Progress in Research on Insect Olfactory Perception of Habitat Odor Molecules

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Abstract   A highly sensitive olfactory system allows insects to precisely identify and position volatile compounds from different sources in their habitats，and plays a crucial role in their foraging，mating，and oviposition activities. During evolution，insects have successfully developed a large and complex olfactory system to adapt to heterogeneous environments，enabling the maintenance of inset population. A comprehensive examination of the olfactory system of insects may therefore yield novel insights into the development of innovative pest control and prevention strategies，as well as the study of olfactory mechanisms in vertebrates and even humans. This paper outlines the current state of research into the signal transduction mechanism by which insects perceive the olfactory molecules of their habitats. The aim of this review is to provide a reference point for future studies into the olfactory perception mechanism and its potential applications in pest management.

Key words   Volatile；Odorant-binding protein；Olfactory receptor；Odorant degrading enzyme；Olfactory receptor neuron

1   Introduction

Olfaction represents a chemical language utilized by animals，with the majority of known invertebrates and vertebrates exhibiting olfactory capabilities. These abilities enable them to perceive and process information from their external environments[1]. The highly specialized and sensitive olfactory system of insects may be one of the reasons why insects have had the most successful evolutionary strategy and the largest number of species in the animal kingdom[2]. The olfactory system of insects plays a pivotal role in regulating a multitude of intricate behavioral responses，including those associated with foraging，aggregation，courtship，avoidance，and the search for suitable egg-laying sites. These processes are of paramount importance for the survival and reproduction of insects. A highly sensitive olfactory system enables insects to accurately identify volatile compounds from different sources in the environment，which plays a critical role in the process of foraging，mating，and egg-laying，as well as in other life activities[3].

It is of paramount importance to elucidate the mechanisms by which insects recognize different chemicals and convert chemical signals into electrical signals that are transmitted to the central nervous system of the brain to inform their behavior，as this will provide insights into the olfactory recognition process in insects[4]. The process by which insects perceive odor molecules is shown in Fig. 1. Briefly，upon entering the sensillum lymph through micropores on the antennae，odor molecules are recognized and bound by odorant-binding proteins（OBPs）or chemosensory proteins（CSPs）in the lymph. These proteins facilitate the transfer of li-pophilic odor molecules across the hydrophilic lymph and the movement to the dendritic membrane of olfactory receptor neurons（ORN）. As a result of the pH change，odor molecules are released and activate odor receptors（ORs）or ionotropic glutamate receptors（IRs）on the dendritic membrane. These receptors convert chemical signals into electrical signals and transmit them into the antennal lobe，which in turn activates the central nervous system of the brain. The brain integrates these signals and sends out commands to produce specific behavioral responses[4]. It is essential that olfactory signaling is rapidly inactivated after transmission. This is because the odorant must be rapidly degraded，terminating the stimulation of odorant receptors by the odorant to prevent the receptors from becoming inactive. This is particularly important for insects that rely on odorants for localization and flight[5].

A consensus on the olfactory perception process in insects is that it can be divided into two main stages. （i）The first stage occurs at the level of peripheral nerves，where the peripheral olfactory system screens and receives odor molecules. These molecules are converted into electrical signals for conduction in neuronal cells. The peripheral sensory system is responsible for identifying odors and is composed of the antennae，mandibular palp，and labial palp[1]. （ii）The second stage occurs at the level of the central nervous system，which is responsible for processing olfactory information，including the antennal lobe，mushroom body，and lateral horn. At the central nervous system level，the central nervous system integrates and processes electrical signals to elicit the corresponding behavioral responses of insects[1,6].

