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Central Mechanisms of Pheromone Information Processing

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Abstract

An advantage of using pheromones in olfactory studies is that they are chemical signals for which receptor neurons are evolved and thus elicite biologically relevant odour-information to be processed in the brain. In many vertebrate and insect species, the olfactory system is separated into a 'main' and an 'accessory' division, the latter mediating pheromone information. In moths, the pheromone information is first processed in the brain in a large and sexually dimorphic structure, the macroglomerular complex (MGC) of the antennal lobe (AL). Also in vertebrates the pheromone information is processed in specific or modified glomerular complexes. One principle question is whether individual olfactory glomeruli are functional units, processing specific information concerning both the chemical quality and spatiotemporal features of the stimulus, like the pheromone plume. Indeed it has been shown that the axons of different pheromone-selective receptor neurons project into different MGC-glomeruli. Intracellular recordings from the AL projection (output) neurons also show that information about single components of the pheromone blend is preserved in some output pathways, whereas other output neurons respond in a unique fashion to the blend. The information about interspecific signals, which interrupts pheromone attraction, is processed in a specific MGC-glomerulus and is to a large extent kept separated from the pheromone information throughout the AL. Many of the output neurons accurately encode changes in the temporal characteristics of the stimulus. **Chem. Senses 21: 269–275, 1996.**

Introduction—accessory olfactory systems

An important advantage of using chemically-identified and behavourally relevant odorants like pheromones in olfactory studies is that they can be used as specific probes to examine odour-information processing pathways in the brain. In many vertebrate and insect species, the olfactory system can be subdivided into a 'main' and an 'accessory' part, involved in detection of food odours and pheromones, respectively. In insect species, like moths, the accessory system in males mediates responsiveness to sex pheromones produced by females. The pheromone information is received by a particular set of receptor neurons and conveyed by their axons to the sexually dimorphic structure, the macroglomerular complex (MGC) of the antennal lobe (AL) in the deutocerebrum. This glomerular complex, which in moths is located at the entrance of the antennal nerve to the lobe, is anatomically separated from the numerous ordinary glomeruli involved in plant odour information processing in these herbivorous species (Boeckh and Boeckh, 1979; Ernst and Boeckh, 1983; Christensen and Hildebrand, 1987; Rospars and Hildebrand, 1992). In several species of fish, a similar subdivision is described; the medial portion of the olfactory bulb and the medial olfactory tract mediate responsiveness to pheromones,

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whereas the lateral olfactory bulb and the lateral olfactory tract convey information about food odours (Døving *et al.*, 1980; rev. by Dulka, 1993). In goldfish, it has been shown by extracellular recordings from mitral cells that the neurons responding to stimulation with identified sex pheromones are located in the medial portion of the olfactory bulb (Fujita *et al.*, 1991). In the same species, further examination using multi-unit recordings revealed that responses to pheromones are transmitted via the medial olfactory tract, whereas responses to amino acids and crude food odours, but not pheromones, are transmitted by the lateral tract (Sorensen *et al.*, 1991). The olfactory systems of terrestrial vertebrates are also characterized by the presence of a distinct accessory subsystem, including an accessory olfactory bulb (Halpern, 1987; Meredith, 1991). The input to the accessory bulb arises from receptor neurons of the vomeronasal organ which is separated from the main olfactory epithelium. This accessory system is also associated with responsiveness to pheromones and can be considered as analogous to the medial portion of the olfactory system in fish. Another distinct pathway mediating pheromone information in mammals is identified in rats, where a subpopulation of receptor-neuron axons project to a histologically distinct 'modified glomerular complex' in the dorsomedial olfactory bulb, that is important in processing odour information about suckling pheromones (Greer *et al.*, 1982; Jastreboff *et al.*, 1984). In each of these accessory systems, the pheromone information is apparently processed in a restricted number of glomeruli. When comparing functional similarities of the accessory olfactory systems of the various groups of organisms, it is also important to point out their characteristic differences, such as the distances over which the chemical signal is able to stimulate the receptors. Whereas the chemicals stimulating the receptors of the vomeronasal organs in mammals have a low volatility, requiring close contact of the olfactory organ to the odour source, the pheromone molecules of insects may be received by the olfactory receptors at kilometer distances from the emitting female.

