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Pheromones, Insects

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Glossary

Aggregation pheromone One sex produces the signal, and both sexes are attracted to the signal.
Anosmia Inability to detect or perceive a chemical compound.
Detection Identification of the presence of a signal.
Hormesis Dose-response phenomenon whereby a low dose (e.g. of insecticides) gives a high behavioral response, while at higher doses the response is reduced.
Natural selection Selection exerted by other species (biotic factors) or by abiotic factors (temperature, light).
Perception Detection of a signal including the interpretation of the signal after integration in the brain center.
Pheromone Infochemical that conveys information between individuals of the same species.
Pheromone component Chemical that has been behaviorally tested and confirmed to attract potential mating partners, in contrast to a pheromone compound, which has been chemically identified to be in the pheromone blend but not confirmed to be behaviorally important for attraction.
Plasticity Variation within individuals during development, sexual maturation, aging, or upon experience.
Reception Detection of a signal at the receptor level.
Sex pheromone Attractant between the sexes (one sex produces and emits the signal, and the other sex from the same species perceives and responds/is attracted to the signal).
Sexual selection Selection exerted by potential or rival mating partners within a species.

Abbreviations

CHC Cuticular hydrocarbon
GR Gustatory receptor
MGC Macroglomeruli complex
OR Odorant receptor
ORN Odorant receptor neuron
PKK Pickpocket ion channel
PBAN Pheromone biosynthesis activating neuropeptide
JH Juvenile hormone

What are Insect Sex Pheromones?

Sex pheromones are ubiquitous in the animal kingdom and present in all insect orders (Gomez-Diaz and Benton, 2013). Since the first identification of the sex pheromone in the silkmoth *Bombyx mori* in 1959, the sex pheromones of more than 1500 insect species have been identified (Pherobase.com). Generally, sex pheromones consist of a blend of at least two chemical components. Species or race specificity is ensured by the blend composition and the ratios of the components. The most famous example is the European corn borer, *Ostrinia nubilalis*, which consists of two pheromone races that have opposite ratios of the same two pheromone components.

There is enormous diversity in the chemical nature of sex pheromones, as they can consist of saturated or unsaturated hydrocarbon chain carrying an acetate, alcohol or aldehyde function (in most moths), polyenic hydrocarbons, methyl-branched hydrocarbons (e.g. in Lepidoptera and Coleoptera), epoxides, ketones (e.g. in some Coleoptera), terpenes (e.g. in beetles) and terpenoids (e.g. in some geometrids and pyralids), iridoids (e.g. in aphids), as well as alkaloids (e.g. in Scarabidae) (Howard and Blomquist, 2005; Hanks and Millar, 2016; Allison and Cardé, 2016; Jurenka, 2004; Dewhirst *et al.*, 2010; Yew and Chung, 2015). Representative structures of insect sex attractants are illustrated in **Fig. 1**, including those of moths, honeybee, cockroach, bug, and fruit fly.