The elucidation of the molecular mechanisms underlying olfactory perception in insects is of paramount importance for the exploitation of beneficial insects and the prevention and control of pests. Consequently，this paper presents a summary of the current state of knowledge regarding the olfactory sensory mechanisms of insects，with the aim of providing a reference for the development of pest management strategies based on these mechanisms.
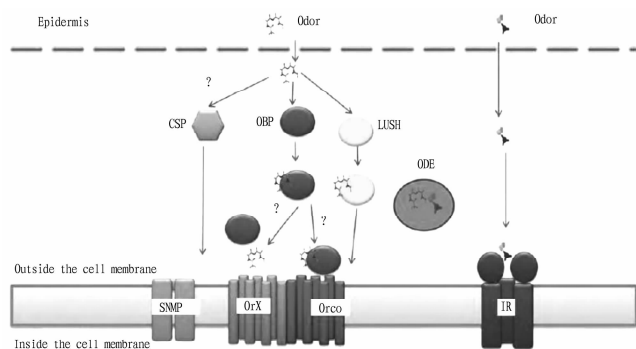
Fig. 1   Schematic diagram of signal transduction in the peripheral nervous system of insects[6]

2   Odor molecules

The odor molecules that insects perceive through their olfactory sense are predominantly fat-soluble molecules, including host plant volatiles and pheromones released by insects of the same species[7]. The olfactory cues emitted by mixtures of different odor compounds at varying concentrations serve as chemical fingerprints that play a pivotal role in the foraging, aggregation, feeding, and searching behaviors of insects. These cues also influence the location of egg-laying sites and the avoidance of egg-laying sites[8-9]. The concentration, frequency, and relative flow rate of odor molecules, in conjunction with the insect's own flight speed and the frequency of wing flapping, collectively influence their olfactory perception of odor molecules[10-11].

2.1   Volatiles of host plants

The volatiles of host plants are primarily identified through gas chromatography-mass spectrometry, which is coupled with a standard sample validation method[12]. The majority of host plant volatiles are composed of alcohols, aldehydes, ketones, esters, hydrocarbons, organic acids, and terpenoids[13].

The volatiles of host plants can be classified into two categories based on their functions and properties. The first category comprises highly specific volatiles, which are formed by the cleavage of secondary metabolites. An example of a volatile belonging to this category is isothiocyanate compounds, which are formed by the cleavage of glucosinolate from cruciferous plants[14]. The second category is plant green leaf odor, which is primarily composed of alcohols, aldehydes, esters, terpenes, and unsaturated fatty acid derivatives, as well as other compounds. They exist in a certain proportion and concentration in plant volatiles to form a chemical fingerprint[13]. Linalool, camphor, and eucalyptol, for instance, are present in a ratio of $2.15 : 1.87 : 1$ in the volatiles of *Cinnamomum camphora*[15].

2.2   Insect pheromone

Insect pheromones are secreted by exocrine glands, which are formed by specialized glandular cells of insect dermal cells that aggregate at specific sites. Those used for intraspecific linkages are designated as pheromones, while those used for interspecific linkages are referred to as interspecific pheromones or allelochemicals[16]. The types of pheromones released by insects are diverse and include sex pheromones, alarm pheromones, aggregation pheromones, tracking pheromones, labeling pheromones, *etc.*[16].

The majority of insect pheromones are $C_{10} - C_{18}$ straight-chain unsaturated fatty acids with oxidized functional groups, such as alcohols, aldehydes, and acetates. Alternatively, they may be $C_{10} - C_{18}$ hydrocarbons with $2 - 3$ double bonds[17]. For example, the sex pheromone of *Helicoverpa armigera* is composed of six compounds, including *cis*-11-hexadecenol, *cis*-9-fulure, *cis*-7-hexadecenal, *cis*-9-hexadecenal, *cis*-11-hexadecenal, and hexadecenal[18]. The ant trail pheromone components Z,E-alpha-farnesene and E,E-alpha-farnesene play a role in maintaining symbiotic relationships between ants and aphids, as well as modulating reproductive behavior in another species[19].

