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UPDATES IN PARASITOLOGY FROM ARGENTINA (A SANCHEZ AND A TOLOZA, SECTION EDITORS)

Chemical Communication of the Head Lice with the Human Host

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Abstract

Purpose of Review Transmission of head lice occurs primarily by direct host-to-host contact and via inanimate objects, called fomites. As for other hematophagous insects, chemical cues are likely involved in host detection, at least in the close range for the case of head lice.

Recent Findings The revision of the literature on the effect of chemical cues from the host on head lice behavior showed that volatiles in a combination but also individually from the human scalp trigger an attraction response on head lice. Studies also show that both infested and non-infested individuals have similar chemical profiles and that lice show no preference for volatiles from either group. Concerning the odors from different body parts, volatiles from scalp, arm, and foot produced similar attraction to lice when compared to volatiles from the scalp. However, complete extracts from different parts of the body (scalp, arm, and foot), lice seem to show a clear preference towards samples from the scalp over samples from the arm or foot.

Summary There is strong evidence of chemical communication between the head louse and its human host. Understanding the biochemical communication between head lice and the human host is essential not only to understanding the biological mechanisms of transmission but also to develop new tools for head lice control.

Keywords Pediculosis · Head lice · Behavior · Chemical communication

Introduction

The head lice *Pediculus humanus capitis* (De Geer) is a cosmopolitan human ectoparasite causing one of the most prevalent human infestations. Pediculosis is a worldwide disease that affects school-age children (5–14 years) in most developed and developing countries [1•]. The rate of head lice infestation varies greatly between ages [1•], being the most susceptible population of children in the early stages of schooling. Transmission occurs mainly through direct contact between persons [2•]. Lice infestation can cause itching, loss of sleep, and social sanctioning [3]. Transmission of head lice occurs primarily by direct host-to-host contact and in minor importance in inanimate objects, called fomites. Although lice have not been incriminated in the transmission of harmful pathogens, it has been suggested that they could be potential transmitters of *Rickettsia prowazekii* Da Rocha-Lima and *Bartonella quintana* Brenner, causative agents of epidemic typhus and trench fever, respectively [4]. These diseases occur in exceptional situations such as war, famine, and deprivation. The incidence of head lice has increased worldwide as a result of pediculocide product failures due to insecticide resistance, misapplication, formulation changes, and misdiagnosis [3].

For insects, the most important source of information for seeking food, shelter, or reproduction is chemical communication. Chemical information can be acquired through smell or taste, or a combination of both. In general terms, smell consists of the detection of signals dissolved in media such as air and water far from their original source [5], while taste is the acquisition of signals by direct contact with the source or with a dissolved product [6].

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The chemical cues for host location studied in hematophagous insects such as mosquitoes reflect different susceptibilities of individuals towards the insects' bite. Certain human odor substances, depending on their concentration, can act as chemical cues either for attraction or repellence of mosquitoes, and these chemicals are secreted naturally in different hosts [7].

Human skin emanates several compounds that contribute to the formation of different odor profiles. The compounds of the skin come from different glands (eccrine, sebaceous, and apocrine). Each gland secretes certain compounds and the interactions of these compounds with the skin microbiota generate a specific chemical profile [8]. Concerning the chemical communication between hematophagous insects and their hosts, 1-octen-3-ol, L-lactic acid and C3-C5 carboxylic acids are present in the skin and are necessary components for the attraction of mosquitoes, kissing bugs, and tsetse flies [9]. The production of these compounds in humans is associated with differential susceptibility to infestation by these insects. For example, high levels of sulcatone and aldehydes are detected in individuals susceptible to mosquito bites compared to non-susceptible [10]. In addition, in bed bugs, there is an attraction/repellence biphasic response (depending on the dose) to compounds present in human extracts, while short-chain aldehydes and sulcatone produce attraction [11]. For the Chagas disease vector, *Triatoma infestans*, the aldehydes octanal, nonanal, and decanal produce a dose-dependent response showing attraction at low concentrations and repellence at high doses [12]. In summary, each person has a distinctive chemical profile and a differentiated susceptibility towards hematophagous insects. That is, the susceptibility to an insect bite can be attributed to the person´s chemical composition.

