



Plasticity in Insect Olfaction: To Smell or not to Smell?

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Abstract

In insects, olfaction plays a crucial role in many behavioral contexts, such as locating food, sexual partners, and oviposition sites. To successfully perform such behaviors, insects must respond to chemical stimuli at the right moment. Insects modulate their olfactory system according to their physiological state upon interaction with their environment. Here, we review the plasticity of behavioral responses to different odor types according to age, feeding state, circadian rhythm, and mating status. We also summarize what is known about the underlying neural and endocrinological mechanisms, from peripheral detection to central nervous integration, and cover neuromodulation from the molecular to the behavioral level. We describe forms of olfactory plasticity that have contributed to the evolutionary success of insects and have provided them with remarkable tools to adapt to their ever-changing environment.

Olfactory receptor neuron (ORN):

sensory structure that receives odor molecules and transduces chemical information into electrical signals

Odorant binding protein (OBP):

protein present in olfactory sensilla involved in the transport of hydrophobic odor molecules

Antennal lobe (AL):

primary olfactory center in the insect brain

Projection neuron:

a neuron that transmits information from the primary olfactory center, the antennal lobe, to higher olfactory centers

Macroglomerular complex (MGC):

enlarged neuropil area within the antennal lobe, specialized in the processing of sex pheromone

Olfactory plasticity:

change in olfactory-guided behavior to a same stimulus due to modulation within the sensory system

INTRODUCTION

Insects rely on olfaction to locate mating partners, food sources, habitats, and oviposition sites, and to escape predators. Insects may encounter odorants emitted from individuals belonging to the same species, such as mating partners (e.g., sex pheromones in moths) and nestmates (e.g., alarm pheromones in ants), or belonging to different phases (e.g., aggregation pheromones in locusts) (130). Insects also exploit odor signals emitted from organisms such as enemies, potential hosts, and food sources, and from other sources of natural or anthropogenic origin, for example, that signify potential oviposition sites (14, 99).

To detect these olfactory signals and cues, insects have developed a sophisticated sensory system consisting of olfactory receptor neurons (ORNs) situated in sensilla on the antennae and mouthparts (64). Odor molecules penetrate through the cuticular pores and then are transported by odorant binding proteins (OBPs) to the ORN membrane, where they interact with receptors, ultimately leading to the generation of action potentials (59, 127). The signal is then transmitted through the ORN axon to the primary olfactory center of the brain, the antennal lobe (AL) (6). There, ORNs make synaptic contact with intrinsic neurons, the local interneurons, and with output neurons, the projection neurons, which transfer information to higher brain centers such as the mushroom bodies (MBs) and the lateral protocerebrum (30). Centrifugal neurons, which have a modulatory role, send axon branches to the AL (6, 56). The AL consists of a species-specific number of globular neuropil, the glomeruli (105), whose activation is odor specific and reproducible within a given species (46). Individual glomeruli become enlarged, such as the macroglomerular complex (MGC) in male moths, in which a large number of ORNs equally tuned to the sex pheromone are present (54).

Insect responses to biologically active chemical stimuli may vary not only according to biotic and abiotic environmental factors and/or previous experience, but also as a function of the physiological state. For development and reproduction to occur, insects must respond to relevant chemical stimuli at the right time. For example, responses to sexual signals should occur at reproductive maturity under environmental conditions suitable for mate finding, mating, and producing offspring. Also, responses to food odors should depend on the state of satiety. Insects must thus respond to odorants in coordination with their own physiological state.

To cope with these variable conditions, insects modify their olfactory systems by neuronal plasticity. Two types of behavioral olfactory plasticity and their neuronal basis have been studied so far: plasticity induced by (a) physiological changes and (b) environment- (e.g., biotic and abiotic factors) or experience-induced changes (e.g., different forms of learning). Here, we focus on the first type of plasticity in adult insects. Adaptations to physiological changes, either as short-term modifications (e.g., via modulation) leading to changes in neural activity or as long-term modifications (e.g., via life-history traits) leading to changes in gene expression and neural structure, are common in animals.

We summarize the recent literature on olfactory plasticity in insects, including economically important insect groups such as pollinators, agricultural pests, and disease vectors. Experience-dependent olfactory plasticity has been well summarized elsewhere (4, 24, 34). Here, we focus on modulatory effects of the physiological state that occur gradually, such as age-dependent, feeding state-dependent, and circadian rhythm-dependent effects, or immediately, such as mating-dependent effects. We describe both behavioral modifications and, where known, the neural mechanisms underlying modulation, from peripheral detection to central nervous integration.