3   Signal transduction in the peripheral olfactory nervous system

3.1   Antennae and olfactory receptors

The technique of electroantennography (EAG) was initially employed to demonstrate that female pheromones in silkworm moths elicited an electroantennogram response in males, thereby confirming the antennae as the primary olfactory receptor organ of insects[1]. During evolution, antennae evolved from primitive filaments into a variety of specific shapes, including feathers, gills, knees, and serrations, in order to increase the surface area and accommodate as many receptors as possible[20]. The disparity in the number of receptors on the antennae of most insects between males and females is relatively modest, with a few exceptions. One notable example is the female moth of *Antheraea polyphemus*, which has nearly 13 000 receptors on its antennae, while the male moths have nearly 10 times more than the females, with about 126 600 receptors[21]. Additionally, olfactory receptors have been identified on the maxillary palp of insects. For instance, the maxillary palp of trypetids exhibits three distinct types of receptors, including sensilla chaetica (SC), microtrichia (MI), and sensilla basiconica (SB)[22].

Receptors have been classified by scanning electron microscopy into three categories: wall pore type, roof pore type, and no pore type[23]. Basiconic sensilla are located in the antennae and maxillary palps and are primarily responsible for detecting ester, alcohol, and aldehyde odors. Trichoid sensilla are located in the antennae and are primarily responsible for detecting sex pheromones. Finally, coeloconic sensilla are located in the antennae and are primarily responsible for detecting acidic and amine odors[24].

3.2   Transport and signal transduction of odor molecules

3.2.1   Odorant-binding proteins (OBPs).

Insect antennal OBPs are widely distributed in the lymphatic fluid and interact with odor molecules as the initial biochemical step in the recognition of external odors by insects. Hydrophobic odor molecules must bind to OBPs in order to successfully cross the aqueous environment of the lymphatic fluid of the antennal receptor and to activate ORs on the dendritic membranes of ORNs[25]. Typical OBPs are soluble proteins with a molecular weight of $12 - 20$ kDa. The full length of the polypeptide chain contains $120 - 150$ amino acids and is characterized by a signal peptide sequence with six conserved cysteines, six α-helices, three internal disulfide bonds, and an N-terminus[26].

Insect antennal OBPs include three distinct protein families:

pheromone-binding proteins (PBPs), general odor-binding proteins (GOBPs), and antennal-binding proteins (ABPX). GOBPs are present in both sexes and function as carriers of host odors. For instance, GOBP2 is involved in the olfactory perception of host odors by *Dichocrocis punctiferalis*. Additionally, GOBPs have been found to interact with CSPs, thereby enhancing the perception of host volatiles[27]. In addition to their involvement in the olfactory perception of host volatiles by insects, OBPs are also involved in the localization process of pests by natural enemy insects. For example, the OBP of *Aphidius gifuensis* (AgifOBP6) parasitizes aphids by recognizing the aphid alarm pheromone E-β-farnesene (EBF)[28]. GOBPs that bind host odors are predominantly distributed on basiconic sensilla, whereas PBPs that specifically bind sex pheromones are distributed on trichoid sensilla. This suggests that the physiological function of receptors influences the distribution of different OBPs on different receptor types[29].

The binding and release of odor molecules to OBPs is dependent on changes in the pH of the surrounding environment. At pH 7.4, the OBP of *Tetradacus citri* BminOBP6 has a strong ability to bind to the odor molecules 1-undecanol and (+)-limonene. Conversely, when the pH is reduced to 5.0, BminOBP6's ability to bind to (+)-limonene is diminished, and its ability to bind to 1-undecanol is lost[30]. The C-terminus of PBPs rapidly binds sex pheromone molecules at neutral pH. Upon transport to the receptor, the C-terminus of PBPs undergoes a conformational change due to the low pH of the environment, which releases the sex pheromone molecules from the binding pocket to activate the receptor[31-32].

3.2.2 Olfactory receptors (ORs). OR specifically recognizes odor molecules and converts chemical signals from odor molecules into electrophysiological signals through selective ion channels, thus playing a pivotal role in the signal transduction pathway[33]. Once an odor molecule has interacted with a receptor, it must be inactivated immediately to ensure the receptor's continued activity and sensitivity to the odor molecule. This is essential for the receptor to accurately recognize the new odor molecule. For instance, the half-life of the drop in receptor potential triggered by a sex pheromone is 1 sec, indicating that the odor molecule must be deactivated within 1 sec[34].