Host Detection by Head Lice

In relation to human lice, [13••] used an experimental arena to expose body lice to paper rubbed on head scalp versus clean paper, and noted a clear preference of lice towards the rubbed paper. More recently, [14••] demonstrated that exposure of head lice to filter papers containing scalp compounds resulted in decreased locomotor activity and complete arrest of the insect on the treated paper. However, the authors found that neither the sex nor the age of the scalp sample donor played a significant role in attracting head lice.

Later, Galassi y colaborators by means of behavioral bioassays, it was investigated whether there is in fact a chemical cue allowing head lice to locate the host within a short distance by using volatiles emanated from the scalp. To carry out this evaluation, an olfactometer device to record the locomotion of lice was placed inside a chamber adapted to emulate the environmental condition of the human head (temperature, humidity, and light).

Lice showed significant attraction towards the side containing the scalp sample (Fig. 1A). The components of the scalp were analyzed using analytical chemistry techniques and the activity of the main compounds detected (sulcatone, geranylacetone, nonanal, and palmitic acid). Of these compounds, head lice showed a binary dose-dependent response to nonanal: at low concentrations, there was an attractant effect and at higher concentrations, a repellent effect was observed (Fig. 1B) [15].

Odor mixtures are used in insects to increase the certainty that an odor source belongs to an expected host [9]. Although individual compounds can trigger behavior

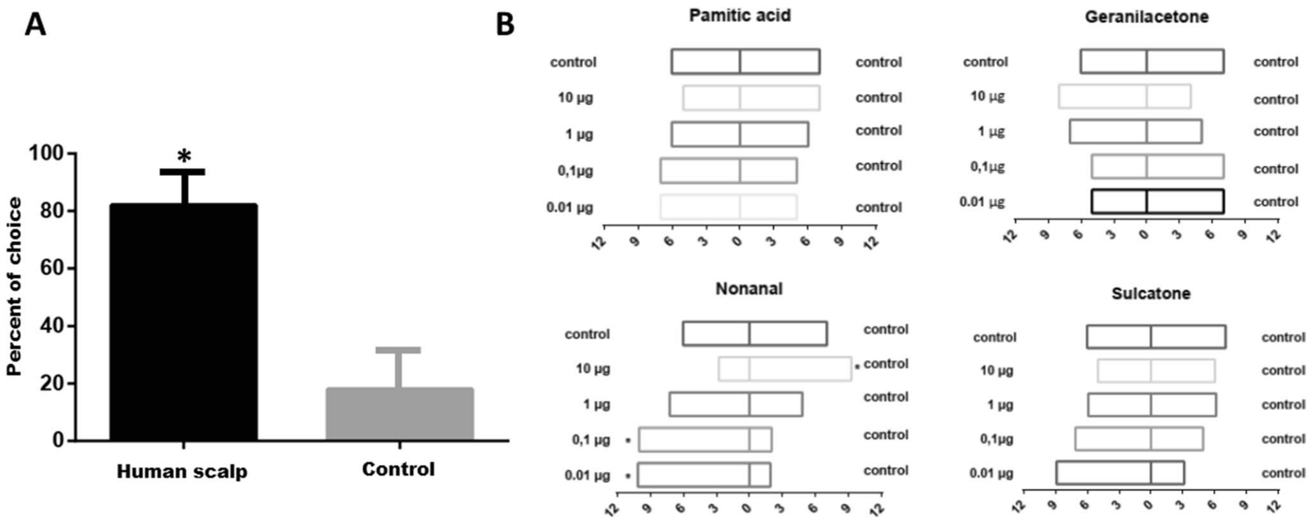

Fig. 1 Lice behavior results. **A** Head lice response to scalp volatiles. **B** Response of the lice against the main compounds isolated in different masses. *means significant difference ($P < 0.001$) [15]

in insects, they generally respond better to mixtures than to single compounds as the effect of attachment decreases [15].

Recently, the majority of compounds detected previously were evaluated and mixed in different proportions to study the effect they had on the behavior of lice. The main compounds previously detected (nonanal, sulcatone, geranilacetone) were evaluated in mixtures in different proportions to study the effect they had on the behavior of the lice. It was observed that the compounds evoked a more attractive response against lice in comparison to the compounds studied individually at the same doses [16].

These works provided evidence on how chemical signals are attractive in certain concentrations and proportions towards lice. This information could be used to further understand the communication mechanisms between lice and their host and may result in tools that alter the transmission.