Sex pheromones can be short(er) carbon chain volatiles that attract potential mating partners from a longer or shorter distance, or long(er) carbon chain cuticular hydrocarbons (CHCs) that are used to identify potential mating partners or rivals upon contact. Volatile and contact chemical cues may be integrated to reinforce or refine selection of the right mating partner. In species with additional cues,
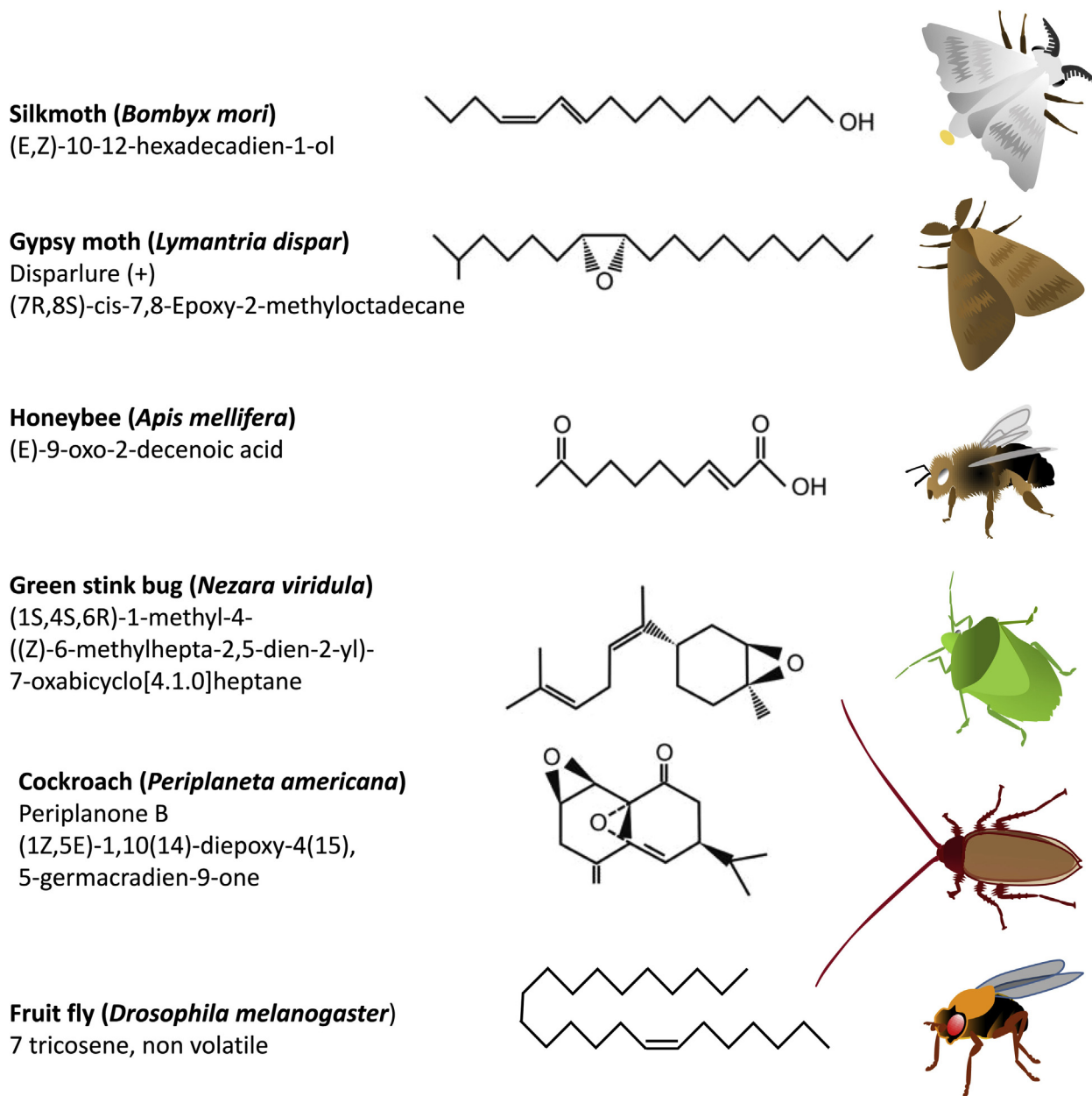
Silkmoth (*Bombyx mori*)
(E,Z)-10-12-hexadecadien-1-ol

Gypsy moth (*Lymantria dispar*)
Disparlure (+)
(7R,8S)-cis-7,8-Epoxy-2-methyloctadecane

Honeybee (*Apis mellifera*)
(E)-9-oxo-2-decenoic acid

Green stink bug (*Nezara viridula*)
(1S,4S,6R)-1-methyl-4-
((Z)-6-methylhepta-2,5-dien-2-yl)-
7-oxabicyclo[4.1.0]heptane

Cockroach (*Periplaneta americana*)
Periplanone B
(1Z,5E)-1,10(14)-diepoxy-4(15),
5-germacradien-9-one

Fruit fly (*Drosophila melanogaster*)
7 tricosene, non volatile

Fig. 1   Representative insect sex pheromone molecules illustrating the diversity of chemical structures.

such as visual and acoustic cues, or species-specific movements, genitalia incompatibility, spatial and seasonal separation of populations, and diel separation of pheromone release, sex pheromones may consist of more ubiquitous compounds. The most striking example is found in aphids, where the sex pheromone of all species consist of nepetalactone and nepetalactol, and the species-specificity mostly comes from the combination of sex pheromone with other environmental cues (Dewhirst *et al.*, 2010). The amount of pheromone that is secreted from or is present in a pheromone-producing gland also varies enormously with species and, to some extent, behavioral function. Sex-attractant pheromones may be present in microgram, nanogram, and even picogram quantities per individual.

