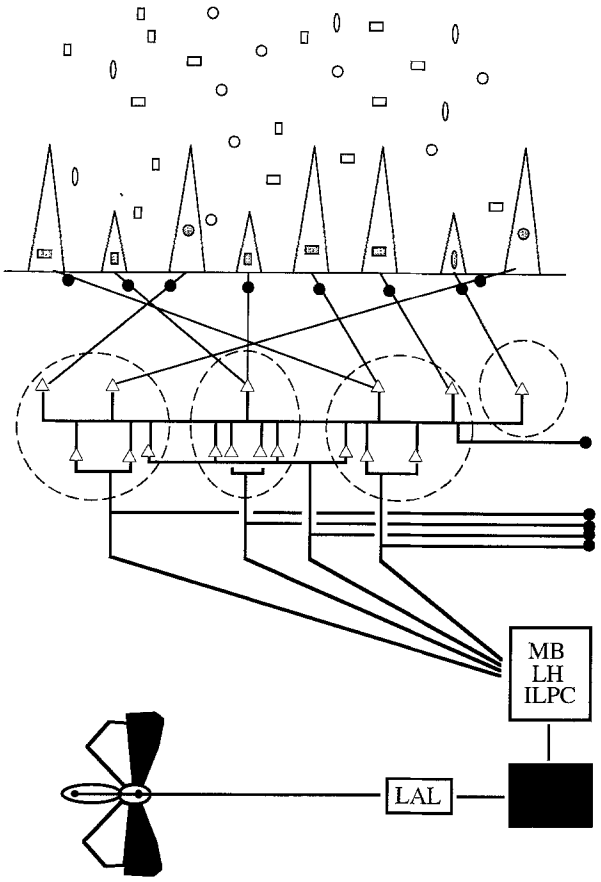

Figure 9. Schematic representation of the signal pathway from detection of an odour molecule to the elicitation of a behavioural response. Molecules in the surrounding air are detected by receptor sites on antennal receptor neurons. From these neurons, the signal is transmitted via chemical synapses (triangles) to local interneurons in the antennal lobe. Receptor neurons detecting the same molecule project to the same glomerulus of the antennal lobe. After integration at the local interneuron stage, the signal is passed on to projection interneurons. These neurons pick up the signal in dendritic synapse sites and transmit the signal through the axon to higher protocerebral centres like the mushroom bodies (MB), the lateral horn (LH) and the inferior lateral protocerebrum (ILPC). At this stage, the knowledge about the processing of the olfactory information is limited, here depicted as a black box. In the lateral accessory lobes (LAL), dendritic branches of descending interneurons overlap with branches of protocerebral odour-stimulated interneurons. The descending interneurons transmit the signal to effector organs like wing muscles, ovipositor muscles or glandular cells through the ventral nerve cord.

and especially of sex pheromones[31,149,160,164,166]. To be able to investigate the presence of different receptor types on the antenna with the EAG technique, adaptation techniques have been developed[156,171]. A combined technique using both a flame ionisation and an electroantennographic detector in the outlet of a gas chromatograph (GC-EAD) has also proven to be very useful in studies of behaviourally relevant odours[8]. To measure pheromone concentrations in the field, methods have been developed where the antenna is mounted and can be used under field conditions[13,174]. One of the more exciting developments of the EAG technique is the 'flying EAG'. By attaching a third antenna, prepared for EAG recording, to the back of a male moth, Vickers et al.[216] were able to record real time EAGs from a flying moth. The electroantennographic measurements do, however, give only very rough estimates of the function of the olfactory system of lepidopterans and other insects.

The function of single lepidopteran olfactory sensilla can be studied by different single sensillum recording techniques, monitoring electric events elicited in receptor neurons when stimulated by different odours. The techniques can be divided into those using tungsten needles as electrodes, and those using glass capillary electrodes. Electrolytically sharpened tungsten needles are used to penetrate the antennal cuticle at the base of the sensillum[82]. After penetration, the very fine tip of the electrode is positioned so that action potentials elicited in the cell bodies present just beneath the sensillum base can be recorded. The great advantage of this technique is the possibility to record from very small sensilla. Glass capillaries are used to make tip-recordings. In this technique, the tip of the sensillum is removed by microscopic knives, and an electrode filled with insect Ringer is slid over the cut surface[86,175,213]. Both the receptor potential and the action potentials can be recorded. Another advantage with this technique is that it gives access to the inside of the sensillum, and the outer dendritic segments of the olfactory receptor neurons. With this access, it is possible to apply different morphological markers to the neurons[70], and to apply different chemicals to change the sensillum lymph experimentally[90,211]. As in the EAG technique, the single sensillum techniques have been exploited to create a very sensitive and selective detector for gas-chromatography, and to make field measurements[214,215,225].

Patch clamp techniques are now being utilised to record from single ion channels situated on the dendritic or on the cell body surface of the RNs, or from the nerve membrane of AL neurons[62]. In patch clamp experiments, an electrode is brought into contact with a piece of active membrane of the nerve cell, and the edges of the electrode are sealed tightly to the membrane by suction. Different types of patch clamp are used, where the different faces of an excised patch of membrane are exposed to the stimulus, or where a whole cell is clamped. Two different approaches have been used to patch clamp moth olfactory neurons. Receptor or AL neuron cells can be cultured in vitro. In this way the whole cell is accessible for patch clamping[78,201,202,233]. In another technique, used only for RN investigations, the dendrite is forced out of a cut sensillum by applying pressure. In this way the dendritic surface is exposed for patch clamping[232].

The RNs present in the sensilla send axons to the primary central olfactory centre, the AL. Extracellular[20] or intracellular[136] recording techniques are used to in-

vestigate function and morphology of interneurons present in the AL and in other olfactory brain centres. Using a fine-tipped glass microelectrode, single neurons can be contacted. By stimulating the antenna with test stimuli, the action potentials elicited in the neuron can be recorded. If the morphological characteristics of the neuron are needed, a morphological marker can be added to the electrolyte in the intracellular electrode. After the physiological experiments, the dye can be injected into the cell by passing a current[33,136]. After dissection, the neuron's morphology can be observed and reconstructed.

