



Chemical ecology and olfaction in arthropod vectors of diseases

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Hematophagous arthropods (ticks and insects, collectively hereafter referred to as vectors) transmit various life threatening diseases resulting in over one million human deaths annually. Exploiting vertebrates for blood demanded extensive sensory and behavioral adaptations that are apparent across the evolutionary range of vector species, from primitive ticks to advanced dipterans. Since animal senses are biological features that have been shaped by natural selection to promote adaptive behavior, a variety of exciting patterns are apparent in *what* they sense and *how*. Vectors display robust olfactory driven behaviors. A distinct yet limited range of volatile organic compounds are parsimoniously used as major cues for tracking in various contexts. These chemicals elicit behaviors such as *attraction* or *repulsion/avoidance* while vectors seek habitats, hosts, mates, or oviposition sites. Interestingly, there is a substantial consilience among olfactory structures and function in arthropod vectors, which is also reflected in the parsimonious use of chemical ligands. A detailed analysis of chemosensory signals and reception by these arthropod vectors can be exploited to identify natural ligands that can be used as baits to manipulate vector behaviors.

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Current Opinion in Insect Science 2015, 10:83–89

This review comes from a themed issue on **Vectors and medical and veterinary entomology**

Edited by **Nora Besansky**

<http://dx.doi.org/10.1016/j.cois.2015.04.011>

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Introduction

Signals and reception rarely arise *de novo* [1], and this reciprocal evolutionary relationship in chemical communication between insects and their hosts was elegantly demonstrated 50 years ago by Ehrlich and Raven in their classical synthesis of evidence from a wide range of insects and their host utilization [2,3]. They coined the term ‘co-evolution’ to describe the evolution of secondary host metabolites and the accompanying

step-wise adaptive responses by insects. Less than optimal signaling severely lowers insect reproductive success and the fitness of their progeny [4,5]. As the most successful and abundant animal group on earth, arthropods display a highly sophisticated system of chemical communication. While this exquisite system has been studied with great enthusiasm within various groups of arthropods from evolutionary and functional perspectives [6,7], recently there has been considerable interest to potentially exploit this understanding of insect olfaction to manipulate vector populations to our advantage [8,9].

Chemical codes

The human ‘volatilome’ consisting of volatile organic compounds (VOCs) derived from exhaled breath, skin emanations, urine, feces and saliva contains over 1700 chemicals [10]. One of the significant discoveries in demonstrating how a single human derived chemical can act as a strong stimulus inducing attraction in host-seeking *Aedes aegypti* mosquitoes came with the discovery of L-lactic acid, isolated from human skin washings [11]. This had led to an early assumption that a single compound on its own can potentially act as an attractant. Subsequent studies however are revealing that complex repertoires of host derived chemicals are often needed to elicit attraction. Currently, over 200 compounds are being suggested as putative attractants for *Ae. aegypti* [12,13]. Extensive analytical work has been directed toward finding chemical attractants for the malaria mosquito, *Anopheles gambiae*. Human feet washing and its derivatives [14] as well as sweat and its constituent chemicals [15,16] are demonstrated as strong chemostimuli in various behavioral assays. Building on the early work by Nicolaides *et al.*, that demonstrated a distinct odor/chemical fingerprint among humans [17], there has been a recent interest in how a diverse human skin microbiota [18] directly impacts the relative attraction of malaria mosquitoes toward particular individuals [19].

A significant development in identifying natural ligands for vectors was the coupling of high resolution chromatography with electrophysiological recordings to selectively isolate biologically active constituents from within a myriad of host derived volatile organic compounds (VOCs). This technique is termed gas chromatography linked electroantennographic detection (GC-EAD), wherein insect antennae are used as sensing elements to isolate a handful of constituents from complex odors as they elute from a high resolution GC capillary column. GC-EAD was developed for the identification of sex pheromones in moths [20], and it was first used to study vector olfaction at the

Natural Resource Institute UK (now part of Greenwich University) in tsetse flies, *Glossina* spp. One alcohol constituent from cow odors, 1-octen-3-ol, generated a strong antennal signal [21]. Subsequent behavioral studies in a laboratory wind tunnel and later field testing demonstrated how this single VOC elicited significant behavioral responses both in laboratory bioassays and field trap captures. Enigmatically, 1-octen-3-ol remains the most common chemostimulus eliciting varied behaviors in almost every hematophagous arthropod studied so far, ranging from ticks, triatomines, mosquitoes, midges, stable flies and sand flies. The GC-EAD method has since been used to isolate and identify important chemostimuli for mosquitoes, triatomines, and tsetse flies with the resulting chemostimuli proving to be behaviorally active [22].

