Parasitol Res (2014) 113:3781–3787
DOI 10.1007/s00436-014-4044-0

ORIGINAL PAPER

Behavioral and electrophysiological responses of *Aedes albopictus* to certain acids and alcohols present in human skin emanations

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Received: 6 May 2014 / Accepted: 11 July 2014 / Published online: 23 July 2014

Abstract Human skin emanations attract hungry female mosquitoes toward their host for blood feeding. In this study, we report the flight orientation and electroantennogram response of *Aedes albopictus* females to certain unsaturated acids and alcohols found in human skin. In the Y-tube olfactometer, odors of lactic acid and 2-methyl-3-pentanol attracted 54–65 % of *Ae. albopictus* females at all doses in a dose-dependent manner. However, at the highest dose (10^{-2} g), the acids repelled 40–45 % females. Attractancy (ca. 62–68 %) at lower doses and repellency (ca. 30–45 %) at higher doses were recorded for 3-methyl-3-pentanol and 1-octen-3-ol, while 5-hexen-1-ol, *cis*-2-hexen-1-ol, and trans 2-hexen-1-ol odor repelled ca. 55–65 % of *Ae. albopictus* females at all doses. Antenna of female *Ae. albopictus* exhibited a dose-dependent EAG response up to 10^{-3} g of L-lactic acid, trans-2-methyl-2-pentenoic acid, 2-octenoic acid, trans-2-hexen-1-ol and 1-octen-3-ol stimulations; however, the highest dose (10^{-2} g) caused a little decline in the EAG response. EAG response of 9–10-fold was elicited by lactic acid, 2-octenoic acid, trans-2-hexenoic acid, and 3-methyl-3-pentanol, while *cis*-2-hexen-1-ol and trans-2-methyl pentenoic acid elicited 1–5-fold responses compared to solvent control. A blend of attractive compounds could be utilized in odor-baited trap for surveillance and repellent molecules with suitable formulation could be used to reduce the biting menace of mosquitoes.

Keywords *Aedes albopictus* · Attractant · Repellent · Host-seeking · Orientation · Olfaction

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Introduction

Mosquitoes use a number of attractive stimuli, e.g., light, heat, moisture, carbon dioxide, and most importantly host odors to locate their hosts (Takken 1991). The odor of human perspiration that we smell is due to saturated and unsaturated C_6 to C_{11} acids, and (E)-3-methyl-2-hexenoic acid is one of the most abundant odoriferous compounds that influence the mosquito orientation to humans (Sastry et al. 1980). Researchers have found that a number of host skin emanation chemicals like 1-octen-3-ol, acetone, short-chain carboxylic acids, ammonia, and L-lactic acid have been found to be attractive to *Aedes aegypti* (L.) females (Bosch et al. 2000; Geier et al. 1999; Schreck et al. 1981). In the gamut of mosquito literature, lactic acid and 1-octen-3-ol has been the most studied chemicals with promising attractiveness to various mosquito genera, thus became an integral part of odor blends used in traps. Chemicals from human skin emanations such as carboxylic acids have recently been shown to influence the orientation behavior of Asian tiger mosquito, *Aedes albopictus* (Skuse) females (Seenivasagan et al. 2014) with the huge potential to be used as attractants in odor-baited traps and as repellents to reduce the biting menace of mosquitoes. L-Lactic acid has been reported as attractant for *Ae. aegypti* (Acree et al. 1968), but its attractancy for *Ae. albopictus* is still debated by many researchers. However, recent reports by Wang et al. (2006) and Hao et al.(2012) demonstrate that significantly more *Ae. albopictus* females were attracted to lactic acid odor in an olfactometer.

Among the well-established mosquito control strategies, notably attractants and repellents play respectively, a predominant role in diverting the mosquitoes to a trap and deflecting the mosquitoes away from human hosts. In the current scenario, researchers are more focused on eco-friendly approaches using semiochemicals (pheromones or parapheromones) of natural and synthetic origin to control hematophagous insects (Seenivasagan & Vijayaraghavan