Peripheral events

The antenna of a moth or of a butterfly is constantly bombarded by molecules present in the surrounding air. Some of these molecules might be of behavioural relevance to the insect, and receptors have evolved for their detection. When a molecule hits a sensillum, it is adsorbed to the surface, and is transported to a sensillum pore by a so far unknown mechanism. Through the pore, the molecule enters the pore tubules, which connect the pore with the sensillum cavity. The electron dense material present in the pore and in the tubules is thought to facilitate transport of the stimulus molecule[102,194,196].

The molecule enters the sensillum cavity, which is filled with the sensillum lymph. The main constituents of this lymph are so-called odourant binding proteins (OBP)[113,118,134,220]. The concentration of the OBPs is very high, calculated to be 10 mM[211]. Two major kinds of OBPs have been identified. One type is located in pheromone detecting sensilla, and is hence called a pheromone binding protein (PBP), while a second type is present in sensilla detecting e.g. host odours, and is called a general odourant binding protein (GOBP)[224]. Antibodies have been raised against both of these types of OBPs in the saturniid *A. polyphemus*. By means of these antibodies, it has been possible to prove that the PBP and the GOBP indeed are present in different sensillum types (fig. 10)[120,197,198].

The function of the OBP proteins has been a matter of discussion. One hypothesis is that the protein acts to bind the odour molecules and transport them to the surface of the dendrites present in the sensillum[124,211,218,221]. A second hypothesis claims that the OBPs should have a function in the inactivation of odour molecules after stimulation[87,98]. Recent data show that the protein might very well perform both these tasks, acting as the binding protein in its reduced form, and in this form interacting with receptor neuron receptor sites. After this interaction, the protein is oxidised, and in this form acts as an inactivator of the pheromone molecule[91].

Molecular biological investigations utilising recombinant DNA techniques have revealed the PBP amino

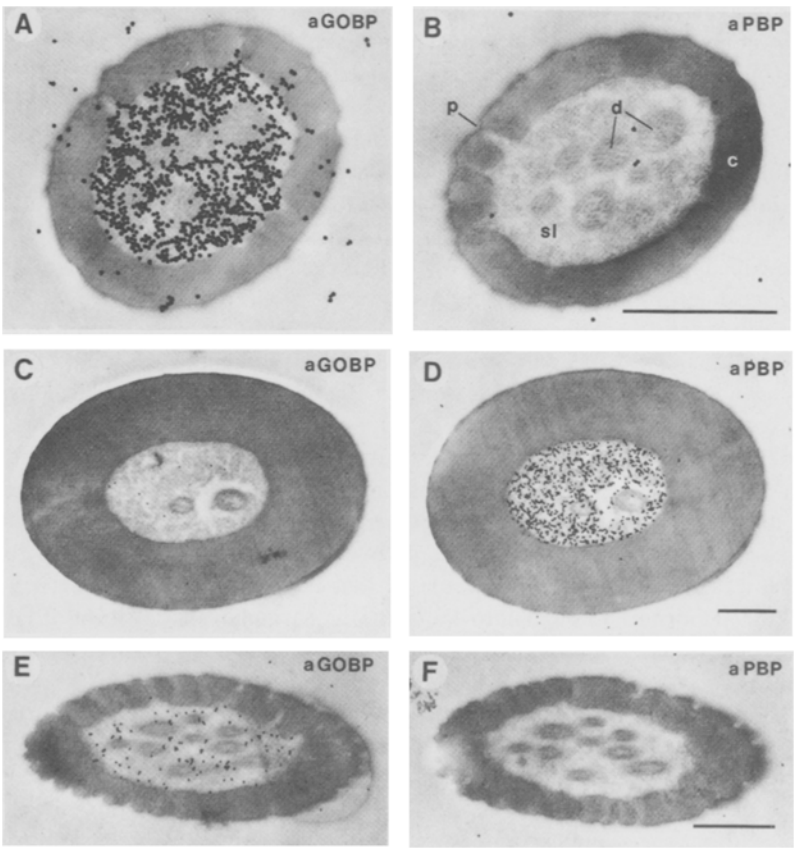

Figure 10. Labeling of olfactory sensilla of the moth *Antheraea polyphemus* with antibodies raised against pheromone binding protein (PBP) and general odourant binding protein (GOBP)[120]. Each horizontal row shows two sections of the same sensillum, but labelled with the two different antisera. *A*, *B*) Female sensillum basiconicum. *C*, *D*) Male s. trichodeum. *E*, *F*) Male s. basiconicum. c = cuticle, d = dendritic outer segments, p = wall pores, sl = sensillum lymph. Scale bars = 1 μm.

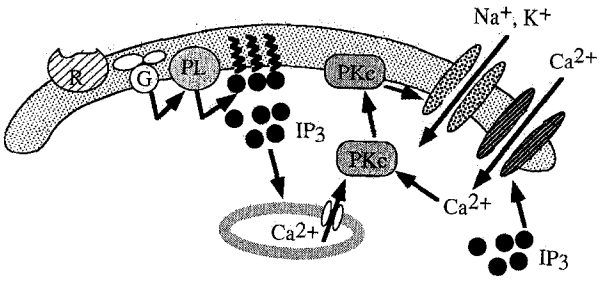

Figure 11. Peripheral events in the lepidopteran olfactory receptor neuron. The odour molecule is detected by the receptor protein (R), which through a G-protein (G) and phospholipase (PL)-mediated reaction causes the release of inositol triphosphate (IP3). The IP3 affects internal calcium stores or ion channels allowing entry of calcium ions into the cell. The calcium activates a calcium dependent protein kinase (PKc) which phosphorylates the ion channel involved in the elicitation of the nerve signal. (Redrawn from an original by R. G. Vogt.)

acid sequences, and the genes coding for these sequences. The PBPs of different species show similarities and all contain two hydrophobic domains. Different PBPs have, however, been identified from antennal preparations of the same species[118], which suggests that the PBPs might have a function in moulding the high specificity of the pheromone receptors.

