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Evolutionary origin of insect pheromones

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Communication via chemical signals, that is, pheromones, is of pivotal importance for most insects. According to current evolutionary theory, insect pheromones originated either from extant precursor compounds being selected for information transfer or by the pheromone components exploiting a pre-existing sensory bias in the receiver. Here, we review the available experimental evidence for both hypotheses. Existing data indicate that most insect pheromones evolved from precursor compounds that were emitted as metabolic by-products or that previously had other non-communicative functions. Many studies have investigated cuticular hydrocarbons that have evolved a communicative function, although examples of pheromones exist that have arisen from defensive secretions, hormones or dietary compounds. We summarize and discuss the selective pressures shaping the pheromone during signal evolution.

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Introduction

The chemical sense and interaction with other organisms via chemical compounds are of pivotal importance to most animals. In particular, insects have exploited chemical compounds in interactions with other organisms, including chemical communication with con-specific and heterospecific individuals, chemical defence against predators and pathogens and chemical cues for locating food and hosts [1]. Interaction via chemical compounds often circumvents the physical constraints imposed by the small body size of most insects with regard to physical interactions and to acoustic and visual signal production and perception. The compounds used in this interaction are named semiochemicals, which are further classified according to their function [1]. The term pheromone was

introduced by Karlson and Lüscher in 1959 [2] and refers to those semiochemicals used in intraspecific communication (see [Glossary](#)). Although chemical communication has been thoroughly studied for several decades, the origin and the evolution of chemical signals remains a major conundrum in chemical ecology.

According to current evolutionary theory, two major hypotheses are proposed for the origin of chemical communication: the sender–precursor hypothesis and the sensory exploitation hypothesis [1,3,4]. The sender–precursor hypothesis predicts that, similar to the evolution of communicative behaviour from functionally different behaviours through a ritualization process [5], chemical communication (pheromones) can evolve from compounds (precursors) with no or a non-communicative function. According to the sensory-exploitation hypothesis, a compound evolves a communicative function because the sender exploits a sensory bias for this compound in the receiver. The major difference between the two hypotheses is that, in the precursor hypothesis, the compound was produced by the sender before the receptor in the receiver evolved, whereas in the sensory exploitation hypothesis, the receptor in the receiver was present before the compound was produced by the sender.

Here, we review the available support for both theories for the evolution of pheromones in insects. We do not aim to provide an exhaustive list of documented cases but hope to give an overview of the current knowledge of the various evolutionary origins of pheromone evolution.

How pheromones evolve through the exploitation of a sensory bias

The sensory exploitation hypothesis argues that a major force shaping the evolution and composition of pheromones is the sensory, that is, olfactory, system of the receiver [6]. Any compound that is released by the sender and that fits a pre-existing sensory bias in the receiver for detecting this compound is likely to be selected over other compounds and might become a pheromone component. The bias for the compound in the receivers sensory system evolved in a different context from the communication with the receiver, for example, to locate food or prey.

Sensory exploitation is a crucial part of many deceptive pollination systems. The flower odours of these plants, which attract the insect pollinator, are similar or identical to compounds used by the pollinators to detect, for example, food, egg-laying sites or mating partners. Data supporting the hypothesis of sensory exploitation in

2 Special section on pheromones

Glossary:

Semiochemical: A chemical involved in the interaction between organisms [16].

Chemical cue: Compounds that supply information without being selected for this function [3].

Pheromone: Molecules that are evolved signals, in defined ratios in the case of multiple component pheromones, which are emitted by an individual and received by a second individual of the same species, in which they cause a specific reaction, for example, a stereotyped behaviour or a developmental process [17].

Pre-existing (sensory) bias: An inherent bias (or ‘preference’) towards certain stimuli in the sensory and/or cognitive system of the receiver that evolves before any trait that exploits this. The most frequently discussed type is sensory bias, which exists at relatively early stages in sensory processing [6].

Sensory exploitation: The evolutionary modification of traits to elicit a stronger response in the receivers sensory system, potentially due to a pre-existing bias in the receiver. Perceptual exploitation involves stimuli exploiting sensory, neuronal, or cognitive processes [6].

91 pollination systems have been found in numerous plant
92 species, for example, in the Araceae and orchids [7,8]. In
93 cases in which the flower odour is identical to a certain
94 model, sensory exploitation leads to chemical mimicry.