2010). *Aedes albopictus* played a major role in the recent outbreaks of dengue and chikungunya in various parts of India, which provoked the need for effective vector surveillance and management strategies using traps that exploit oviposition and host-seeking behavior of mosquitoes. All human beings are not equally attractive to mosquitoes as some of them suffer more mosquito bites, while the others remain almost free from mosquito attacks. It has been found that kairomones in human skin emanations attract *Ae. aegypti* (Dekker et al. 2005) over short distances. *Anopheles gambiae* Giles uses the level of L-lactic acid and CO_2 with kairomones to locate their host (Dekker et al. 2002; Smallegange et al. 2005). Exploiting the host-seeking (Dormont et al. 2013; Logan et al. 2013) and oviposition site-seeking (Bentley & Day 1989; Guha et al. 2012; Seenivasagan et al. 2009a, 2013; Sharma et al. 2009) behavior of mosquitoes ensure effective control of target mosquitoes using suitable attractants and repellents. Hence, vector control using semiochemicals is a promising approach at the ecological system of a target mosquito, where it breeds and survives to inflict damage on residing human population by transmitting diseases.

Although, most of the studies focused on human skin volatiles and their influence on orientation behavior w.r.t *An. gambiae* (Smallegange et al. 2005), *Ae. aegypti* (Logan et al. 2008) and *Culex quinquefasciatus* Say (Puri et al. 2006), the Asian tiger mosquito, *Ae. albopictus* received lesser attention despite its greater role in the recent outbreaks of dengue and chikungunya throughout the world. Further, the role of unsaturated acids and alcohols that mediate such behavior had not been given much importance until recently, wherein, several alkenols and alkynols (Cilek et al. 2011, 2012) have been shown to attract *Ae. albopictus* under semi-field conditions. Accordingly, in this direction, we have evaluated and report hereunder the effect of two saturated branched alcohols viz., 2-methyl-3-pentanol and 3-methyl-3-pentanol; four unsaturated alcohols, such as *cis*-2-hexen-1-ol, trans-2-hexen-1-ol, 5-hexen-1-ol, and 1-octen-3-ol (Bernier et al. 2000); and the most commonly tested acids, such as L-lactic acid, trans-2-methyl pentenoic acid, trans-2- hexenoic acid, and 2-octenoic acid, found in human skin emanations by various researchers around the world on the mosquito behavior. The main objective of this work is to study the influence of these chemicals on flight orientation and electrophysiological response of *Ae. albopictus* females using olfactometer and electroantennogram to identify the effective attractant(s) to utilize them in odor-baited traps.

Materials and methods

Insects and chemicals

Aedes albopictus females used in the experiments were utilized from the laboratory colony maintained in our insectaria. The experiments were performed at 27±2 °C, 75±5 % RH, L10:D14 regime. Females were kept in standard-sized wooden cages (750×600×600 mm) with a sleeve opening on one side (Sharma et al. 2008). Sucrose (10 %) solution was provided *ad libitum* to adults, and females did not have the access to blood meal. Non-blood-fed females (5–7 days old) were used in the olfactometer bioassay. All the chemicals were procured from Sigma-Aldrich, Fluka, Lancaster, and Acros (Table 1). A stock solution of 10 % was prepared in hexane (Merck, HPLC grade) for each acid and alcohol. For each chemical, five concentrations [0.0001 % (10^{-6} g) to 1 % (10^{-2} g)] were prepared freshly by serial dilution, while, L-lactic acid was dissolved in double-distilled water.

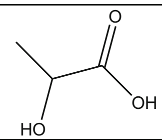
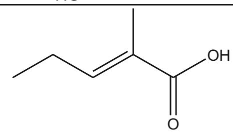
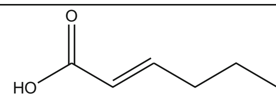
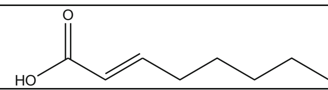
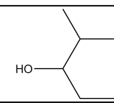
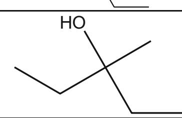
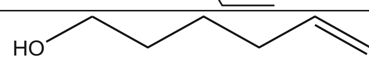
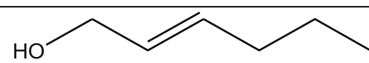
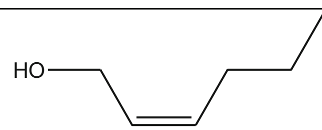
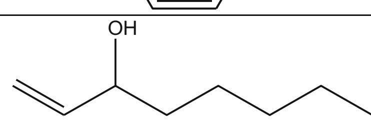
Y-tube olfactometer