When the odour molecule has reached the dendrite surface, it interacts with a receptor site, either on its own or in a complex with the OBP. The insect receptor site is thought to consist of a membrane bound protein just as in vertebrates, even if this so far remains unproven[26,28]. The binding of a molecule into the receptor initiates a cascade of events inside the dendrite. The release and formation of action potentials is preceded by a transduction mechanism activated by the binding of the stimulus molecule. Only one excitatory pathway, involving the second messenger inositol-1,4,5-triphosphate (IP_3) has been described in insects so far. This pathway has been studied in detail by so-called stop-flow experiments[22,23,26]. The transduction mechanisms act on ion channels present in the nerve membrane (fig. 11). Both in cultured RNs from male *M. sexta* and in extruded RN dendrites from *A. polyphemus*, second-messenger dependent, non-specific cation channels have been reported. These channels were activated when the RN was stimulated by pheromone molecules[199–202,232,233].

The change in ion composition is the basis for the receptor potential (RP). The RP is a slow, graded potential, travelling down the length of the dendrite until it reaches the spike initiation site[40,87]. The location of the spike initiation site is uncertain. The location proposed by most researchers is the axon hillock on the cell body, but a pure dendritic origin of the action potentials has also been suggested[39]. From the action potential initiation site, the action potentials are propagated down the axon, mediating the message about the presence of certain types of odour molecules in the surrounding air to higher olfactory centres.

When the pheromone molecule has interacted with the receptor site, it must be inactivated to make the receptor sites accessible for new, incoming molecules. Instantaneous inactivation may be performed by the binding protein (see above). The final task of pheromone degradation has been shown to be performed by special sensillar esterases[205,220,223].

Receptor neuron specificity

RNs housed in lepidopteran olfactory sensilla can display a whole range of specificities, where RNs extremely specialised for sex pheromone detection constitute one end of the specialisation scale, and larval, host odour sensitive neurons represent the other extreme, being very generalised RNs according to present data.

By far the most well-investigated RN types are the sex pheromone-detecting RNs present on the male antenna of most night active and of some day active Lepidoptera. These RNs are characterised by a very high specificity and by a high sensitivity to the molecule to which the neuron is tuned. A few picograms of a stimulating pheromone component is often enough to elicit an electrophysiologically detectable response from one of these RNs, and the response which is behaviourally relevant might be evoked by a stimulus several log units weaker.

The specificity of the pheromone RNs has been investigated in a number of studies. The strategy has been to modify the original pheromone component in small steps, synthesise these analogues, and to test their activity on a RN tuned to the original component. This kind of investigation has been performed both with EAG and single sensillum techniques. However, to be able to draw definite conclusions regarding the function of the receptor site, single RNs have to be recorded from. Thus the single sensillum technique has yielded the most convincing results.

The receptor site challenged with the largest number of different pheromone component analogues is the (*Z*)-5-decenyl acetate (Z5-10:OAc) receptor on the male turnip moth, *A. segetum*, antenna. These recordings, and subsequent calculations using molecular mechanics, have revealed that many analogues can bind to the receptor site. However, the activity shown by each analogue is directly proportional to the energy needed to fold the molecule, so that certain important characteristics fall into the same or a similar spatial location as they would in the lowest energy form of the original molecule (fig. 12). The characteristics that are important are the functional group, the position of unsaturations, and the location of the methyl end of the carbon chain. The chirality of the molecule can also play an important role[16,84,126]. Other investigations give a similar importance to these molecular characteris-

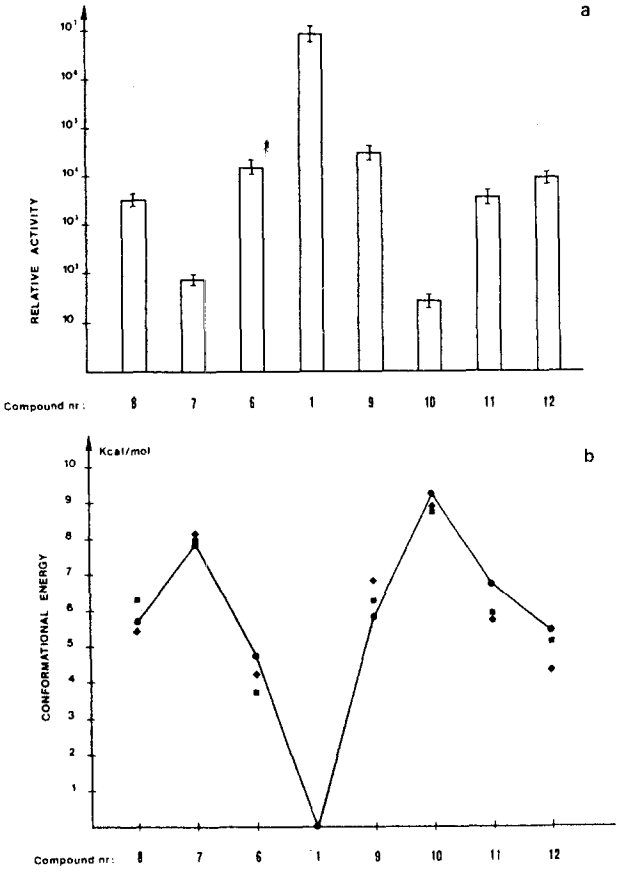

Figure 12. Comparison between single sensillum activity *a*) and conformational energy *b*) needed for a pheromone analogue to assume the position most similar to the actual pheromone molecule (1)[126]. Compounds 6–12 are different analogues of the actual pheromone component.

tics[17,18,163,164]. The investigations of the specificity of single RNs indicate that only a single receptor type is present on each neuron. Some RNs do, however, respond to several different stimuli, and a possible interpretation of this phenomenon would be that several different receptor types are present on the same RN. Experiments utilising differential adaptation[156] have in most cases rejected the hypothesis of multiple-receptor RNs.