Having established the existence of distinct subdivisions within the olfactory systems of numerous species, another important question is whether or not odour information is mapped in a topographic fashion from the periphery to the brain. Studies from widely-differing species indicate that the map of the olfactory system does not follow the precise topographical organizations of other sensory systems. For example, anatomical studies of single glomeruli in zebrafish has demonstrated connections with receptor neurons that are widely scattered over the olfactory epithelium (Baier *et al.*, 1994), and no topographical organization from the vomeronasal organ to the accessory lobe is found in the hamster (Meredith, 1991). Furthermore, the expression of individual putative membrane receptors is random in catfish olfactory epithelium (Ngai *et al.*, 1993) and in mammals, the distribution is also random within a particular expression zone (Ressler *et al.*, 1994; Vassar *et al.*, 1994). It is interesting to note, however, that one such olfactory receptor, OR37, demonstrates a much more restricted pattern of expression (Strotmann *et al.*, 1994), showing that not all olfactory receptors are distributed in the same manner. In insects, olfactory sensilla containing the pheromone receptor neurons are in many species distributed over the whole male antennae, partly intermingled with sensilla containing plant odour responsive receptor neurons. In fact, each antennal segment seems to possess many, if not all types of receptor neurons in some insects. Like in vertebrates, a functional organization then takes place from the receptor neurons to the antennal lobe, where the pheromone sensitive neurons project to the MGC and the plant odour receptor neurons to the ordinary glomeruli (Christensen *et al.*, 1995a,b). Since the MGC is further divided into distinct subcompartments, one important question to arise as a direct result of using pheromones as tools to explore odour information processing pathways is whether the individual MGC-compartments are functionally specified, processing information about specific component qualities and spatio-temporal features of the pheromone plume.

Coding of odour quality

As a result of the identification of pheromones in numerous insect species (cf. Arn *et al.*, 1992), it has become clear that these signals are not only used intraspecifically as pheromones, but also as interspecific signals, particularly for maintaining reproductive isolation between sympatric species (Roelofs and Comeau, 1971; Lanier and Wood, 1975). The typical sex pheromone in moths consists of a mixture of two or several compounds, and the blend evokes upwind flight and attraction toward the pheromone source. Some of the same compounds interrupt the attraction of related sympatric species. Detailed knowledge about the structures of these compounds, their relative amounts in various species-specific blends and careful observation of their behavioural effects, have all been key factors in studies of the central processing of pheromonal information. The first important question concerns the pattern of input to the brain from each type of receptor neuron. Receptor neuron

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specificities are determined by the dose–response relationships to pheromone components, chemical analogues or other relevant compounds which are produced by the particular insect group in question, like the subfamily heliothinae which we are studying (cf. Mustaparta, 1995). These investigations have revealed that pheromonal information is in general received by receptor neurons narrowly tuned to one component. Thus, the information from the conspecific pheromone plend is transmitted to the brain as a pattern or 'ratio' of activities in the different types of receptor neurons, as discussed by Kaissling (1996, this issue). Furthermore, receptor neurons tuned to interspecific signals often exhibit similar specificities as their counterparts mediating pheromonal information (Almaas *et al.*, 1991; Berg *et al.*, 1995; Berg and Mustaparta, 1995).