Flight orientation studies on non-blood fed *Ae. albopictus* females using Y-tube olfactometer was conducted according to Seenivasagan et al. (2014) to different doses of test chemicals. For each replicate, mosquitoes which readily oriented to human hand were aspirated out from the cage in a group of twenty and were used in the experiment. Before stimulation by the test odor, the mosquitoes were given 5 min to acclimatize in the release chamber. Between the replicates, a constant flow of fresh air flushed the olfactometer. The test chemicals (200 μl of odor stimuli) were applied onto a piece of filter paper (10×2.5 cm), placed in an odor cartridge after evaporation of solvent. The airflow was maintained at 50 l/min during the experiment, which was split into two halves by a T-splitter which carried the odor of test chemicals downwind (Seenivasagan et al. 2012). Seven replicates of orientation experiments were conducted for each dose of test chemicals in a dual-choice bioassay, in which the positions of test stimuli were alternated between every replicate. The bioassay was conducted for 3 min; in the given time, all mosquitoes have fled from the release chamber and entered into upwind end of the olfactometer. The olfactometer was cleaned thoroughly after testing each of the chemical. The number of mosquitoes collected in respective chambers of control/treated arm were counted manually to assess the odor preference and used for analysis.

Electroantennogram

The peripheral olfactory response of 5–7-day-old non-blood-fed female *Ae. albopictus* mosquitoes was tested for the test chemicals with seven different antennas constituting seven replicates essentially based on the method described by Seenivasagan et al. (2010, 2012). The EAG responses of non-blood fed mosquitoes were recorded using electroantennogram (EAG) instrument (The Syntech, Hilversum, The Netherlands). The charcoal filtered and

Table 1 Acids and alcohols reported in human skin emanations used in the study

CAS number	Acids	Chemical structure	Purity %	Molecular weight (g/moL)	Source
50-21-5	Lactic acid		98	90.08	Fluka
16957-70-3	Trans-2-methyl-2-pentenoic acid		97	114.14	Aldrich
13419-69-7	Trans-2-hexenoic acid		98	114.14	Lancaster
1871-67-6	2-Octenoic acid		95	142.2	Aldrich
565-67-3	2-Methyl-3-pentanol		> 99	102.18	Aldrich
77-74-7	3-Methyl-3-pentanol		99	102.18	Aldrich
821-41-0	5-Hexen-1-ol		99	100.16	Aldrich
928-95-0	Trans-2-hexen-1-ol		96	100.16	Aldrich
928-94-9	*cis*-2-Hexen-1-ol		95	100.16	Aldrich
3391-86-4	1-Octen-3-ol		98	128.22	Acros

humidified air was delivered continuously through 0.5-cm internal diameter borosil glass tube over the antennal preparation. The test chemical was adsorbed onto a piece of hexane-washed filter paper (5×1 cm) folded in zigzag pattern. Fifty microliters of test stimuli (10^{-6} to 10^{-2} g) were presented to every stabilized antenna for a pulse duration of 0.5 s from lower to higher doses of the test chemicals with 1-min stimulation interval. Each recording session was initiated by application of air, hexane (control), followed by increasing doses of test stimuli and terminated with reverse order of first two stimulations. Acetic acid standard 10 μg was puffed over the antenna at the start and finish of each recording session to test the responsiveness of the antenna. The EAG amplitude (−mV) of blank air was subtracted from other succeeding EAG responses and used for analysis.

Statistical analysis

Percent flight orientation response to treatment odor (T-C/T+C)×100, where T is the number of mosquitoes oriented to test odor, C is the number of mosquitoes oriented to control odor in the Y-tube olfactometer, and EAG amplitude values were subjected to two-way ANOVA using statistical software (Sigma Stat V2.03, SPSS Inc., Chicago, IL). The differences between the treatments were examined by LSD, and $P<0.05$ was considered statistically significant.