Though the GC-EAD technique offered a remarkable advantage over purely chemical-analytical tools by significantly shortening the process of isolating and identifying chemostimuli, its use was challenging in arthropods that have primitive olfactory structures composed of only a small number of olfactory sensilla (bed bugs and triatomines) or do not have a defined antennae (ticks). In these instances, GC was linked to single unit recordings from olfactory sensilla in ticks, bed bugs and triatomines [23]. GC linked single sensillum recordings (GC-SSR) have since been extended to more advanced dipterans with well-developed antenna to search for novel natural ligands, such as in mosquitoes and sand flies [24]. Most recently, olfactory receptor genes (*Ors*) from various vectors have been heterologously expressed into an ‘empty neuron’ in *Drosophila melanogaster* [25**] using the *GAL4-UAS* driver system [26]. Studies utilizing this method have since been used to deorphanize *An. gambiae* ORs by challenging them offline (not connected to GC) with over 100 chemicals implicated as potential chemostimuli [27**,28], and most recently GC-SSR method has been applied to identify a key human odor constituent, sulcatone, that selectively activates an OR from *Ae. aegypti* [29**]. The screening revealed only a handful of compounds (1-octen-3-ol, 2,3-butanedione, 2-ethylphenol and indole) that appeared to be strong chemostimuli. It is worth mentioning that two ORs, each responding to 1-octen-3-ol (OR8) or indole (OR2), are the most sensitive of the receptors deorphanized from mosquitoes. These two ORs responded with the highest selectivity and sensitivity, and they are among the most highly conserved between Culicine and Anopheline species. While the existence of a highly complex chemical landscape in and around arthropod vectors is apparent, the salience of only a handful of these VOCs suggests multiple roles for these chemostimuli in a vector’s life history.

Parsimony in signaling

GC-EAD and GC-SSR studies from a large variety of hematophagous arthropods such as ticks, triatomines bugs, mosquitoes, and sandflies consistently revealed

three major classes of biologically active chemostimuli: 1 — short chain carboxylic acids, 2 — aldehydes and 3 — low molecular weight nitrogenous compounds such as ammonia and alkyl amines. Two other VOCs that also emerge from multiple analyses are 1-octen-3-ol and indole. Finally, a major host metabolite, carbon dioxide (CO₂), induces attraction in every arthropod studied so far, including triatomines bugs, bedbugs, ticks, tsetse flies, sand flies, and mosquitoes. Specialized olfactory receptor neurons (ORNs) detecting CO₂ in various arthropod vectors have been identified [30,31]. It is also worth mentioning that conspecific mating signals, especially pheromones, are not widely recorded in vectors, except in ticks [32] and sand flies [33].

Thus a high conservation in signaling molecules (Figure 1) leads to the intriguing question of why there is such numerical and structural redundancy in VOCs used by vectors. Generally in arthropods, a strong adaptation pressure to use the same chemicals as signals for different purposes is quite common, a trend termed as chemical parsimony [34]. This trend can range from a simple system wherein the same chemical signal can encode different referents based on its concentrations, or simply one chemical serving in a different context. For example, nonanal serves as an attractant in host seeking mosquitoes, while in gravid females it signals as a cue for seeking a suitable site to oviposit; the same chemical also contributes in the recognition of sugar-feeding site (flowers). An elegant example of plasticity can be found in host seeking *Ae. aegypti* that are attracted to human skin washings. Adding lactic acid to the skin extract incrementally increased the attraction, and this chemical alone made totally unattractive animal washings (lacking lactic acid) attractive [35]. It has long been argued that blood from different host sources does not differ much in its nutritive content [36]. Not surprisingly, the host choice for feeding in vectors is quite plastic. An extensive evaluation of the associations between host, habitat and tick spp. associations revealed that host choice in ticks is determined largely by adaptation to a particular habitat type and not by adaptation to a particular host taxon. Many tick species parasitize phylogenetically distant hosts with similar nesting or perching habitats, such as bat ticks that are also found on cave swallows. Bat ticks were therefore considered ‘habitat specialists rather than host specialists’ [37]. Studies of selection in *An. gambiae* mosquitoes showed divergent feeding preferences for humans or cows within five to six generations [38], and cross-mating of zoophilic *Ae. simpsoni* and anthropophilic *Ae. aegypti* generates offspring of intermediate preference [39]. And finally, individual experience and learning in a population has been clearly demonstrated when a first successful blood meal was shown to modulate mosquito preference for the subsequent second blood meal [40]. Though shown to have a genetic basis, host preference of mosquitoes is characterized by high plasticity [41]. Thus,

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