Sex pheromones are not only diverse in terms of amounts, range or ratios of different compounds, but also in terms of enantiomers with opposing, inhibitory effects (Yew and Chung, 2015). For example, closely related species that occur sympatrically and have a similar sex pheromone may avoid hybridization by having different ratios of the same pheromone components or by having additional minor pheromone components that inhibits the attraction of the other species. One example for such behavioral inhibition is found in the gypsy moth (*Lymantria dispar*) and the nun moths (*L. monacha*) that share (+)-disparlure as attractant and live in sympatry in parts of Europe. In addition to (+)-disparlure, the female nun moth produces (−)-disparlure, that inhibits the attraction of male gypsy moths, thus ensuring species isolation. The use of such enantiomers or diastereoisomers in pheromone blends is quite common, especially in species where mate finding relies mostly on sex pheromone communication.

Who Produces Sex Pheromones?

Which sex is the signaler and which sex is the responder varies between insect orders, as well as on the range at which potential mating partners are attracted. The most typical example is found in moths: in most species females adopt a characteristic calling behavior by which they extrude a pheromone gland for emission of a long-range sex pheromone in the air to attract males from a distance. In some lepidopteran species, such as the arctiid moth *Utetheisa ornatrix*, females group together for calling in chorus, which synchronizes and intensifies their signaling, thus favoring attraction. Receiver males fly upwind to the female with a stereotyped zig-zag behavior. Once in the vicinity of the female, males start courtship and in some species produce a close-range sex pheromone that may play a role in female choice. More rarely, as in the sugarcane borer *Eldana saccharina*, male moths emit a long distance pheromone from a gland/hair pencils on their abdomen, or from hair tufts on their wings, so-called coremata. In beetles, flies and several Hemiptera (true bugs), males attract females mostly at close range or upon contact. Tephritid flies display a lek mating system, where males aggregate and emit different visual, acoustic and chemical signals to attract females. Arriving female flies assess the multimodal calling behavior of a number of calling males before selecting a mate among the available ones.

Where are Sex Pheromones Produced?

The locations of the glands or tissues responsible for sex pheromone production are very diverse. Volatile sex pheromones are generally produced in specific glands, such as sex pheromone glands located at the tip of the abdomen in female moths, hair pencils/hair pockets (coremata) in male moths and butterflies, or epidermal glands located under the abdominal tergites of cockroaches. CHCs are produced in oenocytes, which are secretory cells inside the hemolymph (which can be close to epidermis or scattered throughout fat body). *Ips* beetles produce their sex pheromone in the hindgut, the signal being released with the frass. Tephritid flies produce pheromones in salivary and anal glands. In aphids, mature sexual females (oviparae) release a sex pheromone from scent plaques on their hind tibiae which attracts conspecific males (Dewhirst *et al.*, 2010).

Sex pheromones can be produced *de novo* or may be sequestered from plants (Jurenka, 2004). When produced *de novo*, the sex pheromones are generally derivatives from fatty acids (moth sex pheromones and CHCs). In some cases, microbes or symbionts participate in pheromone biosynthesis. For instance, gut microbiota may participate in the verbanone pheromone production in bark beetles. How aphids produce their sex pheromone components (nepetalactone and nepetalactol) is unknown, possibly nepetalactol is produced from a glycoside precursor, a proportion of which is sequentially oxidized to nepetalactone (Dewhirst *et al.*, 2010).