Results

Flight orientation response

Females of *Ae. albopictus* were attracted to odors of lactic acid and 2-methyl-3-pentanol at all doses. Lactic acid elicited dose-dependent orientation ranging from 54 to 65 %, while about 40–57 % orientation was observed for 2-methyl-3-pentanol. Positive orientation toward the odor plume was observed for trans-2-methyl-2-pentenoic acid at 10^{-4} and 10^{-3} g doses, while trans-2-hexenoic and 2-octenoic acids showed attractance at 10^{-5} and 10^{-4} g odor plumes. However, at the highest dose (10^{-2} g), all these acids repelled 40–45 % of *Ae. albopictus* females. In case of 3-methyl-3-pentanol, 10^{-5} and 10^{-4} g plumes showed, respectively, 62 and 68 % attractance, while higher doses exhibited 30 % repellency to female mosquitoes. Similarly, 1-octen-3-ol attracted about 58–64 % mosquitoes at 10^{-6} and 10^{-5} g plume while further increase caused 35–40 % repellence. In contrast 5-hexen-1-ol and both *cis*-2-hexen-1-ol and trans-2-hexen-1-ol odors at all doses repelled ca. 55–65 % of *Ae. albopictus* females (Fig. 1). Significant differences among different chemicals ($F_{9,300}$=9.92, P<0.001), concentration ($F_{4,300}$=17.49, P<0.001), and their interaction ($F_{36,300}$=6.09, P<0.001) effect revealed by two-way ANOVA (Table 2) signify that these chemicals found in human skin emanations did influence the flight orientation response.

Electroantennogram response

Antenna of female *Ae. albopictus* exhibited a dose-dependent EAG response up to 10^{-3} g of lactic acid, trans-2-methyl-2-pentenoic acid, 2-octenoic acid, trans-2-hexen-1-ol, and 1-octen-3-ol stimulations; however, at the highest dose (10^{-2} g), a little decline in the EAG response was observed (Fig. 2). Negative dose-dependent EAG response was observed for 2-methyl-3-pentanol, 5-hexen-1-ol, and *cis*-2-hexen-1-ol, wherein increasing doses reduced the EAG amplitude in contrast to 3-methyl-3-pentanol and trans-2-hexenoic acid which showed increased EAG responses at all doses tested. At the highest dose (10^{-2} g) tested, trans-2-hexenoic acid and 3-methyl-3-pentanol exhibited 9-fold EAG response compared to solvent control. Similarly, lactic acid at 10^{-3} g and 2-octenoic acid at 10^{-4} g elicited 9–10-fold EAG responses significantly different from control. Antennal response ranged from 1- to 5-fold for *cis*-2-hexen-1-ol and trans-2-methyl pentenoic acid compared to control. EAG response to lactic acid was significantly different from other chemicals and both the *cis* and trans geometric isomers of 2-hexen-1-ol differed significantly, while response to octenol, methyl pentanol, hexenoic, and octenoic acids were at par ($F_{9,360}$=31.81, P<0.001) as revealed by two-way ANOVA (Table 3).

Discussion

In our study, we have evaluated lactic acid, three unsaturated acids (C_6 and C_8), four unsaturated alcohols (C_6, C_8) and two saturated branched alcohols (C_6) having molecular weights ranging from 90 to 142 signifying their relative importance to influence the orientation of hungry females toward their hosts. In this study, lactic acid (LA) and 2-methyl-3-pentanol at 10^{-6} to 10^{-2} g attracted >60 % mosquitoes. Similarly, Wang et al. (2006) observed 55–70 % attraction of *Ae. albopictus* to lactic acid odor at 0.01 to 10 mg/l doses. In their olfactometer experiments, LA attracted 25–30 % females at 0.01–100 mg/l doses; however, a significant response (P<0.05) was observed only at 0.1 mg/l compared to control, while Hao et al. (2012) has found 10 % L-lactic acid in dichloromethane attracted more *Ae. albopictus* females than LA alone and human odor. However, Shirai et al. (2001) has reported that L-lactic acid at 0.0001–1 % (10^{-6} to10^{-2} g) significantly reduced the landing of *Ae. albopictus* on human hands compared to water-treated forearms, while Kawada et al. (2007) has reported visual cue +CO_2, visual cue +octenol enhanced the attractiveness to *Ae. albopictus* females. Synergistic blend of lactic acid with acetone, dichloromethane, and dimethyl disulfide attracted more *Ae. aegypti* mosquitoes in a triple-