AGE-DEPENDENT PLASTICITY

The lifespan of adult insects generally varies between a few days and a few weeks; in exceptional cases, such as honey bee or termite queens, adults can live for many years. Depending on its lifespan

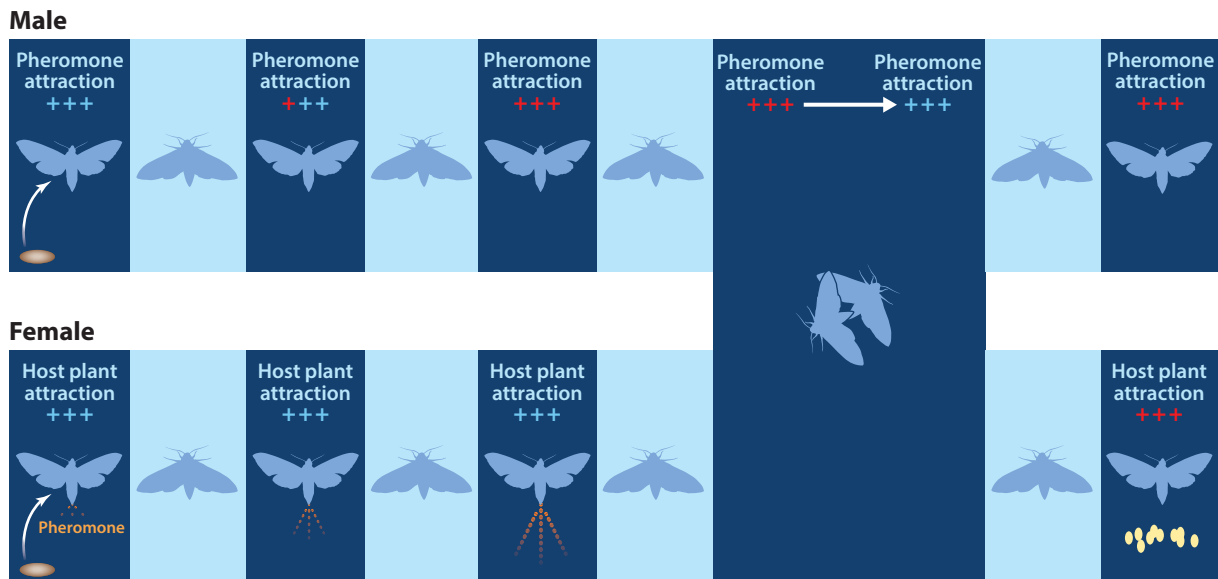


Figure 1

Plasticity in moth olfactory-guided behavior as a function of age, circadian rhythm, and mating. Females emit increasing amounts of sex pheromone and males respond increasingly to this pheromone with age. Both sexes are active only at night. After mating, males transiently stop responding to the sex pheromone until the next night and females begin responding to host-plant odors in search of an oviposition site. Red crosses indicate level of attraction.

and lifestyle, an insect's response to the same odor(s) may change over the course of its adulthood. In males and females, age-dependent olfactory plasticity is linked to maturation of reproductive organs (sexual maturation). This plasticity is, however, not restricted to responses to odors from conspecifics; it also affects responses to hosts, food, or oviposition cues. The best-studied insects in this context are moths and hematophagous mosquitoes and bugs, but we also provide examples from other insects, including flies, wasps, and bees.

Age Modulation of Pheromone-Guided Behavior

For insects in which one sex produces a sex pheromone that attracts the opposite sex, many cases of maturation in early adult life have been reported. In some noctuid moths, for example, males are more apt to respond to the female-produced sex pheromone over the first days following emergence (**Figure 1**) (45, 115, 121), in parallel with the maturation of the male sex accessory glands (SAGs) (36). In tephritid flies, the behavioral response of females attracted to male-emitted sex pheromones depends on ovarian development (41, 73).

In male moths, biogenic amines and hormones are involved in age-dependent behavioral sensitivity to sex pheromones. In *Agrotis ipsilon*, juvenile hormone (JH) biosynthetic activity increases concomitantly with age and pheromone response (36). By manipulating the JH level, researchers could decrease and increase the behavioral response (i.e., the percentage of males flying upwind toward a pheromone source) of sexually mature and young immature males, respectively (45, 62). Similarly, injections of 20-OH ecdysone (20E) increased the behavioral response of young *A. ipsilon* males to pheromone, whereas injections of cucurbitacin, an antagonist of 20E receptors, decreased the responses of sexually mature males (37). Biogenic amines such as octopamine

Sexual maturation:

post-imaginal physiological development of the sexual apparatus and the nervous system to allow reproduction

Sex accessory glands (SAGs):

male glands that produce secretions essential for the transfer of sperm to the female

Juvenile hormone (JH):

sesquiterpenoid insect hormone involved in regulating larval and adult development

and dopamine also influenced age-dependent behavioral olfactory plasticity (2, 62). In *A. ipsilon*, the modulatory action of 20E, octopamine, and dopamine on pheromone-guided behavior seems to occur via their receptors, as the injection of their antagonists or their knockdown strongly decreased the behavioral response of mature males (1, 2, 35, 37).

