CHEMICAL SIGNALS AS ATTRACTANTS, REPELLENTS AND AGGREGATION STIMULANTS

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Summary

Chemical signals in the environment mediate behavioral and/or physiological interactions between different organisms. A chemical signal in the environment may benefit the emitter, the receiver or both, and may evoke a behavioral response such as attraction, repellence or aggregation, responses that are dependent on the nature, quality and quantity of the chemical signal emitted.

1. Introduction

In nature, organisms regularly encounter signals from their environment, signals that may be visual, auditory, physical or chemical, and which influence their behavior. Chemicals in the gaseous phase constitute the odor signals that are conveyed in the air, and are detected by their receivers as a coded message. A coded chemical message may be simple or complex, but when decoded, it may benefit its emitter, the recipient, or both. The message may evoke in the recipient an immediate short-term and reversible behavioral response (releaser effect), or long-term irreversible physiological and/or biochemical changes (primer effect). The latter mainly occur in the endocrine system of the organism. These types of chemical signals are released in minute quantities, in most cases far below human detection by smell. While many of these chemical signals have been discovered mediating interactions among various animal taxa, most of the research has focused on the interaction among insects. An important reason for this is that insects constitute the largest group of animals on earth, with a large number of species being economically important as pollinators, crop pests and vectors of animal and human diseases. Insects exhibit many forms of behavioral patterns, however, this article focuses on chemical signals that evoke three types of short-term behavioral responses in insects: attraction, repellence and aggregation stimulation.

2. Classification of chemical signals

A chemical signal that conveys a message between organisms of the same or different species is referred to as a 'semiochemical' (Gk. *semeon*, sign or signal). Some researchers refer to these types of chemical signals as *infochemicals* since they only convey information in order to distinguish them from venoms and toxins used specifically by certain organisms for defense. Semiochemicals mediate diverse natural interactions involving terrestrial and aquatic organisms. Among insects, interactions with plants, animals, and microbes are recognized. Their sources of production and emission are equally diverse: flowers, leaves, stem bark and roots, microbial secretions, insect body glands, saliva, reproductive organ fluids and excretory products. Semiochemicals are mainly secondary metabolites, produced as by-products from metabolic processes that occur in the tissues of organisms or from enzymatic or microbial activity on ingested food. Although they vary in complexity, semiochemicals that are conveyed in the gaseous phase generally comprise low molecular weight compounds (less than 250 M.W.). Four main classes of semiochemicals are recognized:

- *Kairomone*- Gk. *kairos* (= opportunistic), a message-bearing chemical that provides an adaptive advantage to the receiver (e.g., an *attractant or aggregation stimulant*).
- *Allomone*– Gk. *allos* (= other), a message-bearing chemical that coveys an adaptive advantage to the emitter (e.g., *repellent*).
- *Synomone*- Gk. *syn* (= with), a message-bearing chemical that conveys a mutual advantage to both the emitter and the receiver. (e.g., floral odor attracts pollinating insects, for example honeybee, the flowering plant benefiting from pollination by the insect that in turn is rewarded with nectar or pollen).
- *Pheromone*- Gk *pherein* (= to transfer; *horman* = to excite), a message-bearing chemical emitted and received by an organism of the same species.

Using biological assays, which often involve the application of the chemical to a neutral material, it is possible to discriminate between semiochemical types. For example, an *attractant* chemical will elicit a positive displacement (i.e., movement) of the recipient organism towards it, while a *repellent* chemical will elicit a negative displacement of the recipient away from it. On the other hand, an *aggregation stimulant* will draw individuals of the same species together irrespective of their sexes to group or aggregate. Semiochemicals are usually not restrictive in their function and may exert different effects depending upon the insect species or conditions under which they are presented. For example, a semiochemical released at a given dose may on the one hand function as an attractant for one insect species, while on the other, it may function as a repellent or aggregation stimulant in another species. It may for the same individual insect function as an attractant or repellent at different doses, or evoke no response at all if presented as a single component when activity is due to a blend of components. In the majority of studies, semiochemicals have been found to be composed of blends rather than single components. However, for even simple blends, optimal activity is achieved when the precise ratios of individual components in the synthetic blend simulate the natural situation.

3. Detection and decoding of semiochemicals

Insects detect chemical signals in the environment via sense organs that are endowed with specific receptors, called 'chemoreceptors'. There are two types of chemoreceptors; those that detect chemicals in solution form which are denoted as taste or gustatory receptors, and those that detect chemicals in gaseous form, referred to as olfactory receptors. These receptors are housed in minute or microscopic hair-like structures (setae), which are distributed on various appendages located on different parts of the body. Chemoreceptors can detect and recognize the individual components of a chemical signal in a 'lock and key' mode (i.e., receptor-substrate interaction). While gustatory chemoreceptors are largely concentrated on the mouthparts (maxillary and labial palps, labrum), tarsi, and ovipositor of insects, a large population of the olfactory receptors is located on the antennae. In olfactory reception, an insect exposed to an odor source first detects the chemical signal using its antennae, which involves recognition of the active components in the signal by chemoreceptors according to their structures, or loosely, according to their 'sizes and shapes' or spatial arrangement (enantiomeric composition). These chemoreceptors then relay messages through the antennal nerve to the central nervous system (brain), which decodes the messages via cellular and metabolic activity. This may in turn activate sets of muscles whose reaction may manifest as a behavioral response. The response may be an orientation and/or a displacement towards or away from the source of the chemical signal to signify in the recipient of the chemical signal the presence of an attractant or a repellent, respectively. The accuracy with which a chemical signal is decoded is dependent on the nature, quality and quantity of the signal. In an evolutionary sense, most chemical messages are interpreted in an associative context *i.e.*, as an indicator of an available resource *e.g.* food, a mate, or a suitable egg-laying site. They may also denote the presence of other organisms in the environment that may either be beneficial, or harmful to the recipient.