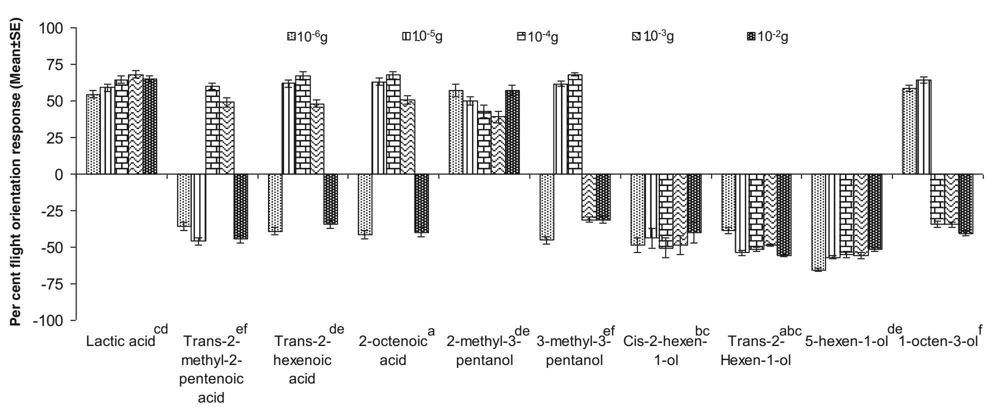


Fig. 1 Flight orientation response of non-blood-fed *Aedes albopictus* mosquitoes in Y-tube olfactometer to acids and alcohols. *Bars* are mean percent orientation response (*n*=7) to the treatment odor, and negative response signifies the repellent effect; in each replicate, 20 females were exposed to odor plumes. *Chemical legends with different alphabet superscripts* are significantly different (two-way ANOVA, *P*<0.001)

Table 2 Results of two-way ANOVA on flight orientation response of *Aedes albopictus* to selected chemicals

Source of variation	Degrees of freedom	Sum of squares	Mean squares	*F* value	*P* value
Total	349	58,689.21	168.164		
Treatment	9	7,720.643	857.849	9.923	<0.001
Dose	4	6,051	1,512.75	17.498	<0.001
Treatment×Dose	36	18,981.86	527.274	6.099	<0.001
Residual	300	25,935.71	86.452		

cage dual-port olfactometer (Bernier et al. 2003). Females of *Ae. aegypti* were repelled by 3-methyl-2-pentenoic acid (65 %), 2-octenoic acid (97 %) at 0.3 mg/cm^2 applied onto a polyester film (Reifenrath 2005). In addition, Mathew et al. (2013) has recently reported that 1-oceten-3-ol and lactic acid, respectively, attracted 60 and 40 % of *Ae. aegypti*, while 1-hexen-1-ol repelled 72 % females in their indigenously designed olfactometer. Differential attractiveness of humans to mosquitoes probably lies in composition of volatile skin emanations, and focus on these differences can lead to the identification of new compounds that mediate the mosquito host-seeking process. Logan et al. (2008) detected benzaldehyde, 6-methyl-hepten-2-one, octanal, nonanal, decanal, naphthalene, and geranyl acetone from less attractive individuals. In addition, our recent findings on orientation response of *Ae. albopictus* to saturated carboxylic acids (Seenivasagan et al. 2014) revealed dose-dependent reversal of response from attraction to repellence for certain chemicals.

In our electroantennogram experiments, we found that the antenna of female *Ae. albopictus*, exhibited a dose-dependent EAG response up to 10^{-3} g of L-lactic acid, trans-2-methyl-2-pentenoic acid, 2-octenoic acid, trans-2-hexen-1-ol, and 1-octen-3-ol stimulations; however, at the highest dose (10^{-2} g), a little decline in the EAG response was observed. Cork & Park (1996) in their effort to identify electrophysiologically active compounds for *An. gambiae* from human sweat extracts has reported that short-chain saturated carboxylic acids elicited significantly larger EAG responses than longer chain saturated carboxylic acids from female *An. gambiae*, while l-octen-3-ol and 4-methylphenol elicited significant dose-dependent EAG responses at the tested doses. However, both compounds elicited smaller EAG responses than the same dose of C_1–C_6 straight-chain aliphatic carboxylic acids. Similarly, isovaleric acid, p-cresol, 1-octen-3-ol, and lactic acid elicited dose-dependent EAG responses in *An. gambiae* s.s. females (Costantini et al. 2001), while the olfactory receptor neurons of both *Ae. aegypti* and *C. quinquefasciatus* had a significantly higher response to the (R)-1-octen-3-ol enantiomer compared to the (S)-1-octen-3-ol enantiomer at 10^{-9} to 10^{-6} g/μl. However, the most notable effect was from an (R:S)-1-octen-3-ol mixture (84:16) that caused significantly more mosquitoes to sustain their flight and reach the capture chambers, suggesting that it may have a behaviorally excitatory effect (Cook et al. 2011). Antennal sensilla of *Ae. albopictus* (Seenivasagan et al. 2009b) plays major role in perception of human odor and guide the mosquitoes to their host. In a recent study, 1-octen-3-ol elicited dose-dependent EAG response in *Ae. albopictus* (Deng et al. 2013) and dose-dependent action potentials from "C"-neuron of basiconic sensilla in *Ae. aegypti* (Bohbot et al. 2013); these finding corroborates our observations that this compound with other attractive chemicals could be useful in developing an attractive bait for day-biting mosquitoes.