Age can also influence the response of insects to other types of pheromones. In the locust *Schistocerca gregaria*, the response to the main aggregation pheromone component, phenylacetone nitrile, is age dependent. Young males and females with low levels of JH display aggregation behavior and are attracted to phenylacetone nitrile, whereas older adults with high JH levels no longer respond to this component (58). In the honey bee, *Apis mellifera*, responses of workers to the queen mandibular pheromone decrease with age (97, 123). Octopamine increased responses of young bees to the brood pheromone, an activator of age- and JH-mediated foraging behavior, and decreased the negative effect on foraging caused by the presence of old bees (8). It is now important to study how the different neuromodulators interact in the different model systems and whether there is a hierarchy in their influence on age-dependent olfactory-guided behavior.

Age Modulation of Behavioral Responses to Nonpheromonal Odors

Behavioral responses to plant or animal host odors as well as nonhost volatiles also underlie age-dependent changes in different insects. Food odor cues are often most attractive in early adult life, and oviposition-site cues become more attractive later. Female mosquitoes begin host searching and blood feeding only 24 to 72 h after adult emergence (65). Before this time, young female mosquitoes search for sugar-rich resources and are not attracted to vertebrate odors. Older *Aedes aegypti* females are more responsive to CO₂ than younger ones are (19, 47). Also, in the obligatory hematophagous triatomine bugs, which have similar host-seeking behavior throughout development, attraction to host cue CO₂ is age dependent. In *Rhodnius prolixus*, recently molted nymphs become highly attracted to CO₂ beginning 7 days after ecdysis, when they are anatomically (e.g., mouthpart sclerotization) and physiologically (e.g., biosynthesis of blood digestive enzymes) mature enough to ingest blood (Figure 2) (17).

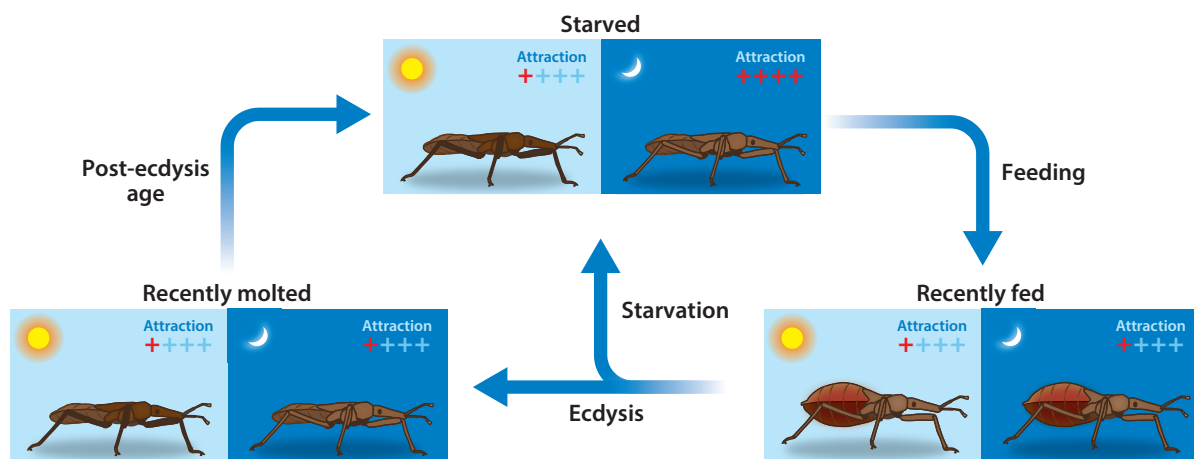


Figure 2

Plasticity in triatomine bug olfactory-guided behavior as a function of age, circadian rhythm, and starvation. Bugs are attracted to hosts during the night. After feeding and following ecdysis, they are transiently no longer attracted to their hosts. Attraction resumes after starvation and time after ecdysis. Red crosses indicate level of attraction.

In females of different herbivorous insects, including moths and beetles, both positive responses to host-plant odors and negative responses to nonhost-plant volatiles can increase with age (7, 87). By contrast, the avoidance response to the fruit-related odor benzaldehyde decreased with age in *Drosophila melanogaster* (32). Also, specificity to and the range of olfactory cues alone or in combination with other sensory cues to which insects respond can change with age. In the pepper weevil, *Anthonomus eugenii*, specificity to host-plant odors increases with age and maturation (3). In the ant *Pheidole dentata*, the range of olfactory cues to which it responds increases with age, in coordination with the number and types of tasks performed in the colony, and this change is accompanied by increasing levels of serotonin and dopamine but not octopamine (113). In the tephritid fly *Neoceratitis cyaneescens*, sexually mature females use a combination of visual and olfactory host-plant cues, whereas immature females and males orient only toward olfactory host-plant cues and largely ignore visual cues (22).