The next question is whether these functional types of receptor neurons project to different glomerular locations in the male specific MGC in the antennal lobe. This has, indeed, been demonstrated, for the first time in the turnip moth *Agrotis segetum* by staining functionally different types of receptor neurons of sensilla trichodea in males (Hansson *et al.*, 1992). It was shown that neurons tuned to each pheromone component had a specific pattern of projections in the four glomerular lobes of the MGC, each receptor cell type projecting mainly to one glomerulus. In another moth species, the tobacco budworm moth *Heliothis virescens*, it was shown that the receptor neurons tuned to the two essential pheromone components (Almaas and Mustaparta, 1991; Berg *et al.*, 1995) projected to the same glomerulus, which is also the largest of four glomeruli in the MGC of this species (Hansson *et al.*, 1995). A third type of receptor neuron, which is tuned to a compound mediating interruption, projected to another glomerulus of the MGC, in which no terminals of pheromone receptor neurons were found. A functional organization of the male-specific MGC has also been demonstrated by intracellular recordings from antennal lobe interneurons. In *Manduca sexta*, it was shown that projection neurons mediating responsiveness to the two essential pheromone components, arborize in different parts of the MGC (Christensen and Hildebrand, 1987; Hansson *et al.*, 1991). Projection neurons activated by antennal stimulation with the major component arborize in the 'toroid' part of the lobe, while neurons responding to the second essential component arborize in the 'cumulus' (Christensen *et al.*, 1995a,b). Some projection neurons responding to both components receive input through interconnections via local interneurons. Similar studies of two sympatric species of heliothine moths have revealed both similarities and differences in the functional and anatomical organization of the MGC. These data suggest that different strategies are used by these two species to process olfactory information in the antennal lobes (Christensen *et al.*, 1991, 1995a,b). Surprisingly, we found that the two heliothine species possess a range of receptor neurons that are similarly tuned, even though their pheromone blends are very different. The major pheromone component (called 'A' for simplicity) is the same for both species, but the second essential component is different (B in *H. virescens* and C in the closely-related species *Helicoverpa zea*; see Figure 1). Compound B actually serves a dual function in that it interrupts the pheromonal attraction of *H. zea* males. A fourth compound, D, produced by other sympatric species, interrupts the attraction in *H. virescens* males (N. J. Vickers, personal communication; see Figure 1A). In these and three other heliothine species studied so far, the two most prevalent groups of receptor neurons are tuned to compound A and B, respectively, suggesting that these compounds have been preserved through the evolution of pheromone communication in the heliothine moths (Mustaparta, 1995). A third type of neuron in *H. virescens* and *H. zea* is tuned to compound D. In order to interpret which receptor neuron types give input to individual projection neurons in the antennal lobe, it is important to know the dose–response relationships of the single receptor neurons. For instance, the very sensitive receptor neurons tuned to compound A also respond to compound B, with a shift of the dose–response curve about 2 log units to the right (Almaas and Mustaparta, 1990; Almaas *et al.*, 1991; Berg *et al.*, 1995). The receptor neurons tuned to compound B also respond to compound C when the concentration is raised about 100 times.

In *H. virescens*, where A and B are the essential pheromone components, most AL projection neurons responding to antennal stimulation with heliothine compounds were excited by stimulation with these two pheromone compounds (Christensen *et al.*, 1995a,b). The responses of many of these neurons reflected the responses of the receptor neurons tuned to the major component A, i.e. they responded exclusively to stimulation with A, or predominantly to A and less so to B. It is likely that these neurons receive input mainly from the receptor neurons tuned to A. Staining revealed that these neurons arborize in the largest lobe of the MGC, corresponding to the lobe where the pheromone receptor neurons projected (Figure 1A). Another large group of AL projection neurons responded about equally to the compounds A and B, indicating that these neurons most likely receive input from both the A- and B-types of receptor

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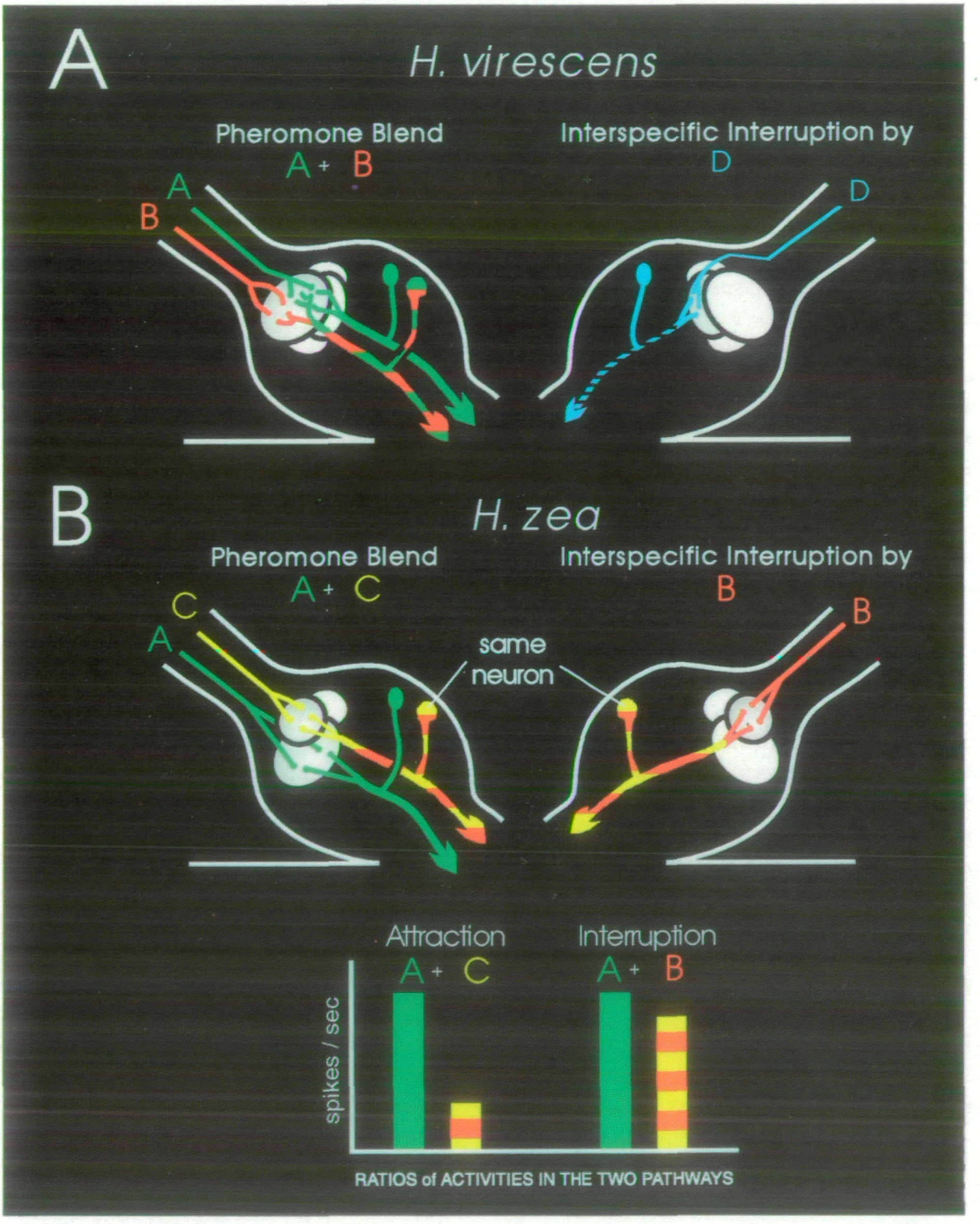