Some insects sequester or acquire host plant compounds and use them as sex pheromones or sex pheromone precursors. The most famous example is the arctiid butterfly *Utetheisa ornatrix* (Arctiidae), whose male courtship pheromone derives from pyrrolizidine alkaloids (PAs), which are ingested at the larval stage from the host plant *Crotalaria spectabili*s. Males also transfer PAs to females during mating as a nuptial gift, which females subsequently use to coat their oviposited eggs, which are then protected against predators (Eisner, 2003). In other arctiids, most Dancinae and Ithomiinae butterflies, males also obtain PAs from plants and use them as pheromone precursors. *Cysseps fulvicollis* (Arctiidae) males produce hydroxydanaidal from PAs of dead and damaged plants, and release it as a sex attractant. Host plant volatile emissions can also have an indirect impact on insect sex pheromone communication, for instance in *Helicoverpa* species where host plant volatiles induce female calling behavior. In some *Ips* beetles, exposure to plant volatile myrcene increases the amounts of ipsenol and ipsdienol pheromones in male hindgut tissues. On the receiver side, sex pheromone detection and processing has been also shown to be modulated by the presence of plant volatiles: chemicals from host plants often synergistically enhance the response of an insect to the sex pheromone, improving temporal resolution of pulsed pheromone signals, while some others can have inhibitory or repellent effects that interrupt the response.

When are Sex Pheromones Produced?

Upon Sexual Maturation

Pheromone emission and sensitivity usually coincide with sexual maturity. In most moth species, females and males start to become sexually active 1–2 days after emergence. In general, pheromone glands contain very low levels of pheromone on the first night after emergence, which then increases sharply in subsequent nights. When females get older or after mating, sex pheromone levels may decline again, at least for a short or a long period. In many moth species, female sex pheromone production follows a diel rhythm that is regulated by the nightly release of the pheromone biosynthesis activating neuropeptide (PBAN) from the subesophageal ganglion (Jurenka, 2004). In some moth species, previously synthesized fatty acids are stored as triglycerides in lipid droplets and mobilized by phosphorylation, while in other species, such as *Trichoplusia ni*, pheromone is continuously produced and not regulated by PBAN. In long-lived insects with multiple reproductive cycles, such as cockroaches, beetles and flies, pheromone production is regulated by juvenile hormone (JH) and ecdysone (Jurenka, 2004). For example, in beetles JH regulates pheromone production of both fatty acid and isoprenoid biosynthetic pathways, while JH in turn is regulated by environmental and physiological factors. In bark beetles, feeding on a new host tree elevates JH titers by stimulating activity of the corpus allatum, the endocrine gland that produces JH. In Diptera, ecdysone instead of JH stimulates egg maturation as well as sex pheromone production, most likely by regulating the fatty acyl-CoA elongases (Jurenka, 2004).

At Specific Times of the Day

Many moth species show specific daily activity rhythms in their sexual activities, some species being sexually active in the day, some early at night, while others are sexually active late at night. This differentiation has been suggested to have arisen to minimize communication interference between closely related species, as co-occurring and closely related species with overlapping sex pheromone blends show a temporal differentiation in their daily sexual activities. For example, in the Mojave Desert of California *Hemileuca electra* calls from mid-morning to early afternoon; the closely related species *H. burnsi*, which shares pheromone components with *H. electra*, calls from midafter-noon to dusk. Without exclusive times for mating activities, these species would cross-attract.

At Specific Times in the Year

Many insect species are sexually active only at specific times of the year, usually in the summer time. When the summer period is long (at lower latitudes), multiple generations may develop in one season, while at higher latitudes only one generation may develop. This is the case for example in the European corn borer, where populations near the Canadian border are univoltine, while more southern populations are bi- or even trivoltine, which genetically isolates these populations. Species may also be sexually active early or late in the season. In migrating species, such as the monarch butterfly *Danaus plexippus* and the noctuid moth *Helicoverpa armigera*, adults become sexually active only after arriving at their breeding site.

Variation and Plasticity in Insect Sex Pheromones

Geographic variation in sexual communication signals and responses has been found in many species, even when sex pheromones are mainly used as species-specific recognition cues, which inhibits variation and promotes retention of the species-specific blend (Allison and Cardé, 2016). This already indicates that environmental cues influence sexual communication; both the signal and response can be affected by both abiotic and biotic factors, such as photoperiod, temperature, the occurrence of closely related species that may interfere in the sexual communication when the sexual signals are very similar, and presence of predators and parasitoids that may home in on the sex pheromone to find their prey (Fig. 2). Since many female moths produce their sex pheromone *de novo* every night, females may adjust their pheromone blend depending on the current local environmental conditions.