Host Selection (Susceptible vs Non-Susceptible)

Human populations can have different head louse infestation levels. For example, school children are most affected by head lice. However, there are cases of pediculosis in adults. [17–20]. In a study of 1800 infested children in schools in Buenos Aires, Argentina, 37.82% corresponded to boys and 53.07% to girls within the same age range [1•]. This same trend has been reported in children from other countries such as the UK, South Africa, Turkey, and Brazil [18–21]. Some researchers hypothesized that these differences in infestation rates were related to the behavior of adults versus that children's. In the case of children, girls spending more time in close contact with each other (compared to boys) and thus facilitating head-to-head transmission.

To evaluate if there is a chemical component to the susceptibility, Galassi et al. analyzed possible differences in the chemical composition of the scalp volatiles between susceptible and non-susceptible individuals independently of their gender. They also studied if there is a differential response of the lice against the volatiles generated by the infested versus non-infested subjects.

Regarding chemical analysis, no qualitative or quantitative differences were observed between the compounds emitted by infested and non-infested individuals (Table 1). In all cases, aldehydes and sulcatone were detected at higher proportions, and when were individually tested they showed an attractance effect. Comparing the profiles of both groups, a higher number and proportion of acid compounds were found in non-infested individuals.

Thus, although the study showed that there was a difference in infestation rate among children of a certain age range and sex, the difference cannot be explained by the host's compound composition of the scalp.

The susceptibility of an individual is not only determined by its capability to be detected as a host but also for the suitability of its head environment to develop a lice colony. Considering that these parasites complete their entire cycle on the host, several factors are involved in the establishment of the colony, such as the quality of the food and nesting that are usually different among person like other hematophagous insects [30]. For this reason, there is a need to study these factors in order to elucidate the mechanism behind these different infestation rates.

Ecological Niches of Head Lice in the Body Parts

Humans can be parasitized by three species of lice that live on different parts of the body: *P. humanus capitis*, *P. humanus humanus*, and *P. pubis*. Two of them belong to the genus *Pediculus* (*Pediculus humanus capitis* and *Pediculus humanus humanus*) and have a great morphological and genomic similarity, but develop their colonies in different parts of the human body [27]. *Pthirus pubis* found in the pubic area and known as the pubic or crab louse. Head lice live on the human head and spend their entire lives on it, while body lice live on clothing and approach the body to feed. Regarding their ecological niche, both species have different temperature and humidity conditions, that is, both exploit different areas to feed and nest [22, 23]. Galassi and collaborators studied if head lice recognize the skin emanated compounds (both the volatile fraction and the whole extract) from different parts of the human body and if they prefer those from the head over those from other areas of the body [28]. As a result, they obtained that the lice had a clear preference for the human sample (head, arm, or foot) over the control (paper without sample) as expected.

Comparing samples from different body parts, when the volatile extract of the different body parts was compared, lice did not show a preference. However, when they were offered to choose between the total extract from the head versus that of the arm or foot, head lice showed a statistically significant preferential response towards the head sample compared to samples from other parts of the body [29] (Fig. 2).

These results demonstrated that head lice are attracted to volatile human odor compounds regardless of the body area, showing no preference towards volatiles from the head compared to volatiles from other parts of the body (arm and foot). In contrast, when lice were exposed to samples containing whole extracts (volatiles plus non-volatiles) from different parts of the body, the insects showed a clear preference for head samples compared to foot and arms.

Table 1 Identification of the volatiles generated by the scalps of 6 volunteers between adults and children. The amounts of each compound are estimated by the relative areas of the peaks. ***area percentage greater than 10%, **area percentage between 1 and 10%, *area percentage less than 1%. (a) Similarity between the sample and the library greater than 92% (b) similarity between the reference index (c) obtained by comparison against chemicals standards (Sigma-Aldrich) [29]