The function of the long range pheromone detection system: the periphery

An important feature of the sex pheromone detecting system is the ability to discriminate the conspecific female from other species' females, so that the male does not waste energy and time being attracted to females with whom he cannot reproduce successfully. Closely related species or pheromone strains within a species can utilise very similar pheromone blends, sometimes containing the same chemical compounds, but in different proportions[114]. The male must therefore be able to detect the components of the female pheromone, and in what proportions they are emitted, with high sensitivity. The sensitivity of the olfactory system is further increased in the CNS. From the antenna, tens of thousands of pheromone-specific RNs project into the AL. The output neurons, the PNs, are approximately a thousand-fold fewer[80]. By this strong convergence, the male moth increases the already very high sensitivity of the antennal receptors by another 100 to 1000 times.

The molecule identification is performed by receptor sites on antennal RNs. Numerous studies have been performed to establish the properties of these neurons, both by EAG and single sensillum techniques. The investigations show that antennal preparations are extremely sensitive to the components involved in sexual communication. As the pheromone is usually composed of several components, RNs with different specificities are present on the antenna. The RNs can be situated together in the same sensillum as in the European cornborer, *Ostrinia nubilalis*[73,85] and the sphinx moth, *M. sexta*[89], or can be located in separate sensilla as in many noctuid species[5,133,142,207]. When more than one RN is present in a sensillum, the physiological responses can most often be separated by the RNs having different action potential amplitudes. As a rule, the pheromone-detecting RNs are excited when stimulated. Only in two moth species have RNs been inhibited when stimulated with a pheromone component[74,207].

In many species, RNs detecting pheromone-like compounds not present in the conspecific pheromone blend have been demonstrated[3,55]. Often these RNs are specifically tuned to pheromone components of closely related species, or other species competing in the chemical communication channels, i.e., making use of the same type of chemical substances for their communication. Responses from these RNs usually evoke an inhibitory effect on the sexual behaviour of the male. These compounds are therefore named behavioural antagonists, and make up another important feature of the male's species identification system. Another hypothesis for the presence of some of these detectors is that they detect breakdown products of the actual pheromone molecules, and could thus be satiation detectors[207].

One of the most well-investigated species at the peripheral olfactory level is the cabbage looper moth, *Trichoplusia ni*. Several researchers have spent much effort in elucidating the specificity and function of antennal pheromone-specific RNs in the male. The RN type tuned to the major pheromone component, an acetate, was identified in early investigations along with a RN present in the same sensillum, and responding to the corresponding alcohol[53,125,137,150,151]. The investigation of further RNs with different specificities could take place only after a detailed chemical and behavioural study, revealing a redundancy in the pheromone communication system of the species. In a behavioural study, it was shown that six different compounds, all

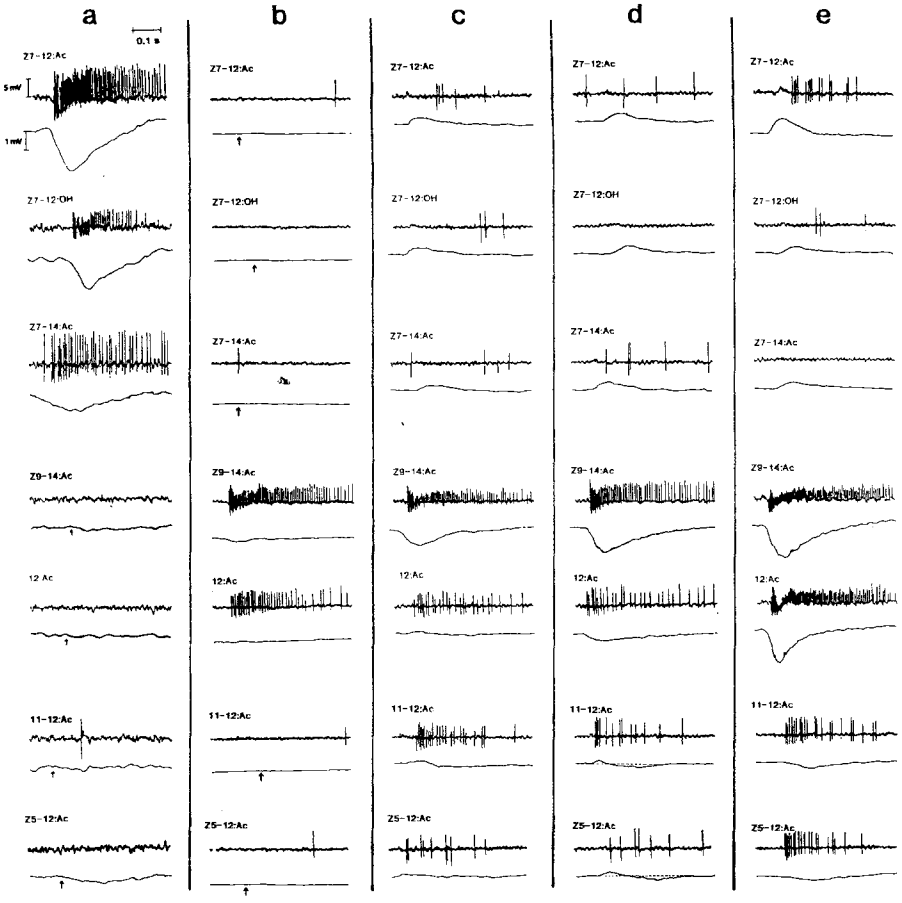

Figure 13. Single sensillum responses to the different components involved in the pheromone communication system of the cabbage looper, *Trichoplusia ni*[207]. AC and DC responses from receptor neurons within five individual sensilla are shown. Note the different specificity of the receptor neurons present in the sensilla. Due to the recording method the AC response (upper trace) is not always mirrored by the DC response (lower trace). (Z)-7-dodecenyl acetate is abbreviated Z7–12:Ac. Other compounds are abbreviated accordingly.

produced by the conspecific female, were involved in the attraction of male cabbage looper moths[127]. When the search was directed by this finding, RNs tuned to the minor pheromone components were indeed found (fig. 13)[138,139,207]. The cabbage looper was also the first moth species where a clear correlation between pheromone-detecting sensillar morphology and function was demonstrated[152]. Similar correlations have since been shown also in other species[72,128].