The sex pheromone signal may vary in quantity as well as in quality. The quantity is mainly affected by host plant volatiles, nutrition and temperature, while the quality can be affected by immune defence responses and experience. For example, when *Heliothis subflexa* females emerged and remained in the odour of the closely related species *H. virescens* for three days, females contained

+/- ? Photoperiod: seasonal and/or diurnal rhythms of sexual activities
+/- ? Dessication: dual role of cuticular hydrocarbons

+ Host plant volatiles synergizing with sex pheromones
+ Sequestration of sex pheromone components (or precursors)
- Negative interactions with host plant compounds or insecticides

- Competition among signalers
+ Chorusing of signalers

Communication interference between closely related species with similar sex pheromone blends

Pathogens may affect sexual communication directly or indirectly

Attraction of mating partners

Predators or parasitoids homing in on sex pheromone to locate prey

Competition among receivers

+ Increases the attraction of the signaling sex and/or reinforces the species-specific sexual signal
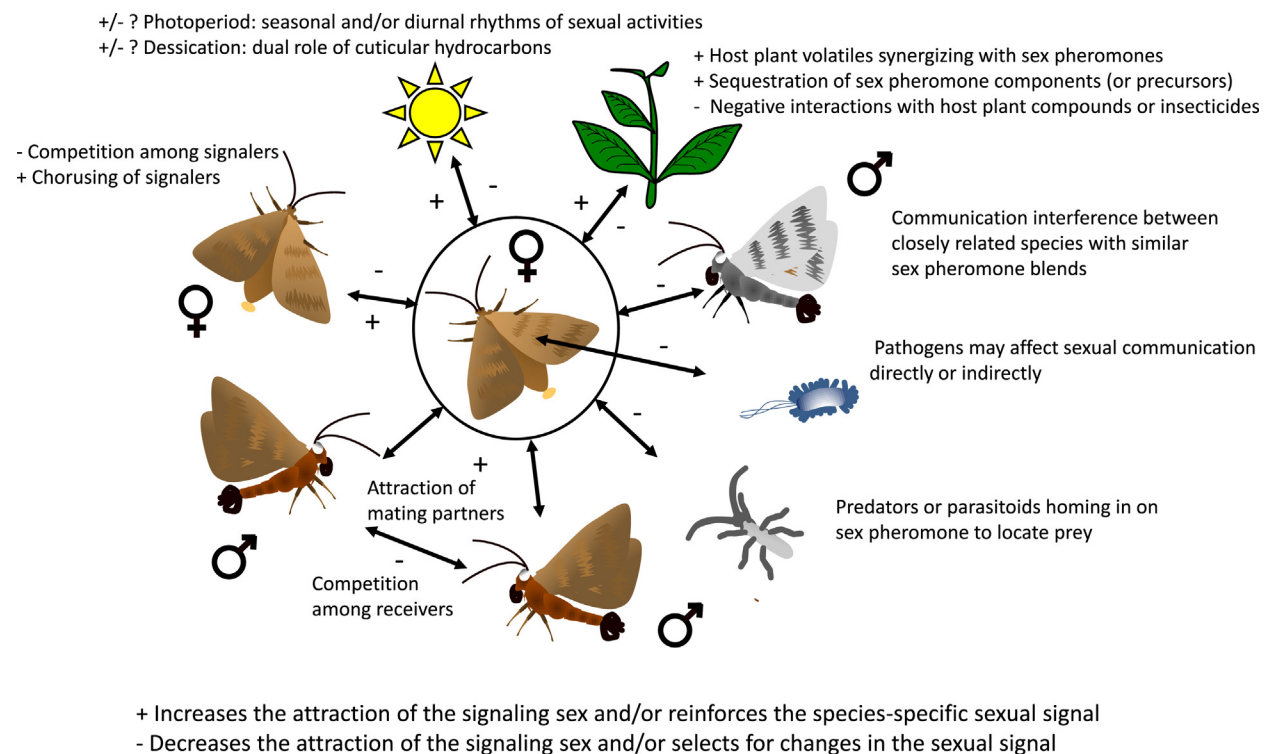- Decreases the attraction of the signaling sex and/or selects for changes in the sexual signal

Fig. 2   Factors that may affect sex pheromone communication in moths.

significantly more of a sex pheromone component that not only attracts conspecific males but also inhibits the attraction of *H. virescens* males. Thus, early-adult experience of different chemical environments affects the sex pheromone composition in *H. subflexa* females. In aphids, the ratio between the two pheromone components nepalactone and nepelactol varies depending on the age of the females, increasing after maturation and then decreasing at later ages, which may be a symptom of senescence (Dewhirst *et al.*, 2010). In the cockroach *Nauphoeta cinerea*, the male sex pheromone varies depending on the carbohydrate intake, and a higher intake increases the male attractiveness, thus increasing their reproductive fitness. Changes in CHC composition have been found in the housefly *Musca domestica*, where the melting temperature of the surface lipids isolated from female houseflies decreased from 39°C to 35°C as the females attained sexual maturity and produced sex pheromone, whereas those prepared from males did not change with age.