ORs belong to the G-protein-coupled receptor (GPCR) family, which are ubiquitous in the animal kingdom. The first OR gene was identified in *Drosophila melanogaster*[35]. Insect GPCRs share a common feature of the presence of seven transmembrane α-helical structures. These receptors are connected by three extracellular and three intracellular loops, with the amino terminus intracellularly and the carboxyl terminus extracellularly. They play a key role in the selection of odor signal specificity in the peripheral olfactory system of insects[5,36]. The function of each type of neuron is dedicated to the detection of a specific set of odors. Only one OR is expressed in an ORN. However, there are instances where two receptor genes are expressed in the same ORN. Odor tuning profiling studies have demonstrated that only one receptor gene determines the tuning function of an ORN[37-38]. Insect odorant receptors are divided into two classes: the first is the traditional odorant receptor x (ORx), which contains the common OR and

the sex PR (pheromone receptor). The ORs exhibit low homology among different insects despite they are numerous[39]. The second class is the atypical odorant receptor co-receptor (Orco), which is highly conserved and belongs to the OR83b family of receptors. Typically, only one Orco is found in an insect[40]. Orco does not bind to ligands and does not affect the specificity of ligand recognition by ORs. However, it forms a heterodimer with ORx, which improves odor recognition and binding efficiency and promotes accurate localization of ORs in neuronal dendrites and maintains their stability. Additionally, it does not alter the ligand binding range of ORs[41-42].

3.2.3 Sensory neuron membrane proteins (SNMPs). Signal transduction in the peripheral olfactory system of insects is facilitated by the involvement of SNMPs, which play a pivotal role in the process of olfactory perception in insects[5]. SNMPs are dual transmembrane proteins belonging to the CD36 family. At least two SNMP family genes, SNMP1 and SNMP2, are present in insect antennae. For example, sex pheromone induces the Eobl-SNMP1 of *Ectropis obliqua* to be highly expressed specifically on male antennae, while EoblSNMP2 is highly expressed on female antennae, male antennae, and other chemosensory tissues. Additionally, both EoblSNMP1 and EoblSNMP2 are centrally expressed in trichoid sensilla, which are in the same distributional position as the PBPs for receptor pheromones. Collectively, these findings support the conclusion that trichoid sensilla are located in the antennal main receptor pheromone[43].

SNMPs are involved in the binding and subsequent unbinding of odor molecules from OBPs and odor molecule complexes. SNMPs can also form complexes with ORs to facilitate odor molecule binding to receptors and participate in olfactory recognition responses. Finally, SNMPs act as a novel transporter protein to transport odor molecules to dendritic membranes of olfactory neurons[44].

3.2.4 Odor degrading enzymes (ODEs). If an odorant persists in stimulating an insect's olfactory receptors, it can cause damage to its olfactory nervous system. Consequently, the dynamics of the olfactory system necessitate rapid degradation of the odorant, particularly in insects that rely on the odorant to localize their flight. A number of ODEs have been identified that are capable of rapidly degrading odorants, such as the recently identified aldehyde oxidase (AOX) in the antennae of moths and butterflies, the esterase in the antennae of *Spodoptera frugiperda*, and the cytochrome P450 enzyme. However, the P450 enzyme is an intracellular enzyme, and only odor molecules entering the cell can be degraded by the P450 enzyme[45-47]. Alternatively, the olfactory system of insects employs a "molecular trap" odor scavenging mechanism that terminates the stimulation of odor substances to ORs in order to maintain receptor activity[48].

3.3 Olfactory conduction Upon the introduction of an odorant into the antennae of insects, the level of inositol trisphosphate (IP3) within the antennae reaches a maximum value within 50 ms, subsequently declining to a minimum value and returning to the normal value within approximately 200 ms[49]. High concentrations of IP3 may facilitate the opening of calcium channels in the dendritic membrane, thereby altering the ion permeability of the membrane. This results in a transient inward flow of calcium

ions out of the dendritic membrane and the formation of a calcium ion current, which may subsequently activate potassium and chloride channels. This, in turn, further depolarizes the membrane and generates a receptor potential in olfactory receptor cells[50].