95 However, studies supporting the role of sensory exploi-
96 tation during the evolution of insect pheromone are rare.
97 Confirming the hypothesis requires not only to demon-
98 strate that the compound is released by the sender and
99 that the receiver has a preference for the compound, but
100 also that the preference, and not the compound, is found
101 in ancestors.

102 The most convincing examples come from the European
103 bee-wolf *Philanthus triangulum*: females of this solitary
104 wasp exclusively hunt honeybees to provision their larvae
105 and make use of the honeybee alarm pheromone (*Z*)-11-
106 eicosen-1-ol to recognize their prey. Males exploit the
107 sensory bias in females who have evolved to use (*Z*)-11-
108 eicosen-1-ol in order to hunt prey, by producing (*Z*)-11-
109 eicosen-1-ol as a male sex-pheromone to attract females
110 [9–11]. The piece of the puzzle that is missing, however,
111 is the evidence for the preference and lack of the com-
112 pound in the male pheromone in ancestors or closely
113 related species. Another example is found in the phero-
114 mone communication of *Drosophila melanogaster*. The
115 male-produced antiaphrodisiac (*3R,11Z,19Z*)-3-acetoxy-
116 11,19-octacosadien-1-ol (CH503) is transferred onto the
117 female during mating and suppresses courtship from other
118 males. CH503 also suppresses courtship from males of
119 other *Drosophila* species who do not produce the com-
120 pound themselves, indicating an ancestral bias for the
121 compound in males is likely [12*]. Unfortunately, the
122 context in which the bias for CH503 in males has evolved
123 remains unclear. A sensory bias might also have played a
124 role in the evolution of the honeybee queen mandibular
125 pheromone (QMP), which is produced by the queen and
126 used to regulate the behaviour and physiology of the
127 workers. Homovanillyl alcohol (HVA) is one of the major

components of the QMP and interacts directly with 128
dopamine receptors in the bee, suggesting that HVA 129
evolved as a pheromone component to match the pre- 130
existing dopamine receptors [13]. 131

The way that pheromones evolve from 132 chemical cues 133

The sender–precursor hypothesis predicts that phero- 134
mones can evolve from any compound that is released 135
by one individual and detected by another individual of 136
the same species. Precursors can be waste products, by- 137
products from physiological processes or compounds with 138
a function different from communication. Pheromone 139
evolution starts if the receiver is able to detect the 140
compound and to associate it with a condition of the 141
releasing individual, for example, a condition that can 142
simply be his or her presence. At this stage, only the 143
receiver can respond and benefit from detecting the 144
compound. In this spying phase, the compound is used 145
as a chemical cue, namely it provides information without 146
being selected for this function. If the receivers response 147
benefits both the releasing and the receiving individual, 148
then the chemical ritualization of information transfer via 149
this compound may result in it becoming a true chemical 150
signal [1,3]. 151

Finding support for this evolutionary route usually 152
requires finding a species in which the same compound 153
is used for two functions (a phenomenon called semio- 154
chemical parsimony [14]), one of which is communica- 155
tive. However, the original function of a pheromone 156
component might have been lost during evolution or 157
the compound might have been modified during the 158
ritualization process, both of which make it difficult to 159
identify the original function of the compound. Further- 160
more, if the pheromone precursor is a metabolic by- 161
product, the identification of the evolutionary origin of 162
the pheromone will also be challenging. However, a 163
recent study of the parasitic wasp *Nasonia vitripennis* 164
has demonstrated that even newly produced compounds 165
can evolve and persist in the sender, because they are 166
initially unperceived by the receiver and therefore not 167
selected against [15*]. Such behaviourally neutral phero- 168
mone compounds might provide the basis for the rapid 169
evolution and diversification of insect pheromones. 170

Pheromones originating from cuticular lipids 171

Cuticular hydrocarbons (CHCs) are a class of insect 172
pheromones for which the original function is known 173
and rarely lost. CHCs (and other lipids) are found on 174
the cuticle of almost all insects and primarily function as a 175
desiccation barrier. Many insect species use CHCs for a 176
variety of communication processes, such as sex phero- 177
mones or for nest-mate recognition ([18], but see [17] the 178
distinction of pheromones and signature mixtures). The 179
CHC profile of an insect usually consists of more than 180
20 compounds, with variations in the number and position 181

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