Further investigations were performed on the chemical communication interactions between the cabbage looper and a closely related sympatric species, the soybean looper. The soybean looper utilises the same main pheromone component as the cabbage looper. It was shown that the soybean looper possessed RNs tuned to one of the cabbage looper pheromone components[55]. In behavioural experiments it was demonstrated that this component acted as a strong antagonist for the soybean looper, preventing cross-species attraction.

In the cabbage looper, early studies implied a blend specificity of antennal RNs, i.e., a blend of two pheromone components evoked a higher response than the sum of the response to the two components individually[150,151]. This type of interaction has, however, since been questioned[138], as the results from the initial study could not be repeated. In another species, the red-banded leafroller moth, *Argyrotaenia velutinana* an initial conclusion of RN blend specificity[150a] also failed to be proven in repeated experiments[1,2].

Another well-investigated sympatric species pair is *Heliothis virescens* and its close relative *Helicoverpa (Heliothis) zea*. Both species utilise the same major pheromone component. *H. virescens* possesses antennal RNs tuned to its two pheromone components and to a third substance of potential behavioural antagonistic significance[4,5]. In *H. zea*, RNs tuned to the major pheromone component were identified, while the second RN type found was tuned to one of the minor components of the *H. virescens* pheromone[3,52]. This compound has a clear antagonistic effect on the attraction of *H. zea* males[190]. The RN tuned to the behavioural antagonist, however, also responded to the minor pheromone component of *H. zea*, but to a lesser degree[3]. The action as pheromone receptor or antagonist receptor turned out to be a pure concentration effect[217]. When the RN was weakly stimulated, it mediated a behaviourally positive signal. When it was strongly stimulated, the signal became inhibitory for male attraction.

Interactions between pheromone communication systems of closely related species has also been studied in e.g., *Lymantria dispar* and *L. monacha*[63,64,180], in the

two *Antheraea* species, *polyphemus* and *pernyi*[141] and among species of the genus *Yponomeuta*[129,212,213].

In the turnip moth, *A. segetum*, the geographical variation of the male pheromone detection apparatus was investigated. Traditionally, the pheromone detection system, being subject to heavy stabilising selection, has been considered very homogeneous over a species range. In the study of turnip moth populations from different European, Asian and African locations, a strong variation in the number of RNs tuned to different pheromone components was, however, demonstrated. These differences were matched by a parallel variation in the female pheromone production[75,132].

According to evolutionary theory, the traits involved in sexual communication should be tightly linked genetically to protect the communication system from breakdown. This hypothesis was tested in the European cornborer, where two pheromone strains occur. The females of each strain and hybrids of the strains could be identified by analysing pheromone production, and the males of the two strains could be recognised by their RN setup in the sensilla. Both RN setup[73] and female pheromone production[115,167] were inherited autosomally, but when the genetic system was further dissected, it was shown that these traits of male and female sexual communication were probably inherited on different chromosomes, thus not genetically linked at all[130]. A further complication of the system was found when the male behavioural response was demonstrated to be modified by a third, sex-linked genetic factor[167]. In another species, *Ctenopseustis sp.*, it was shown that the male sensillum setup was inherited on one of the sex determining chromosomes[71].

In about 80% of the species where both female sex pheromone production and male sex pheromone detection at the RN level have been investigated, the major pheromone component is detected by a RN with a relatively larger spike amplitude, as compared to RNs responding to minor components or behavioural antagonists. In the European cornborer, it was shown that larger action potentials are produced by larger RNs[69], thus suggesting an adaptive explanation as to why the main component – large action potential coupling occurs, as larger RNs are safer and faster signal conductors. A similar investigation in the saturniid moths *A. polyphemus* and *A. pernyi* failed to show a correspondence between large action potential – large RN[99].

Pheromone detection in females

The female ability to detect pheromone has been investigated to a lesser degree than in the male. In several species, the female antenna has, however, been challenged with stimulations of the sex pheromone produced in her own pheromone gland. In several of these species, no responses whatsoever were evoked[69,76]. In a few species responses were, however, recorded even if to a much lower degree than in the male. The most well investigated female pheromone auto-detection is the one present in the *S. littoralis* female. This female possesses antennal RNs tuned to her own main pheromone component, and these neurons are just as specific and sensitive as those in the male. The sensilla housing this RN type are, however, about five times fewer than in the male, so the overall sensitivity to pheromone is considerably lower in the female[128]. A similar case has also been reported in investigations of the cabbage looper female[206].

Detection of male-produced, close range pheromones has been studied in a number of species, and both moth and butterfly females possess RNs tuned to the male compounds[56,57,181,186]. The male odours are, contrary to the female's, food-derived. It has been demonstrated that males having consumed a higher amount of a pheromone precursor have higher success in getting mated. The pheromone concentration can thus provide the female with a way to judge the male quality[133a].

In the moth *Utethesia ornatrix* males are attracted to odours emitted by the female, and upon arrival the male displays eversible glandular brushes, so-called coremata[54]. The odour is detected by specific antennal RNs[54]. In two *Creatonotos* species, the male coremata emit pheromones attracting both males and females, thus forming lek aggregations. The female in these species has also been demonstrated to possess RNs tuned to the male pheromone components[229]. Role reversals in the pheromone communication system have also caused female moths to acquire sensitive male pheromone-detecting RNs in some pyralid species[231].