In contrast to increasing olfactory sensitivity during maturation in early adult life, senescence or aging can negatively affect olfactory responses. For example, *D. melanogaster* showed an age-dependent aversion to or a decrease in attraction to innate odors from approximately 14 days post eclosion (52). Investigations into the potential aging effects on longer-lived insects would be valuable.

Age Modulation in the Peripheral Olfactory System

Sensitivity of insect antennae to pheromones, as measured by electroantennographic (EAG) or single sensillum recordings, can either increase with age or be independent of age. In a few moth species (*Ostrinia nubilalis*, *Spodoptera littoralis*, and *Pseudaletia unipuncta*), the pheromone-detecting sex showed increasing EAG or ORN responses with age (33, 84, 112), whereas in *A. ipsilon* no effects of age were found in EAG responses to sex pheromone (45). In *S. littoralis* males, EAG responses increasing with age were correlated with changes in the expression of certain ecdysone receptors in the antennae: Whereas expression of *SIEcR* was constant throughout adulthood, expression of both *SIUSP* and *SIE75* increased steadily (15). Also, age-related changes in behavioral responses to aggregation pheromones in locusts and to the queen mandibular pheromone in honey bees were not reflected by changes in EAG responses (58, 97). The decreasing behavioral attraction of honey bee workers to the queen mandibular pheromone correlated with changes in the expression of biogenic amine receptors in the antennae. The expression of the dopamine *Amdop2*, the octopamine *Amoa1*, and the tyramine *Amtyr1* receptors increased with age, whereas expression of *Amdop3* decreased (86, 123).

EAG responses to nonpheromonal odors increased with age, e.g., *S. littoralis* females to plant odors (84) and female *Phormia regina* blow flies to odors from oviposition substrates (26). In the mosquito *Ae. aegypti*, the sensory neurons on the antennae and maxillary palps respond increasingly to lactic acid and CO₂, respectively, with age in correlation with increasing behavioral responses to these host odors (28, 47). Bohbot et al. (19) correlated an increased response of octenol-sensitive ORNs on the antennae of *Ae. aegypti* with an increase in odorant receptor gene expression from day 1 to day 6 post emergence. Investigations using molecular genetics tools with *D. melanogaster* need to confirm whether observed correlations between gene expression and antennal sensitivity indeed have a functional connection.

Age Modulation in the Central Olfactory System

Clear correlations between changes in the central nervous system and age-dependent modulation of olfactory-guided behavior have been found in some insect species. Most of the described

Odor-guided behavior: locomotion elicited by an odorant

effects occur at the AL level, but age-dependent changes within the MBs have also been observed. *A. ipsilon* males demonstrate prominent changes in the sensitivity of sex pheromone–responding AL neurons in accordance with age and hormone levels: AL neurons become increasingly sensitive to the sex pheromone as the insect ages, and high levels of JH, 20E, octopamine, and their receptors allow this increase in sensitivity (2, 5, 43, 62). Central processing of plant odors, by contrast, is age independent (48). An anatomical correlate of olfactory maturation has been found within the AL of the sphingid moth *Manduca sexta*. The relative size of the pheromone-processing MGC glomeruli increases during the first days of adult life (57). Contrary to findings on sex pheromone responses in male moths, AL sensitivity to aggregation pheromones in the locust *S. gregaria* decreases with age and JH level, consistent with observed behavioral changes (58).

In social insects such as honey bees and ants, but also in *D. melanogaster*, correlates of age-dependent behavioral changes have been identified within both the AL and the calyces of the MBs. Owing to an increase in synaptic density in honey bees and *D. melanogaster*, certain glomeruli of the AL increase in size with age (32, 128). Also, in vivo optical imaging experiments have shown that odor responsiveness increases within the AL glomeruli of honey bee workers during the first days of adult life (125). At the MB level, the volume of the calyces increases with age while the density of synaptic microglomeruli decreases (49). Within the calyces, the membrane surface area of projection neuron synaptic boutons increases and the number of postsynaptic partners (Kenyon cells) decreases with age (50). In the carpenter ant *Camponotus floridanus*, both the AL and the MBs increase in size and contribute to increasing brain volume with age, correlated with an increase in the complexity of worker tasks (51). Whether the neuromodulators and their receptors involved in age-dependent physiological changes also play a role in the anatomical modifications would benefit from further investigation.

FEEDING STATE-DEPENDENT PLASTICITY

For many insects the attractiveness of food/host odors is dependent on the delay after the last food intake. Generally, food odors become more attractive as starvation is prolonged. This form of plasticity, however, has been studied predominantly in blood-sucking insects, as many of them transmit infectious diseases to humans. In addition, after a blood meal, insects engage in different activities related to their biology, such as mate finding, searching for oviposition sites, or returning to refuges.