N° Peak	Compound	Non infested			Infested		
		1	2	3	1	2	3
1	Octanal $_{(a)(b)(c)}$	**	**	**	**	**	**
2	Sulcatone $_{(a)(b)(c)}$	***	***	***	***	***	***
3	1-hexanol $_{(a)(b)(c)}$	*	-	-	-	-	-
4	Nonanal $_{(a)(b)(c)}$	***	***	***	***	***	***
5	Tetradecane $_{(a)(b)(c)}$	-	-	-	-	-	*
8	Acetic acid $_{(a)(b)(c)}$	**	**	***	**	**	-
9	2.6-dimetil 7-octen-2-ol. $_{(a)(b)}$	-	*	**	**	-	**
10	Decanal $_{(a)(b)(c)}$	***	***	***	***	***	***
11	Propanoic acid $_{(a)(b)(c)}$	*	*	**	*	-	-
14	3,7-dimetil 1,6-octadien-3-ol $_{(a)(b)}$	-	-	**	**	-	*
15	2-methyl-propanoic acid $_{(a)(b)}$	-	**	**	-	**	*
16	1-octanol $_{(a)(b)(c)}$	-	-	-	**	**	-
17	6-methyl-3,5-heptadien-2-one $_{(a)(b)}$	-	-	-	-	-	**
19	Undecanal $_{(a)(b)(c)}$	-	-	-	-	**	*
20	Butanoic acid $_{(a)(b)(c)}$	*	**	-	*	-	-
21	1,2-hexanediol $_{(a)(b)}$	-	-	-	-	-	**
22	3-methyl-butanoic acid $_{(a)(b)(c)}$	**	**	**	-	*	*
23	2-decen-1-ol $_{(a)}$	-	*	-	-	-	-
24	1-nonanol $_{(a)(b)(c)}$	*	-	-	*	-	-
25	2-undecanal $_{(a)(b)}$	-	**	-	*	-	-
26	3,7-dimethyl-2,6-octadien-1-ol $_{(a)}$	-	-	-	*	**	-
27	3,7-dimethyl-6-octen-1-ol- $_{(a)(b)}$	*	*	*	**	*	-
28	4-methyl pentanoic acid $_{(a)(b)}$	-	**	-	-	-	-
29	6-methyl-2,4-heptanedione $_{(a)(b)}$	-	-	-	-	-	*
30	Hexanoic acid $_{(a)(b)(c)}$	**	***	**	*	*	-
31	Geranylacetone $_{(a)(b)(c)}$	***	**	***	**	**	**
32	2-ethyl-hexanoic acid $_{(a)(b)(c)}$	-	*	**	-	*	-
33	Heptanoic acid $_{(a)(b)(c)}$	-	**	*	-	-	-
34	1-dodecanol $_{(a)(b)(c)}$	-	**	**	**	**	**
35	Octanoic acid $_{(a)(b)(c)}$	**	***	**	**	*	**
36	Nonanoic acid $_{(a)(b)(c)}$	**	***	*	**	*	*
37	1-tetradecanol $_{(a)(b)(c)}$	*	*	-	**	-	-
38	1-hexadecanol $_{(a)(b)(c)}$	-	**	**	**	**	-
39	Dodecanoic acid $_{(a)(b)(c)}$	*	**	*	**	-	-
40	1-octadecanol $_{(a)(b)(c)}$	-	-	**	-	*	*
41	Tetranoic acid $_{(a)(b)(c)}$	**	*	*	*	-	*
42	Pentadecanoic acid $_{(a)(b)(c)}$	*	*	*	*	-	-
43	Hexadecanoic acid $_{(a)(b)(c)}$	**	**	***	**	**	-
44	Squalene $_{(a)(b)(c)}$	-	-	-	-	-	**

Human lice do not have to travel long distances to find their host, as they do not survive outside of it. This is because lice lose humidity outside the scalp, become dehydrated and die within a few hours. The sources of infestation are generated mainly directly (contact between hosts). In other words, lice do not have the need to distinguish odors over long distances to detect the host, but they do have the need to reach the host's head to install the colony. In addition, a recent study by Ortega and coll. [24] demonstrated that lice have the ability to select different sources of human versus neutral odors by using chemoreceptor antenna structures. Possibly, for this reason, they can discriminate the odors of different parts of the human body at a very short distance and this would be associated with substances of lower volatility, differentiating the area they infest. The mechanisms by which they can make this discrimination are still unclear, but we hypothesize that it is based on its olfactory and/or taste system.