The function of the long range pheromone detection system: the CNS

When the molecules involved in the sex communication system have been detected by antennal RNs, the signal is transmitted along the RN axons to the AL MGC[70,116]. There the signal is transferred mainly to AL LNs, and from interactions between the LNs with other LNs, with PNs and probably with CNs[37], the output signal from the AL is formed[32–36,66,68,95]. In an early study, Boeckh and Boeckh[20] demonstrated by extracellular recordings that pheromone-responding neurons occur in the ALs of *A. polyphemus* and *A. pernyi*. In a similar study, performed with an intracellular technique, Matsumoto and Hildebrand[136] could correlate physiological and morphological characteristics of the AL interneurons. Similar studies were performed also in the silk moth, *B. mori*[96,97,155].

The interaction between LNs and PNs was shown in double impalements including an interacting pair of one of each of these neuron types. When the LN in such a pair was experimentally hyperpolarized, the PN was

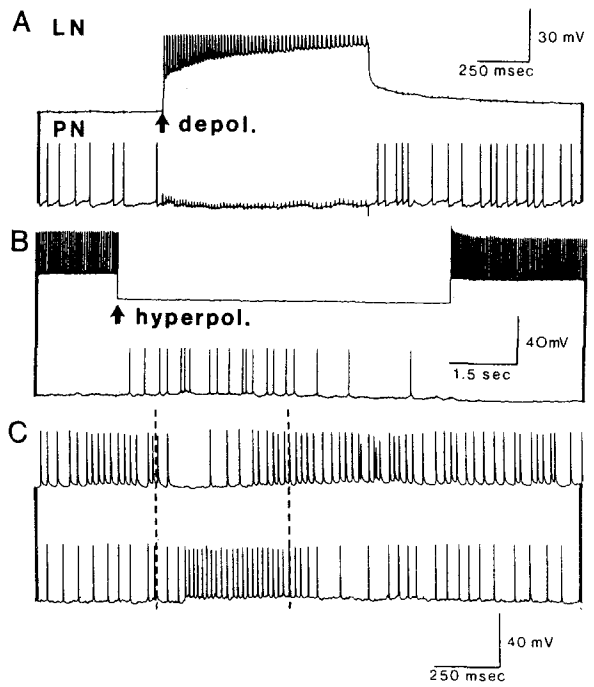

Figure 14. Example of the way projection neuron activity is released through disinhibition[37]. By experimental depolarisation of the local interneuron, the activity in the projection interneuron is suppressed *A*), while by inhibiting activity in the local interneuron, the projection interneuron is activated *B*). In *C*) the interaction of the two neurons following delivery of an odour stimulus to the ipsilateral antenna is shown.

depolarized (fig. 14). These responses suggest that at least some of the excitation observed in PNs may be mediated through disinhibitory interactions[37]. The PNs would thus have a very high spontaneous activity which is constantly suppressed by the activity of inhibitory LNs. When the activity of these LNs is decreased, the suppression of the PN activity is weakened, and the PN starts firing. These results agree well with earlier investigations showing that many LNs are GABA immunoreactive[81], and that PN activity is inhibited by GABA[226]. Very few LNs inhibited by pheromone stimulation have, however, been found[37].

Information about single pheromone components is sometimes conserved even in the AL output neurons, the PNs. In such a case, a labelled line is said to reach beyond the AL. In other PNs, much more complex responses are recorded, where the neuron is excited or inhibited by several different components[33,35,36,66]. When signals from RNs of different specificity are mixed in such a way, the system displays across fibre patterning. In different species, labelled lines and across fibre patterning seem to occur to different degrees, and occur at different levels of the olfactory pathway. When it comes to AL function in the most well-investigated species, the sphinx moth, *M. sexta*, the labelled lines persist in many PNs, so that information about the presence of single pheromone components is conserved in protocerebral olfactory centres[33,68,95]. In the turnip moth, *A. segetum*, the labelled lines are significantly fewer, as only very few AL output neurons are found responding to single sex pheromone components[66]. In another noctuid, *Helicoverpa zea*, labelled lines beyond the AL were commonly found for one of the major pheromone components, but none was found for the other[36].

In the female *S. littoralis*, AL neurons specifically tuned to female-produced pheromone components were identified. In the female moth, both labelled lines and across fibre patterning were observed at the LN and PN level[7].

Some labelled lines do probably end after the AL output neuron level, while others are found to persist all the way to descending interneurons[93]. The number of labelled lines that persist to higher levels in the olfactory system seems to vary greatly between species.

The task of identifying the components of the sex pheromone, and conveying this information along labelled lines, is thus solved. Another important feature for species recognition does, however, remain; the identification of the blend. As mentioned earlier, different species may differ only in the specific blends that they produce, blends composed of the same chemical compounds. Blend detection at the RN level has been reported, but was later questioned (see above). The possibility of blend recognition by antennal neurons is unlikely. This process must thus take place in the CNS. In recordings from AL neurons, some are found to respond to several pheromone components. These neurons, however, cannot be called blend detectors, as they only respond to the presence of the single components, much like the labelled line neurons. Another type of AL neuron, present both among LNs and PNs, will not respond or responds very weakly to the single pheromone components. However, if this neuron type is stimulated by the mixture of the major pheromone components, a strong response is evoked. These AL neurons are blend detectors, and have so far been reported mainly in noctuid moths (fig. 15)[35,36,66]. The higher potency of the blend, as compared to the single components, persists, and is better represented at higher levels of the olfactory pathway. In both protocerebral and descending neurons, long lasting excitations were only observed when the antennal RNs were stimulated with the pheromone blend, while the single pheromone components gave rise to brief excitations[93,94].