Figure 1 Scheme of the pathways for pheromone and interspecific signal information in *Heliothis virescens* (A) and *Helicoverpa zea* (B), showing that the two kinds of information are processed in different MGC-lobes in *H. virescens*. This is also the case for the information about the major component A and the interspecific signal B in *H. zea*. However, in *H. zea* components B and C are encoded by the same population of output neurons. The conspecific component C evokes low spike activity, whereas the interspecific component B evokes higher frequency firing. Differential levels of activity in the two pathways shown may result in the different behavioural reactions.

neurons (Christensen *et al.*, 1995a,b; Figure 1A). Only occasionally, a synergistic effect of compound A and B was recorded, where stimulation with one compound hardly had an effect, but the combination of A and B evoked a strong long-lasting response. It suggests that some neurons detect the whole pheromone blend in this species. Other neurons

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which were not excited by the pheromone compounds responded selectively to antennal stimulation with compound D which is here the interspecific signal. Unfortunately, these neurons were not stained and, therefore, correlations could not be made with the projections of the receptor neurons tuned to compound D. However, it is likely that these AL projection neurons receive input only from the D-type of receptor neurons projecting into the separate MGC-lobe (Figure 1A).

In *H. zea*, where compound A is also the major pheromone component, a large number of neurons exhibited the same response characteristics as neurons encountered in *H. virescens*, i.e. strong activation by antennal stimulation with compound A, showing either selective responses to A or strong responses to A and weaker responses to B (Christensen *et al.*, 1991). Again, the responses of these AL neurons reflected the responses of the receptor neurons tuned to the major pheromone component A, suggesting that they receive input from this type of receptor neurons. Differences between the two species were found with respect to responses elicited by stimulation with compound B, which has different functions in the two species (the second essential pheromone component in *H. virescens* and an interspecific signal in *H. zea*). Whereas the information about compound B was completely integrated with the information about the major component A in *H. virescens*, it seems to a large extent to be kept in separate pathways through the AL in *H. zea*. In this species, about one-third of the identified AL projection neurons, responded predominantly to stimulation with compound B, weaker to compound C and not at all to compound A. These responses reflected the responses of the receptor neurons tuned to compound B and suggested that they receive input from these receptor neuron types (Christensen *et al.*, 1991). Staining showed that these AL projection neurons had a restricted arborization in one dorsal lobe of the MGC, suggesting that the interspecific signal information is processed in this particular MGC-lobe (Figure 1B). Like in *H. virescens*, a few neurons responding synergistically to antennal stimulation with compound A and B were also encountered in *H. zea*. However, in the two species the messages mediated by these neurons may be different; in *H. virescens* it is most likely the presence of the conspecific blend and in *H. zea* it may be the presence of the sympatric species' blend.