The quality of the sex pheromone may also be affected by immune defence responses, as generally hypothesized by the Zahavi handicap principle (i.e., hypothesis proposed to explain how evolution may lead to "honest" or reliable signaling between animals which have an obvious motivation to bluff or deceive each other). The level of sexual attraction may signal the level and extent of health. However, if sexual attractiveness and immunity compete for the same resource pool, they may negatively affect each other. For example, the sex pheromone blend of *Heliothis virescens* females shifted towards an unattractive blend when females were infected with an entomopathogenic bacterium.

How are Sex Pheromones Perceived/Detected?

Mechanisms of Pheromone Detection in the Receiver

Volatile pheromones are detected by the olfactory organs of insects, the principal one being the antennae. These antennae harbour cuticular expansion called sensilla, many of which are dedicated to pheromone reception in the receiver sex (Fig. 3(A)). For instance, male silkmoth *Bombyx mori* antennae are covered by dizaines of thousands of pheromone sensitive sensilla. In addition, antennae may have a sophisticated shape, such as the pectinated antennae of the silkmoth that increase their surface to accommodate larger numbers of pheromone-sensitive sensilla. These sensilla usually house one or two olfactory receptor neurons (ORNs), which are bipolar cells that ensure the transformation of the chemical message into an electrical message that will be transmitted to the brain (Kaissling, 2014; Fig. 3(B)).

Pheromone-sensitive neurons usually respond to a single pheromone component, rarely two. This situation is clearly different from the responses of "generalist" ORNs that are usually activated by a family of related chemicals. The ORN dendrites extend in the sensillum lumen filled with the sensillum lymph, whereas their axons group together in antennal nerves that enter the antennal lobes (the primary processing center in the central nervous system) where they synapse with central neurons in glomerular
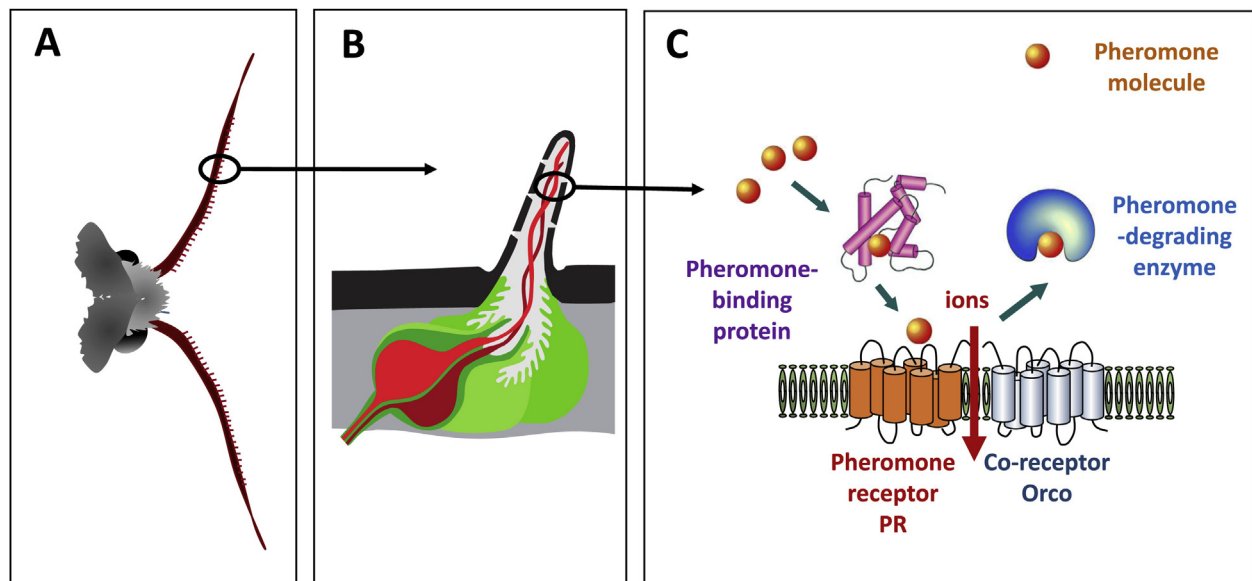