The function of the long range pheromone detection system: dynamic properties

An additional important feature of the lepidopteran olfactory system is the ability to follow rapid changes in concentration of odour molecules of behaviourally relevant stimuli. A natural odour plume is not a continuous cloud of molecules. It looks more like the smoke from a

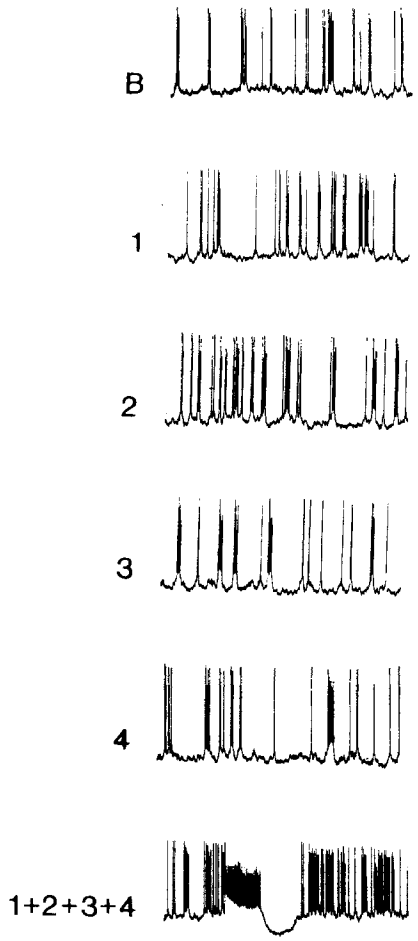

Figure 15. A blend-specific projection interneuron in the male *Agrotis segetum* antennal lobe. This neuron did not respond to the blank (B) or to any of the single pheromone components (1–4). When stimulated with the full pheromone blend, the neuron did, however, give a strong response.

cigarette in a very weak wind. Filaments with relatively high concentration drift downwind, but are interspersed by practically odour-free air[145]. While flying through the air, a moth will encounter pheromone pulses at between 1–10 Hz. To be attracted, a male moth requires this kind of plume structure. If the pheromone level is too high, or too uniform, the male moth will abort its flight towards the pheromone source[106,107,228]. Both these phenomena can be partly explained at the peripheral level, when considering the ability of the RNs to detect pulses. The RNs present on the antenna are capable of following pulses up to 10 Hz[11,12,51,88,135]. When the pheromone content is too uniform, the pulsed signals from the RNs disappear, and when it is too high the total input relating to pheromone presence ceases, as the RNs become adapted (fig. 16A)[11,12]. In the turnip moth, *A. segetum*, it was also shown that different RN types, detecting different pheromone components, adapted at different rates. Therefore, at high concentrations the moth receives a skewed impression of the pheromone blend present in the air[67].

The adaptation of antennal RNs has been suggested as one of the possible explanations of pest control by pheromone confusion. Control by this method is achieved by 'saturating' an area, e.g., an orchard, with pheromone. This treatment breaks the pheromone communication of the target species, and has been observed to make the males passive[30a,140a]. Another hypothesis claims central nervous adaptation, or habituation, to be the cause of communication break-down. Several other, more behaviour-oriented hypotheses have been proposed, but no hypothesis have so far been proven true[14a,140a].

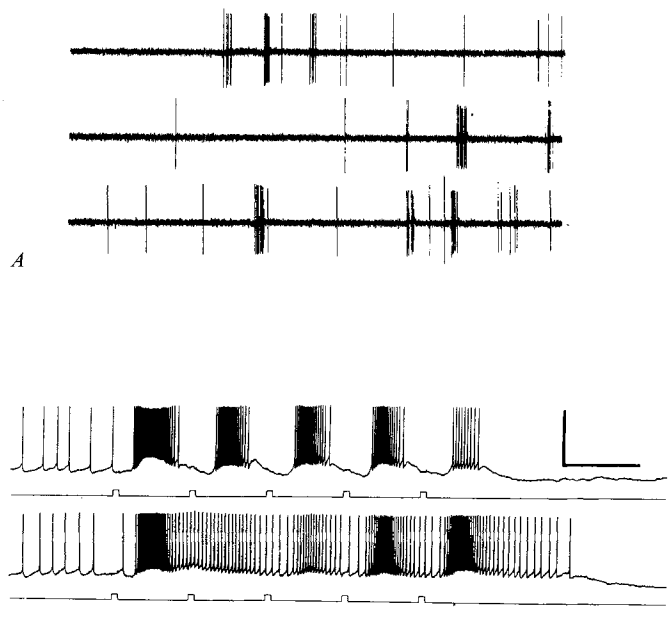

Figure 16. Pulse detection at the peripheral[67] *A*) and the central nervous *B*) level[34]. In *A*) an antennal receptor neuron is challenged with a natural pheromone plume. The filamentous nature of the plume is demonstrated by the intermittent stimulations of the receptor neuron. At the antennal lobe level, the pulse-following capability is totally dependent on inhibitory input from local interneurons. If the GABA-mediated inhibition is counteracted by a GABA inhibitor, the pulse following is stopped *B*).

Some of the AL interneurons display special features, making them very good pulse followers. In some neurons investigated in *M. sexta*, one pheromone component excited the neuron and another component inhibited it. These features were shown to be very important for the ability to follow fast odour pulses, as the excitation and inhibition acted in concert, to accentuate the pulses. When the antennal RNs were stimulated with single pheromone components at 2 Hz, the neuron was not able to follow pulses, as it was when the two components were presented together (fig. 16B)[34]. Similar pulse-following capabilities have been reported in investigations of AL interneurons in two heliothine species[35].

Food and host odour detection

The larva needs to identify suitable host plants. The identification of suitable substrates by larvae has in choice tests been shown to depend partly on olfactory information[38,44,45,65]. Larval olfaction has been studied by single sensillum techniques in different species. The results show that the RNs housed in the larval olfactory sensilla, both on the antenna and on the maxillae, respond to a wide spectrum of plant-produced odours[46,48,185]. Taste receptors in larvae have also been shown to be able to detect odours over short distances[203]. A broad profile of response to different compounds might imply an unspecific olfactory system. No RN, however, has the same response spectrum to the odours tested, and specificity might be achieved by across fibre patterning[48,184]. Recordings from central olfactory neurons in larvae also show responses to general green leaf volatiles (GLV) such as E-2-hexenal and Z-3-hexenol and to host plant extracts[83].