The integrated results show that the ALs of the two species process differently the information from the similarly 'labelled' primary axons. However, one similar principle in the two species is that the information mediated by the interspecific signals is to a large extent kept in separate pathways throughout the antennal lobe and is processed in a separate or particular MGC-lobe. In contrast, the information about the two pheromone components in *H. virescens* seems to a large extent to be integrated in the antennal lobe, where the information about the second essential component is completely mixed with that from the major component. More analyses concerning synaptic connections between the primary afferents and the projection neurons are needed in order to find out whether the two types of receptor neurons project to separate areas of the particular MGC-lobe. In *H. zea*, where the information from the second essential component C is mediated via the receptor neurons tuned to the interspecific signal B, the information from both compounds is obviously transmitted to the AL-neurons in the same dorsal MGC-lobe (Almaas *et al.*, 1991; Christensen *et al.*, 1991; Vickers *et al.*, 1991). Since both types of projection neurons, mediating responsiveness to the pheromone compound A and to the interspecific signal B, arborized in this MGC-unit, the possibility exists that the information about compounds C and B may become separated at this level. However, since no projection neurons were encountered that responded predominantly to compound C or to compounds A and C, it seems likely that the information about B and C are further conveyed along the same output axons to protocerebrum.

The data provided so far from the morphology of functionally identified receptor neurons and AL-projection neurons in the two heliothine moths demonstrate that the MGC is subdivided into functional units, where the pheromone and interspecific signal information is processed in separate lobes. The data from *H. virescens* and *M. sexta* demonstrate that the information from different pheromone components is integrated by some projection neurons, whereas others mediate responsiveness about single components. Furthermore, the data from the heliothines show that the antennal lobes of two related species process differently the input which is similar in the two species, transmitted by receptor neurons of the same specificites.

Coding of odour intensity and temporal features

Other important features of the AL projection neuron responses are the dynamic concentration range and the inhibitory input. In general the projection neurons in heliothines (as in other species; Boeckh and Boeckh, 1979) showed much stronger responses to a given concentration

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of the stimuli than the receptor neurons, although the sensitivities of both kinds of neurons varied with a factor of 1000 (Almaas and Mustaparta, 1991; Almaas *et al.*, 1991; Christensen *et al.*, 1991, 1995a,b). The data obtained in heliothines suggests that projection neurons exhibiting a high sensitivity may receive input from very sensitive receptor neurons, whereas the less sensitive receptor neurons provide input to the projection neurons exhibiting a lower sensitivity (Christensen *et al.*, 1991, 1995a,b). This implies that the mechanisms for detecting increased concentrations of the filaments in the pheromone plume, is a recruitment of receptor and AL projection neurons of lower sensitivites, in addition to a temporal summation of increased firing rates in the receptor neurons. During the males' flight in a pheromone plume consisting of intermittent odour filaments, the receptor neurons are exposed to pulsed odour stimulations. The temporal response pattern of the receptor neurons and their ability to respond to odour pulses is discussed by Kaissling (1996, this issue). The pulsed response characteristics observed in receptor neurons seem to be accentuated in the AL. When stimulating the antenna with pheromone pulses, many of the projection neurons show excitatory responses to each pulse, followed by an inhibition, where the neurons are able to encode pulse frequencies up to about 12 Hz (Christensen and Hildebrand, 1987; Christensen *et al.*, 1991). The inhibition is explained by input from the local GABA-ergic AL interneurons to the projection neurons (Christensen *et al.*, 1993). Some AL projection neurons do not show the ability to follow pulses, and a very few neurons display exclusively inhibition in responses to antennal stimulation with pheromones (Christensen *et al.*, 1991). Different abilities of neurons to follow pulsed stimulation may be important for the orientation in the pheromone plume, where some neurons detect each pulse and others continue firing when the male comes outside an odour filament or the plume. These response characteristics suggest that in addition to detecting different qualities of pheromone blends produced by conspecifics and sympatric females, the AL projection neurons in males are also coding intensities by both temporal summation and recruitments of neurons, as well as coding the spatial features of the pheromone plume.

In conclusion, the different glomerular compartments of MGC seem to be functionally specified, but they all operate as a unit to process the various features of the insect produced stimuli.

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