Effects of Feeding State on Behavioral Responses to Odor

The nutritional state of the insect influences odor-guided behavior in both blood and nonblood feeders. Sugar feeding influenced parasitoid wasps' choice between host and food cues (77, 82), and in *D. melanogaster*, starvation increased the attractiveness of food-odor sources (38). In mosquitoes, a blood meal distends the abdomen and the subsequent ovarian development suppresses host-seeking behavior, which in *Ae. aegypti* (69, 70) and *Anopheles gambiae* (119) is generally restored 24 h after oviposition. Once a blood meal large enough to initiate ovarian development has been obtained, mosquitoes are attracted to olfactory cues associated with suitable oviposition sites (68).

In the case of triatomine bugs, the response of all developmental stages to CO₂ and other odors depends on their feeding status (**Figure 2**). *R. prolixus* starved for a short duration is attracted to host-related cues and repelled by aggregation pheromone, whereas insects starved for a long duration are attracted to both (102). Unfed *R. prolixus* is highly attracted to CO₂, whereas 48 h after a blood meal, the bug becomes unresponsive to CO₂, which then becomes repellent after 72 h and remains repellent or neutral for at least 20 days (16, 18). Moreover, insects fed saline

solution or even starved bugs injected with hemolymph of fed insects are also unresponsive to or repelled by host cues such as CO₂ and heat (18). Postfeeding behavioral aversion to CO₂ seems to be induced by a mechanical distension of the abdomen and by an unidentified factor in the hemolymph that modulates olfactory responses (18). Blood feeding triggers physiological processes such as molting in nymphs or egg-laying in adult females and modifies host attraction behavior, with different time courses for different insects, according to their life-history traits. A high sensitivity to host odors when blood feeders are engaged in other relevant tasks would be a waste of energy and even life-threatening as hosts often display defensive behavior.

***Aedes aegypti* head peptide I (Aea-HP-I):** peptide suggested to inhibit host seeking in *Aedes aegypti* mosquitoes

Effects of Feeding State on Peripheral Detection and Central Processing of Odors

In blood-feeding insects, both down- and upregulation of the sensitivity to host and oviposition-related odors, respectively, has been found on the antennae following a blood meal. In *Ae. aegypti*, a humoral factor downregulates the sensitivity of lactic acid receptor neurons situated in grooved peg sensilla, which are used during host localization (23, 29), whereas ORNs in trichoid sensilla increase their sensitivity to oviposition site-emitted compounds 72 h after a blood meal (117). In *An. gambiae*, there is a complex change of ORN responses after blood feeding: Depending on the neuron types, both up- and downregulation of responses to different odors were found (98). By contrast, ORNs of starved tsetse flies, *Stomoxys calcitrans* stable flies, and triatomine bugs were more sensitive to host-related odors (93, 101, 126).

Proteins involved in peripheral odor detection, such as odor receptors (ORs) and OBPs, are suggested to modulate the peripheral system. In *An. gambiae* the putative odorant receptor *AgOr1*, which is expressed only in female antennae, is downregulated 12 h after blood feeding (42), during which olfactory responses to human odorants are substantially reduced (119). Likewise, down- and upregulation of genes, such as those encoding for ORs and OBPs in *Ae. aegypti* and *An. gambiae*, have been documented as changes in transcript accumulation induced by a blood meal (20, 83, 103). Similarly, the expression of antennal OBPs in *Glossina morsitans morsitans* and the transcript levels of the antennal olfactory co-receptor genes in *R. prolixus* vary as a function of the nutritional state (75, 80).

Neuromodulators, such as peptides and serotonin, regulate numerous feeding functions (91, 114). Physiological analyses of *D. melanogaster* indicate that increased attraction to a food odor after starvation might originate from rich temporal dynamics of gene expression and modulation by insulin and the short neuropeptide F at the first synapse within the olfactory system (39, 104). Insulin signaling regulates the expression of the short neuropeptide F, leading to increased sensitivity of presynaptic neurons within the AL and therefore to more robust food-searching behavior in starved flies (104). In *R. prolixus*, the level of serotonin circulating in hemolymph increases after blood feeding (74). Furthermore, serotonin-immunoreactive neurons innervating the AL of mosquitoes display volumetric changes in their varicosities in response to blood feeding, indicating serotonin release at the synapses (116). Whether serotonin influences olfactory responses related to host-seeking behavior needs to be confirmed. In *Ae. aegypti*, the head peptide, Aea-HP-I, released from neurosecretory cells in the brain and midgut, was suggested to inhibit host seeking after a blood meal (23). Despite these findings, we are only beginning to discover how neuropeptides modulate the olfactory system.