4. Approaches to isolation and identification of semiochemicals

The message content of a chemical signal is often complex, composed of a range of chemical compounds. An insect exposed to the chemical signal selectively responds to the active components in the signal. The active components in the chemical signal can be isolated and identified using interdisciplinary approaches involving insect behavior, sensory physiology, analytical and organic chemistry, biochemistry and ecology. Recent years have seen breakthroughs in analytical techniques, which now permit for rapid screening of semiochemicals in more sensitive bioassays and their isolation and identification from relatively smaller amounts of material. There are several non-destructive methods available for collecting natural odors from living organisms, which excludes the introduction of artefacts. Examples include the adsorption of odors on different polymer matrices contained in cartridges or filters. Trapped odors can be desorbed thermally or eluted with organic solvents followed by analysis using gas chromatography. The direct coupling of a chemical (flame ionization or mass spectrometer) and a biological detector (insect antenna) permits for simultaneous isolation and identification of active components from trapped odors. Furthermore, the discovery of more efficient chemical synthetic methods now permit for the synthesis of semiochemicals in a state of high purity whose field activity may provide some answers to certain ecological and evolutionary questions associated with the importance of the chemical in the behavior of the insect being studied. Semiochemicals have so far been found in nearly all insect taxa. Table 1 and Figure 1 represent a few examples of the many compounds identified as attractants, repellents and aggregation stimulants mediating interactions of insects.

Compound	Source	Insect
Plant-produced attractants		
1,8-cineole (**1**), methyl salicylate (**2**)	orchid flowers	*Euglossa* spp. (orchid bees)
(*E*)-2-Hexen-1-ol (**3**) (green leaf volatile)	potato plant	*Leptinotarsa decemlineata*
		(Colorado potato beetle)
(*E*)-4,8-dimethyl-1,3,7-nonatriene (**4**)	Corn leaves	*Cotesia sesamiae* (parasitoid)
dipropyl disulfide (**5**)	onion plant	*Delia antiqua* (onion maggotfly)
Vertebrate-produced attractants		
carbon dioxide (**6**), acetone (**7**)	bovine breath	*Glossina* spp. (tsetse flies)
1-octen-3-ol (**8**)	bovine breath	*Glossina* spp.
3-n-propylphenol (**9**)	bovine urine	*Glossina* spp.
Sex attractant		
(*R*)-japonilure (**10**)	female	*Popilla japonica*
		(Japanese beetle)
(*S*)-japonilure (**11**)	female	*Anomala osakana* (Osaka beetle)
(*E*)-9-oxo-2-decenoic acid (**12**)	queen bee	*Apis mellifera* (honey bee)
(*Z*,*E*)-9,11-tetradecadienyl acetate (**13**)	female	*Spodoptera littoralis*
		(cotton leafworm)
Plant-produced repellents		

(*Z*)-3-hexen-1-ol (**14**), (*Z*)-3-hexenyl acetate	*Nicotiana tabacum*	*Heliothis virescens*
(**15**), (*Z*)-3-hexenyl isobutyrate (**16**),	(tobacco plant)	(tobacco budworm)
(*Z*)-3-hexenyl butyrate (**17**)		
(*Z*)-3-hexenyl tiglate (**18**)		
Aggregation stimulant		
phenylacetonitrile (**19**), guaiacol (**20**),	male	*Schistocerca gregaria*
phenol		(desert locust)
(*R*)-ipsdienol (**21**)	male	*Ips pini* (bark beetle)
(S)-ipsenol (**22**)	male	*Ips paraconfusus* (bark beetle)
See Fig. 1 for structures corresponding with numbers in parentheses		

Table 1: Examples of attractants, repellants and aggregation stimulants of selected insects

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Biographical Sketch

Dr Baldwyn Torto is a Senior Scientist within the Behavioural and Chemical Ecology Department at the International Center of Insect Physiology and Ecology (ICIPE). He plans and conducts research on insect behaviour-modifying chemicals for integration with other pest management technologies for ICIPE target pests. His research includes studies on the chemical ecology of arthropod pests, elucidating the signals involved in pest-plant interactions to improve traditional IPM strategies for smallholder farmers and the use of semiochemicals and natural products for Integrated Vector Management (IVM). Dr Torto has a BSc in chemistry and biochemistry, MSc in natural product chemistry, and a PhD in applied natural product chemistry, with a major in insect chemical communication from the University of Ghana. He was a Postdoctoral Research Associate at the University of Maine, USA, then later moved to ICIPE, first as Research Scientist then as Senior Scientist working on the chemical ecology of the desert locust and other insect pests. He has been a Rothamsted International Fellow at the Institute of Arable Crops Research, UK, where he worked on the chemical ecology of cereal panicle pests. Dr Torto has also served as a lecturer at the University of Ghana, Legon and Egerton University, Kenya. He is presently a Visiting Scientist at the USDA/ARS-Center for Medical, Agricultural and Veterinary Entomology in Gainesville, Florida.