Fig. 3 Illustration of pheromone detection in moths. (A) Head of a moth with two antennae. Antennae carry cuticular expansions called sensilla, some of which are devoted to pheromone detection. (B) Pheromone sensitive sensilla usually house one to three olfactory receptor neurons (red) surrounded by accessory cells (green). The dendrite expands in the cuticular lymph while the axon goes to the central nervous system for signal integration. (C) Molecular mechanisms of pheromone reception. The pheromone molecule (orange) enters the sensillum via cuticular pores. It travels in the sensillum lymph bound by pheromone-binding proteins (PBPs) to the membrane bound pheromone receptor (PR). PR works together with a co-receptor (Orco) to transform the chemical signal into an electrical signal via ion channels opening. Modified from Kaissling, K.-E., 2004. Physiology of pheromone reception in insects (an example of moths). ANIR 6, 73–91.

structures. Axons of pheromone-sensitive neurons have a specific neural circuit as they project to a sexually dimorphic macroglomerular complex dedicated to pheromone signal integration. Pheromone information is relayed via antennal lobe projection neurons to both the mushroom bodies and the lateral protocerebrum. Understanding how the pheromone cues are converted *in fine* to the appropriate behavior is still a scientific challenge.

At the molecular level, the pheromone molecules enter the pheromone sensitive sensilla via cuticular pores. Most pheromones being hydrophobic, they are supposed to be solubilized by dedicated soluble proteins, the so-called pheromone-binding proteins, to cross the aqueous sensillum lymph and reach specific pheromone receptors (PRs) located in the dendritic membrane of the ORNs (Vogt, 2005; Fig. 3(C)). These PRs are part of the insect odorant receptor (OR) family, an unusual family of seven transmembrane domain ionotropic receptor proteins totally unrelated to mammal ORs. After pheromone interaction with its receptor, signal termination may be ensured by pheromone-degrading enzymes abundantly expressed in the sensillum lymph. A fast inactivation is indeed necessary for an efficient orientation behavior to the pheromone source. Although we still lack a consensus view on the exact function of each protein family, the occurrence of a diversity of members in each family accounts for their participation in the specificity of pheromone recognition. The combinatorial expression of these proteins within a sensillum may ensure the specificity, the sensitivity and the dynamic of the olfactory reception, defining the functional phenotypes of pheromone-sensitive neurons.

Most of the PRs functionally characterized to date – meaning their pheromone ligand is known – are from moths, and few others have been characterized in Diptera – mainly fruit fly–, Coleoptera – mainly Cerambycidae – and Hymenoptera. The general observation is that PRs tuned to the major pheromone components are usually very selective, like the ORNs that express them, while some others can recognize pheromone components from closely related species as well as behavioral antagonists (Montagné *et al.*, 2015; Zhang and Löfstedt, 2015).

Non-volatile close range pheromones are detected by contact chemodetection that involves taste structures such as the labellum or forelegs, for instance in the fruit fly. There, gustatory receptors (GRs) that are structurally related to ORs and/or two transmembrane domain Pickpocket (PKK) ion channels would ensure the signal recognition.

Who is the Receiver?

Because sex pheromone signaling is from one sex to the other, one would expect that only the opposite sex receives the emitted signal. Indeed, females of the silkmoth lack the specific receptor to the sex pheromone bombykol, they are thus anosmic to the pheromone they emit. However, females from other moth species express pheromone receptors as in males – although in a smaller amount – and autodetection by the signaler is frequently observed. The elicited behaviors are usually gender-specific: each sex exhibits a different behavior when exposed to the same cues, probably due to sexually dimorphic connectivity in higher-order neurons. In moths, while males would use the pheromone signal to detect an appropriate female, the female may detect its own pheromone to autoregulate its biosynthesis. Alternatively, detection of conspecific sex pheromone may allow evaluation of the local female density and thus the mating success probability. In the fruit fly, the male-specific sex pheromone cis-vaccenyl acetate (cVA) is detected by a pheromone receptor expressed in both male and female antennae. In males, cVA inhibits male–male courtship, while in the female it increases its sexual behavior.