ORs and Orco form a dimer that serves as a gated ion channel for signal transduction. Odor molecules stimulate the ORs to directly open the ligand-gated ion channel, allowing the cation to enter the cell. This generates a receptor potential, which diffuses to the olfactory receptor cell via the dendrites. At the same time, it is transmitted to the central nervous system via the axon, completing the release of an action potential.

3.4 Coding characteristics of odor by the peripheral olfactory nervous system

Peripheral olfactory receptors serve the function of rapidly transmitting qualitative and quantitative information about an odor in an odor mixture to the central nervous system. This process can be studied extracellularly by odor-induced electrophysiological responses using single-cell recording methods[20,51]. The olfactory receptor nerves encode odors in terms of whether the nerve cell produces an excitatory, inhibitory, or no response to the odor, as well as the strength of the response.

The coding characteristics of the peripheral nervous system for odors are as follows. (i) Selectivity. Olfactory neurons are selective, and a specific olfactory neuron can exhibit a response threshold to one or more odors, which is the tuning nerve of the odor. Single-cell recordings revealed that almost every ORN exhibited a distinct degree of selectivity for the odor molecules in the test. Furthermore, the selectivity of the ORNs was also demonstrated by an excitatory response to one odor and an inhibitory response to another odor[52]. (ii) Sensitivity. Olfactory neurons are capable of responding to absolute concentrations of odors or changes in concentration. For instance, the carbon dioxide ORN in the maxillary palp of Aedes egypti is capable of responding to subtle concentration changes. The dose-response intensity curve varies over a range of carbon dioxide concentrations that extends beyond the range of carbon dioxide concentrations observed in natural conditions. This allows for the detection of changes in odor flow with greater precision[53]. (iii) The co-location effect between olfactory neurons enhances the precision of inter-odor ratios and also ensures the detection of whether two or more odors are mixed in the same airflow or from different airflow sources. Insects possess an exceptional ability to discern the proportions of mixed odors. It has been demonstrated that ORNs tuning mixed odors are frequently distributed in the same receptor. Furthermore, insects are capable of distinguishing between two sources of unevenly mixed odors that are in close proximity through the use of the co-location effect. For instance, *Helicoverpa zea* is capable of distinguishing between sex pheromones that are separated by a mere 1 mm, and its antagonist[54]. (iv) Acclimatization and acclimatization release are intimately linked to odor concentration and exposure time. Insects depend on this information for the immediate transmission of exposed odors to the central nervous system[55]. When the ORN encounters two odor streams of the same concentration in a time shorter than the time of acclimatization release, the latter does not trigger an action potential. Alternatively, exposure to a high concentration odor stream does not result in a response to a later exposure to a low concentration odor stream for a short period of time due to acclimatization, a phenomenon known as temporal equilibrium. Insects utilize temporal equilibrium to regulate their response to odor concentration and frequency in order to maintain a relatively stable central nervous system signal amidst a stream of constantly changing odor concentrations.

4 Signal transduction in the central nervous system

Odor molecules cause action potential signals generated by receptor cells to be transmitted first to the antennal lobes of the central nervous system, which represent the initial level of the olfactory information processing channel. The axon of olfactory neurons in the adult antennae enters the antennal lobe directly, where numerous bundles of nerve fibers are present in the periphery of the antennal lobe. The glomerulus serves as the primary site for signal processing and integration, as well as signal amplification. These functions are essential for the initial processing of olfactory information, which occurs within the context of the neuropile. Prior to entering the antennal lobe, the axons of olfactory neurons undergo a process of recombination, whereby they are reorganized into a chemical assembly from a proximity assembly. This occurs within a defined zone, where functionally similar neurons form a bundle of axons[56].