Female choice of host plant for oviposition is often crucial for larval survival, as many newly hatched larvae have a very limited possibility to change plants. It is also important for the female to try to optimize the chances of survival for her offspring in other ways. Moth and butterfly female antenna abound with RNs tuned to different plant-produced odours[15] (Anderson et al., unpubl.). In early investigations, the impression was that the female receptors resembled the larva's in being very non-specific[15,76], responding to a wide spectrum of GLVs. Investigations performed on the female *S. littoralis* antenna, however, show that RNs tuned very narrowly, and with a very high sensitivity to a particular plant volatile, are present (fig. 17) (Anderson et al., unpubl.). In the investigation of *S. littoralis*, strong responses were elicited by plant odour concentrations similar to those used in investigations of male pheromone detection. The impression of generalism probably stems from the utilisation of too high stimulus doses. With very high GLV concentrations, strong responses can indeed be evoked even in pheromone-specific RNs in males[76]. In the female *S. littoralis*, RNs

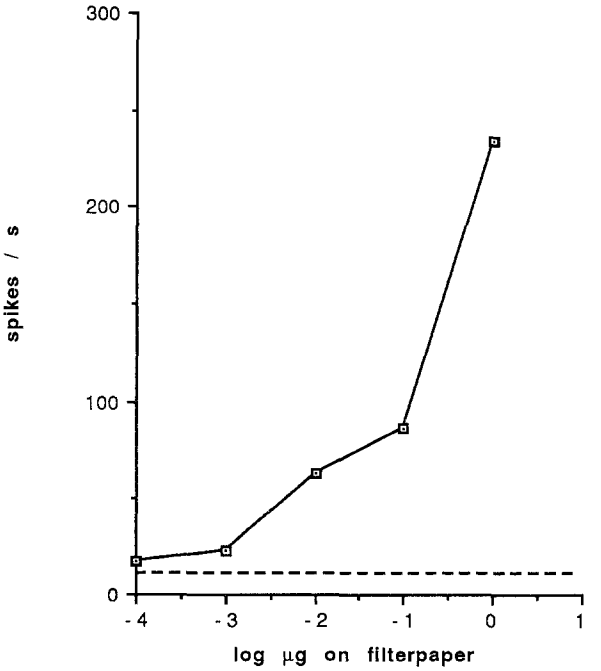

Figure 17. Plant odour detection by an antennal receptor neuron in a female *Spodoptera littoralis*. The neuron displays a sensitivity and specificity as high as that found in male pheromone-detecting neurons. The stimulus was humulene, a terpene constituent of the odour of cotton, one of this moth's preferred host species. No comparable response was obtained to any of approximately 30 other host plant, oviposition deterrent or pheromone odours (Anderson et al., unpubl.).

tuned to GLVs were also found. The maximum response of these neurons, however, was achieved by stimulation with seven carbon compounds. This finding contrasts with the earlier use of six carbon GLVs, like E-2-hexenal and Z-3-hexenol, as the typical GLVs (Anderson et al., unpubl.).

To further optimize the choice of oviposition site, the female *S. littoralis* has been shown to have highly sensitive olfactory detectors tuned to odours of oxidised plant compounds produced in the larval frass, compounds that together produce a strong oviposition deterrence[6]. Most of these compounds are terpenes, both cyclic and acyclic. Different degrees of RN specificities could be observed, so that one RN type was excited only by a single frass compound, while another was excited by all the cyclic terpenes. Receptors tuned to these oviposition-deterring components have also been found on the male antenna (Anderson et al., unpubl.).

In both male and female Lepidoptera, adult insects thus have sensitive and specific antennal RNs tuned to different plant-produced compounds. A second olfactory pathway involved in detecting host odours is the labial palp pit and its RNs. In the moth *H. armigera*, these receptors have been shown to be very sensitive to minute changes in the CO_2 concentration in the moth's immediate environment[191]. Carbon dioxide is also a plant-produced odour, and just like the GLVs, very general.

Like the pheromone information, the plant compound information is transferred via the RN axons to the AL glomeruli. The pheromone specific RNs project to the MGC, while the plant odour-specific RNs project to the sexually isomorphic, ordinary glomeruli. All projections observed have been monoglomerular. In the female moth, only the ordinary glomeruli are present. In an investigation of antennal lobe processing of a large number of plant and larval odours in the female *S. littoralis*, no clear correlation between glomerulus position and specificity to a certain stimulus was found[7]. Neurons responding to the tested GLVs, to flower odours and to larval odours were found and neurons integrating the responses to these odour classes were also demonstrated.

Conclusion

Olfaction in Lepidoptera, and especially in the moths, has been a subject of intense research over the last 20 years. Many morphological, physiological, biochemical and molecular characteristics of both peripheral and central nervous neurons involved in the olfactory sense have been defined. An important factor making research in lepidopteran olfaction so successful is the parallel development of studies of the nature of the chemicals detected by the system, and studies performed on the behaviours elicited by the system. Specifically, the pheromone communication system of moths has been intensely studied. Without the chemical and behavioural background, investigation of the olfactory system would not have progressed to its present status.

Much has been done, but even more remains to be done. Many new avenues of research are open for research in the lepidopteran olfactory system. Molecular techniques are just starting to be utilised. In the not too distant future, the first moth olfactory receptor protein will be identified. The pheromone detection system has been heavily exploited, but now interest is being directed towards the much more versatile and challenging host odour detection system. The function of the olfactory system under natural conditions is just starting to be unravelled. These areas and many more lie ahead of us who have the great fortune to work in the field of lepidopteran olfaction.

Acknowledgements. I am very grateful to Drs T. J. Almaas, P. Anderson, S. Anton, T. A. Christensen, S. Erland, E. Hallberg, R. A. Steinbrecht and J. L. Todd, and two anonymous referees for valuable comments on the manuscript. I am also deeply indebted to Dr. E. Hallberg for his expert help with the electronmicrographic material. The writing of this review was funded by the Swedish Natural Science Council (NFR).

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