RHYTHM-DEPENDENT PLASTICITY

Olfactory-guided behavior, similar to many other activities, varies according to the time of day. Circadian rhythms help animals remain tuned to their environment, allowing them to anticipate

Zeitgeber: sensory cue present in the environment that helps synchronize the internal circadian rhythm

the arrival of near-future cyclic conditions. Oscillations are recurrent approximately every 24 h and persist under constant conditions. Although an endogenous rhythm is defined as self-sustainable, an animal's internal clock is sensitive to external cues such as light, temperature, humidity, food-related cues, and social interactions, which serve as zeitgebers to maintain a rhythm

Rhythm-Dependent Behavioral Responses to Odors

A circadian rhythm of olfactory sex communication occurs in cockroaches (76, 132) and moths (**Figure 1**) (25, 55, 78, 79, 118). This rhythm is maintained in constant darkness at least for some time, and other zeitgebers such as pheromone exposure can replace cyclic light conditions (118). In the diurnal gypsy moth, *Lymantria dispar*, octopamine injected prior to the onset of scotophase increased the percentage of contacts with pheromone sources during both photophase and scotophase, whereas an injection in early photophase did not have any effect (79). Studies with moths have demonstrated that synchronizing female calling with male orientation responses during the photoperiod minimizes metabolic costs (25, 55, 118).

Circadian rhythms of behavioral responses to olfactory stimuli have also been reported for blood feeders (**Figure 2**). Nocturnal triatomine bugs seek a blood meal mainly at dusk (81) and are guided by CO₂ (among other cues) released by sleeping hosts (12). Correspondingly, during this time the bugs are maximally attracted to CO₂ (12, 13, 16) and do not orient toward aggregation pheromones released by conspecifics around shelters (16). Conversely, at dawn, after feeding, they return to their shelters and are highly responsive to aggregation pheromones (16). Experiments under constant darkness reveal that the responsiveness to CO₂ is controlled by a circadian clock, whereas the response to the aggregation pheromone is not (12, 16). Circadian rhythms are thus important for the odor-guided behavior of insects with different life styles, helping them elicit appropriate responses at the appropriate time, but more case studies are needed to expand general concepts.

Rhythm-Dependent Antennal Function

In many insect species, the sensitivity of ORNs to odors, measured by EAG and single sensillum recordings, appears to be under circadian control. In the cockroach *Leucophaea maderae* and in *D. melanogaster* a circadian clock regulates antennal responses to food-related odors (71, 94). In blood-feeding insects such as triatomine bugs, tsetse flies, and mosquitoes, antennae respond to host-related stimuli in synchrony with their behavioral rhythm of response: Antennae are more sensitive when the insects seek a host (21, 101, 106, 122). In moths, peripheral pheromone detection is generally independent of the circadian rhythm (95, 129); however, in *S. littoralis* males pheromone sensitivity decreases significantly at the end of scotophase, which correlates with rhythm-dependent expression of an odorant-degrading enzyme gene in the antenna (89). Also in mosquitoes, olfactory-related genes, including OBPs, sensory appendage proteins, and the olfactory co-receptor Orco, underlie a circadian rhythm of expression (27, 106, 108). Quantitative proteome analysis revealed that the expression of OBP transcripts (from genomic analysis) corresponds with a peak in protein abundance at the same time of the night (i.e., dusk) and EAG olfactory sensitivity to host odorants (106, 107). Altogether these results show that the olfactory machinery of mosquitoes is tuned for host odor detection and location as a function of their activity period.

The existence of peripheral oscillators necessary to mediate rhythmic olfactory responses was first shown in the antennae of *D. melanogaster* (120). Mutant flies lacking the clock genes *period* and *timeless* lost their ability to respond to odors in a rhythmic fashion, further confirming control by a circadian clock (71). Abolishing the clock by molecular targeting of transcriptional regulators of the core clock mechanism showed that the antennal ORNs, but not central neurons, can function

as autonomous pacemakers (120). Rhythmic expression of clock gene products has since been observed in the antenna of many insects, suggesting that antennal oscillator-modulating olfactory sensitivity is a common feature (88, 89, 111).

MATING-DEPENDENT PLASTICITY

Many insects undergo significant physiological changes during mating. These modifications induce often drastic changes in male and female responses to odors involved in sex recognition, such as sex pheromones, or host attraction, such as host-plant odors in herbivores or animal host odors in blood-feeding insects; the female response to oviposition-site cues undergoes changes as well. Generally, responses to sex attractants are switched off after mating, whereas responses to host odors or oviposition-site cues are switched on (i.e., postmating switches). In most species these effects are reversible and after a species-specific time interval, the original state is resumed.

Mating-Induced Changes in Behavioral Responses to Sex Pheromone

Mating-dependent olfactory plasticity has been studied in detail in the male noctuid moth *A. ipsilon* (Figure 1). In this species, the olfactory switch-off occurs very rapidly after the onset of copulation and lasts throughout scotophase (44, 124). This behavioral switch-off seems to be independent of JH, 20E, and the biogenic amines octopamine and serotonin (11, 36, 124) and originates from the SAGs (124). Moreover, this inhibition is restricted to sex pheromone, as newly mated males still respond to plant odors (9). Interestingly, the addition of sex pheromone inhibited the response of mated males to even flower odors, but enhanced the response to sex pheromone in virgin males (9). Similarly, mating decreased responses of *Plutella xylostella* males to sex pheromone or mixtures of pheromone and host-plant odors, even though the addition of plant odors strongly increased the response of virgin males to sex pheromone in the field (100). In *S. littoralis*, newly mated males ceased to respond not only to sex pheromone but also to host-plant odors (cotton leaves), whereas they still responded to food odors such as lilac flowers (72) (Figure 1).