The differentiation of odor molecules in the natural environment by the antennal lobe is the coding of the "quality" of odor molecules. The judgment of the concentration of odor molecules is the coding of the "quantity" of odor molecules. The odor flow in the air is not continuous, and the solution to the problem of discontinuity in the odor flow is the coding of the "spatio-temporal dynamics" of the odor flow[57]. The activation of different odorants by different groups of output neurons in the antennal lobe results in the formation of coding groups for specific odorants. These coding groups are composed of multiple output neurons. The mechanism of the coding group is the synchronous discharge between output neurons. This synchronous relationship is continuously updated with the chemical composition and concentration of the odorant. A multivariate recording study of the antennal lobe of *Manduca sexta* reveals temporal and spatial variations in the coding of the antennal lobe[58]. The antennal lobe is connected to the forebrain, the next level of the insect's central nervous system, through five tactile channels. These include the inner tactile channel, the middle tactile channel, the outer tactile channel, the dorsal tactile channel, and the dorsal middle tactile channel. The processed electrical signals are transmitted to the forebrain by the output neurons of the antennal lobe, which is the high-level center of the insect's olfactory system. The olfactory information transmitted by insects is conveyed from external afferent neurons to the calyx in the forebrain and from the mushroom bulb by external efferent neurons[59]. The lateral forebrain, situated on both sides of the forebrain, is a network of nerve fibers with no fixed structure. It contains the lateral horn, which receives information from the antennal lobe, the gyri-cerebrales, and the mechanoreceptive center of the midbrain. The neural spheres, located behind the antennal lobe and on the lateral-ventral surface of the centrosome, are lateral attachment balls that are intimately connected to the centrosome

and receive olfactory-related information transmitted from the lateral horn. This information is exchanged between the two lateral attachment balls via a long-distance pathway[60].

5　Summary and prospects

The odor environment in which insects live is exceedingly intricate, comprising a vast array of odor molecules and their diverse combinations. The primary challenge facing the olfactory system of insects in the context of a rapidly changing odor environment is to effectively utilize odor information to enhance their survival prospects. Insects have evolved an olfactory sensory system that is capable of accurately and sensitively determining various combinations of odors or changes in odor dynamics. This may be one of the reasons why insects have become competitive winners.

　　Research on the molecular mechanism of olfactory sensation in insects is of great significance and offers considerable potential for future development. It represents an important avenue for the discovery of new methods of pest control and prevention. A comprehensive examination of the molecular mechanisms underlying olfactory perception in insects can elucidate the influence of olfaction on insect behavior. Moreover, it can provide a theoretical foundation for the development of novel, effective, and environmentally friendly behavioral modifiers for the targeted control of agricultural and forestry pests or hygienic pests, thereby advancing the goal of sustainable pest management. The olfactory mechanism of insects is currently understood to a greater extent than previously thought, but there are still a number of elements that require further study and determination. These include the question of whether odorants activate ORs alone or in the form of a complex, the specific physiological functions of olfactory-related proteins, the interaction mechanism between various olfactory-related proteins, how the chemical information is translated during the specific signaling process and connected with the motor center to make the insects react accordingly, and the difference in olfactory sensory mechanisms of insects in different habitats. In light of the rapid advancement and ongoing refinement of experimental techniques, a multidisciplinary approach integrating electrophysiology and molecular neurobiology, such as optical conformation, multivariate recording, patch clamp technology, laser confocal imaging technology, and molecular genetics, is essential for elucidating the complexities of olfactory sensation in insects and exploring the potential of interfering with target genes involved in olfactory perception for pest management. Furthermore, the olfactory recognition system of insects can be emulated to develop highly sensitive biosensors. The structure, physiological functions, and odor recognition mechanisms of the insect olfactory system exhibit numerous parallels with those of vertebrates. Consequently, a comprehensive examination of the insect olfactory system can serve as a robust foundation for the investigation of the olfactory mechanism in vertebrates and even in humans. This will facilitate the comprehension of the cognitive processes of the human brain and the exploration of the deeper neuroscience.

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