Evolution of Pheromones and Their Role in Speciation

Insect sexual communication can be under different types of sexual and natural selection. Sexual selection may be exerted by the receiving sex when sex pheromones are used to choose among potential mating partners within a population (or species), or by the producing sex when mate competition occurs (Groot *et al.*, 2016). For example, in *Drosophila* flies and *Heliothis* moths, males perfume the females with their short-range sex pheromone, which inhibits the attraction of other, rival males. Natural selection can occur when other, predatory or parasitoid, species home in on the pheromone signal to locate their prey. A famous example is the bolas spider that can mimic the sex pheromone of different moth species. Natural selection can also occur when the pheromone has a dual function, which has been found to be the case in CHCs, as these also prevent insects from desiccation (Chung and Carroll, 2015). This has been illustrated in *Drosophila serrata* and *D. birchii* that co-occur in Australia and exhibit strong pre-mating isolation. *D. serrata* is a habitat generalist, with high amounts of methyl branched CHCs that prevent water loss and affect mating success, while *D. birchii* is a habitat specialist occurring in the humid rainforest, which is much less desiccation resistant, and produces only trace amounts of methyl branched CHCs that do not play a role in mating success.

When sex pheromones are subject to both sexual and natural selection, diversification of sex pheromones may be enhanced when both selection forces are in the same direction (as the example of CHCs). When sex pheromones are mainly used as species-recognition cues, i.e. to distinguish conspecific from closely related heterospecific individuals, and closely related species produce very similar sex pheromone blends that may only differ in the ratio of the different pheromone components, sex pheromones seem to be under stabilizing selection; For the signaler any deviation away from the mean lowers the probability of attracting the right (conspecific) mating partner. For the receiver, attraction to an off-blend can increase the chance of being attracted to another closely related species with a very similar sex pheromone. Counter-selection forces may occur when predators or parasitoids home in on the sex pheromone signals, which causes a trade-off between attraction to potential mating partners or to the enemy.

The use of sex pheromones in pest management may also cause selection towards alternatives sex pheromone blends (Witzgall *et al.*, 2008). For example, mating disruption is used in moth pest management: by saturating the air with synthetic sex pheromone

lures, the males are unable to locate the females, which thus prevents matings. However, this may pose selection to both the female signal and the male response to vary their sexual communication such that they will be able to find each other again. Such changes have for example been found in the summer fruit tortrix *Adoxophyes honmai*, where males did not respond to the common female pheromone blend anymore.

Pheromone Communication in a Changing World

Since pheromone signals and responses can be affected by many external biotic and abiotic factors (such as presence of plant volatile compounds, insect density, temperature, wind, humidity, pollution), global changes may also affect sex pheromone communication, either with direct effects on the insect physiology, or via modification of environmental factors that influence the pheromone communication. For example, as host plant volatile emissions have an impact on insect sex pheromone communication, one can expect temperature, CO_2 and ozone increases in the coming years to affect plant volatile emission and thus to impact the sex pheromone communication and by consequence the reproductive success of many insects.

Another interesting anthropomorphic impact is the effect of insecticides. Whereas the sex pheromone communication is generally altered when insects are exposed to insecticides, exposure to sublethal doses of some insecticides such as organochlorides, neonicotinoids or pyrethroids, has been shown to enhance reproduction abilities, a phenomenon called hormesis. Although neglected for long, insecticide-induced hormesis showing such a reversal of response between low and high doses of insecticides has been found in a number of species. The underlying mechanisms remain largely unknown, but the olfactory system appears to be affected and pheromone detection and associated behavior enhanced. For instance, chlordimeform treatment at low-dose induced a very high sensitivity to sex pheromone in the oriental fruit moth and the cabbage looper, and deltamethrin enhances the male response to pheromone in the cotton leafworm. Such phenomenons may participate in pest insect resurgence.

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Relevant Website

http://www.pherobase.net/. –Database of pheromones and semiochemicals.