Similar effects occur in species in which males produce the sex pheromone to attract females. In several true fruit flies and the parasitic wasp *Nasonia vitripennis*, mated females cease to be attracted to the male-emitted pheromone and this inhibition can last up to four weeks, depending on the species (41, 60, 61, 63, 109). Females begin instead to be attracted to fruit odors after mating, as shown in the Mediterranean fruit fly, *Ceratitidis capitata* (60, 61). The lack of behavioral responses to sex-related cues after mating is thus a common phenomenon in insects, but different neuromodulators seem to be involved, leading to different time courses for the switches in behavior.

Mating-Induced Changes in Behavioral Responses to Oviposition and Host Cues

Behavioral responses to plant odors may also vary in female herbivores according to mating status. Behavioral responses to host-plant odors are often enhanced after mating, as females must find a suitable oviposition site (Figure 1). Indeed, mated female moths are more attracted to host-plant volatiles than virgin females are (85, 110).

In female blood-feeding insects, mating inhibits host search but elicits responses to oviposition-site cues. Only mated female mosquitoes are highly attracted to oviposition-site stimuli (68). Secretions of the male SAGs induced virgin females to engage in oviposition site-seeking behavior (131), and transplanting conspecific male SAGs with their major peptide component, Aea-HP-I, into virgin *Ae. aegypti* females significantly reduced their host-seeking behavior (40, 90). After

Postmating switch:
behavioral changes in
odor responsiveness of
males and females
following mating

oviposition, *Ae. aegypti* females gradually recover their behavioral and physiological responses to host cues and are no longer behaviorally attracted to oviposition cues (66). These mechanisms, however, cannot be generalized to all mosquito species: Male *An. gambiae* SAG content neither initiates refractory mating behavior nor stimulates oviposition (67). Different mechanisms in different insect species thus seem to modulate behavioral responses to oviposition and host cues.

Mating-Induced Modulation Within the Olfactory Pathway

As for other types of modulation, sensitivity changes occur at different levels of the olfactory system after mating, depending on the insect species. In *S. littoralis* males, EAGs, single sensillum recordings, and in vivo calcium imaging revealed that antennal neurons were less sensitive to the sex pheromone and host-plant odors after mating, whereas neuronal responses to flower odors were not modified (72). In *S. littoralis* females, the behavioral postmating olfactory switch from food odor to host-plant odor originates also from modulation in the peripheral olfactory system (84, 110). In *A. ipsilon* males, on the other hand, no difference in antennal sensitivity to the sex pheromone was observed, and responses to flower odor were enhanced after mating only at high stimulus doses (10, 44). Also, in other moth species such as *Vitacea polistiformes* and *Cydia pomonella*, EAG responses to the sex pheromone did not differ between virgin and mated males (31, 96). In *A. ipsilon*, modifications to odor sensitivity have been found within the AL: Neurons are less sensitive to the sex pheromone by several orders of magnitude after mating, whereas AL responses to a flower odor are not modified (9, 10, 44). Nevertheless, when presenting the sex pheromone and the flower odor simultaneously, flower-odor-responding neurons within ordinary glomeruli of the AL in virgin males show synergistic responses to the mixture, but high doses of the sex pheromone inhibit mated males' responses to flower odor (9). Neither octopamine nor serotonin seems to be involved in mating-induced sensitivity changes in the AL (11). The mechanisms by which peripheral and central neurons change their sensitivity after mating remain to be investigated.

CONCLUDING REMARKS AND PERSPECTIVES

We have reviewed the plasticity of insect olfaction as a function of the physiological state. This plasticity of sensory systems, together with experience-induced plasticity, is an important evolutionary strategy that optimizes vital resources for survival and reproduction. High sensitivity has metabolic costs (92) and should therefore only be present when a resulting behavioral output leads to an increase in fitness. In addition, locomotor activity in response to a sensory cue would be a waste of energy if the organism's physiology were not ready for the final behavioral output. Most studies reviewed here were performed under laboratory conditions and did not take into consideration the metabolic costs. Future investigations should confirm in a more natural context the findings from laboratory studies in conjunction with metabolic costs.