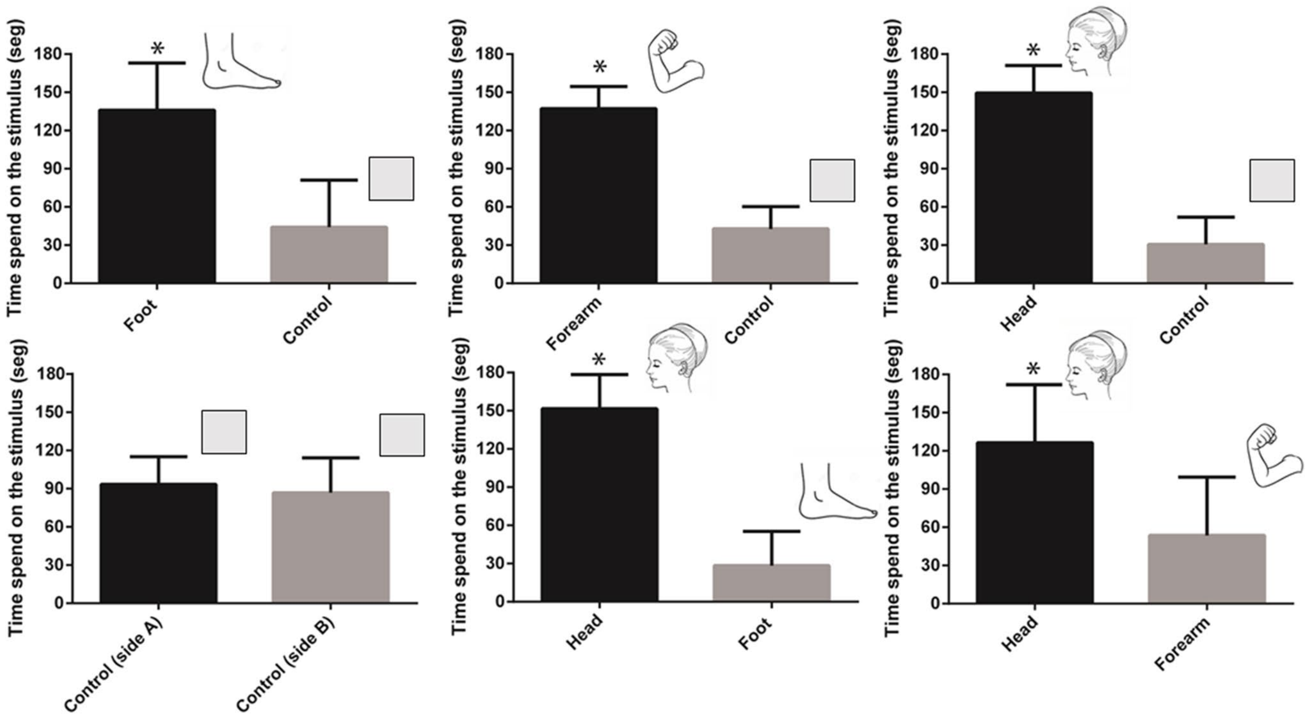

Fig. 2 Preferencial response of lice towards the whole extracts head, arm, or foot sample. *Indicates significant differences

Conclusions

Throughout this work, the behavior of head lice against chemical stimuli from the host was reviewed. In summary, the main results are as follows:

1. The mixture of volatiles from the human scalp triggers an attraction response on head lice.
2. Individually, nonanal bioactivity showed a significant biphasic response, producing attraction at low concentrations and repellence at high concentrations.
3. Individuals infested by lice show similar composition of major volatiles of the scalp than those not infested. Accordingly, head lice did not show a preference for volatiles from the infested over the non-infested group.
4. Volatiles from different parts of the human body (scalp, arm, and foot) produce similar attraction to lice when compared with clean samples and lice did not no show a preference for volatiles from the scalp.
5. Samples of whole extracts of different parts of the body (scalp, arm, and foot) also elicit an intrinsic attraction towards lice. However, the lice show a clear preference towards the sample from the scalp over the arm or foot samples.

This review synthesizes evidence of chemical communication between the head louse and its human host. The results showed that lice are oriented towards the volatiles emitted by their human host (and/or some of their main components) and that they clearly prefer samples of all the compounds from the scalp compared to samples from other parts of the body (arm and foot).

This suggests that the insect primarily uses volatile or contact chemical cues to orient towards the human, and contact chemical cues to orient towards the head. The chemical communication demonstrated for the head louse, together with other physiological mechanisms, conditions the behavior of this important human parasite and lays some foundations for the transmission of pediculosis. New studies are necessary to discriminate the mixtures and proportions of the compounds that determine the behavior of lice, as well as the importance of the scalp's microbiota associated with lice infestation.

Likewise, the results of this work are relevant not only from the perspective of the biology of the head louse but also in the framework of the development of new tools against pediculosis thus by, reducing or replacing current pediculicides and developing environmental friendly products.

Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

Human and animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any authors.

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