Behavioral changes in accordance with age, feeding status, circadian rhythm, and mating status have been investigated primarily in insects with well-described olfactory communication systems, such as cockroaches, bees, locusts, and moths, and in blood-feeding species, such as mosquitoes and triatomine bugs. These organisms have enabled researchers to describe changes in sensitivity along the olfactory pathway. However, very little is known about the role of higher brain centers in physiological state-dependent forms of plasticity. In some cases the role of hormones and neuromodulators such as biogenic amines and peptides has been described (Figure 3), but synaptic plasticity at the anatomical, physiological, and molecular levels should be studied. With the molecular, biochemical, and genetic tools emerging for an increasing number of species, it might now be possible to identify genes, and the corresponding proteins and neurons in which

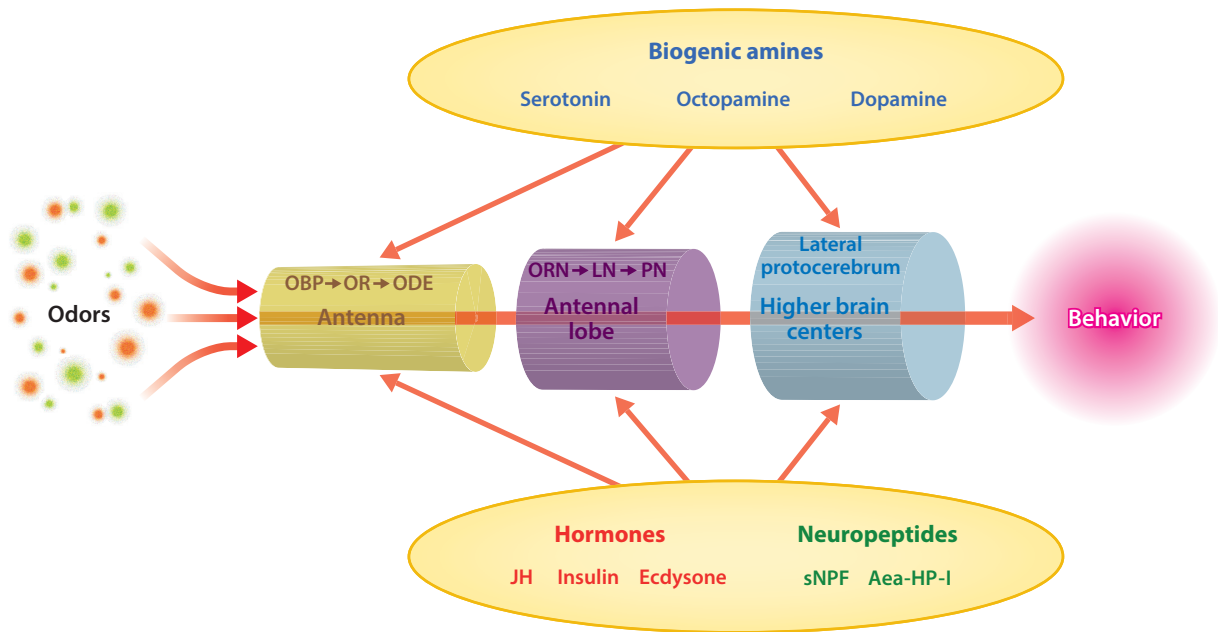


Figure 3

Actors of olfactory plasticity at different levels of the olfactory pathway. Biogenic amines, hormones, and neuropeptides modulate the peripheral and central nervous systems, leading to changes in sensitivity to behaviorally active odors and thus to changes in behavior. Abbreviations: Aea-HP-I, *Aedes aegypti* head peptide I; JH, juvenile hormone; LN, local interneuron; ORN, receptor neuron; OBP, odorant binding protein; ODE, odorant degrading enzyme; OR, olfactory receptor; PN, projection neuron; sNPF, short neuropeptide F.

they are expressed, that play a role in physiological state-dependent plasticity not only in model organisms but also in nonmodel insects. From a socioeconomic point of view, investigations into disease vectors, agriculturally important insects, and their natural enemies will provide scientists new opportunities to develop alternative control strategies by exploiting the knowledge on naturally plastic behavior and the underlying neural mechanisms in species that rely heavily on their sense of olfaction to reproduce.

SUMMARY POINTS

1. The physiological state of insects influences olfactory-guided behavior by modulating peripheral detection and central nervous processing of odors.
2. Odor-guided behavior in response to intraspecific (i.e., pheromone) and interspecific (i.e., host odors) cues is influenced by age and adult development. Such modulation occurs at the peripheral and central nervous system levels.
3. Responses to food odors depend on the development of the feeding organs and the degree of starvation or satiety, signaled, for example, via stretch receptors in the abdomen and factors circulating in the hemolymph. So far, evidence has been found primarily for modulation of peripheral sensitivity.

4. Circadian rhythms coordinate insect communication and adapt behavior to the ecology of an insect species. Clock genes in the antennae allow autonomous rhythmicity of odor detection.
5. Mating switches the odor responses of both male and female insects. Whereas responses to sex pheromones and animal host odors are usually switched off after mating, responses to host-plant and oviposition-site cues are switched on.

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