Both the electroantennogram and orientation response of *Ae. albopictus* females exhibit significant correlation on their relative sensitivity and perception of odors at tested doses, signifying olfaction-mediated upwind flight into the

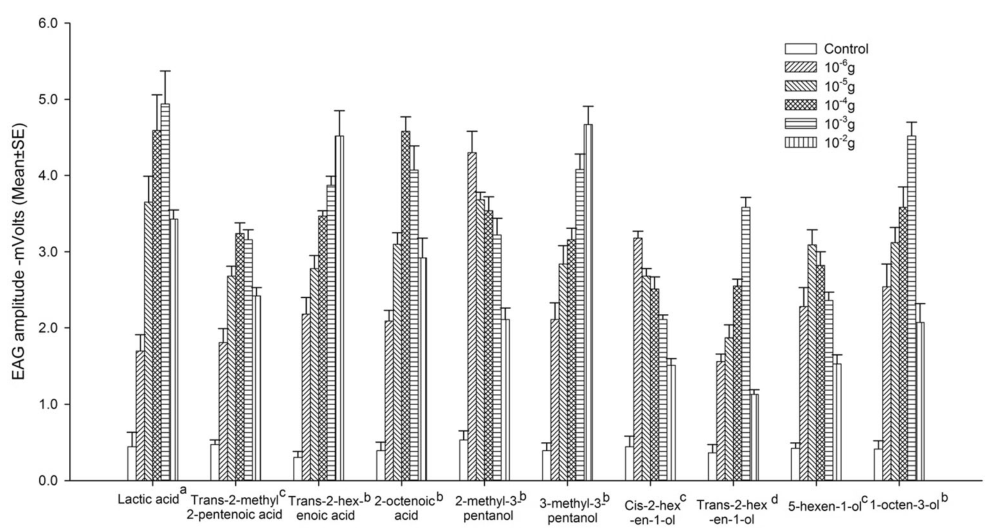


Fig. 2 Electroantennogram response of non-blood-fed *Aedes albopictus* mosquitoes to acids and alcohols. *Bars* are mean EAG response (n=7); in each replicate, antenna of seven females were stimulated by odorants. *Chemical legends with different alphabet superscripts* are significantly different (two-way ANOVA, P<0.001)

Table 3 Results of two-way ANOVA on electroantennogram response of *Aedes albopictus* to selected chemicals

Source of variation	Degrees of freedom	Sum of squares	Mean squares	*F* value	*P* value
Total	419	795.066	1.898		
Treatment	9	76.284	8.476	31.814	<0.001
Dose	5	458.377	91.675	344.092	<0.001
Treatment×Dose	45	164.491	3.655	13.72	<0.001
Residual	360	95.914	0.266		

olfactometer. Relatively lesser EAG response (1-5 folds) of females to *cis* and trans geometric isomers of 2-hexen-1-ol as well as 5-hexen-1-ol odors compared to other chemicals has correlated with the diminished orientation of females, thus signifying a moderate repellent or attraction inhibition effect by hexen-1-ol odor in the olfactometer. Although dose-dependent EAG was observed for both lactic acid and octenol, female *Ae. albopictus* experienced a mild repellence by 1-octen-3-ol odor at doses above 10^{-4} g in the flight orientation. The position of –CH_3 in the second and third place of methyl-3-pentanol exhibited contrasting EAG response depicting positive and negative thresholds, however, increased sensitivity to 3-methyl-3-pentanol at 10^{-3} and 10^{-2} g resulted in reversal of orientation by *Ae. albopictus* females. Additional evidences emerge on response threshold in both EAG and orientation responses that at the optimum doses (10^{-5} to 10^{-3} g); these chemicals could guide the olfactory responses of these mosquitoes.

In conclusion, the Asian tiger mosquito is diurnally active and highly anthropophilic in nature and uses visual and chemical cues to find their hosts. A thorough evaluation of individual compounds and testing them in various combinations with other physical and chemical cues is required to make an effective odor baits. Our effort is a small initiative toward this goal, and the findings of the current study would lead to further ventures in this area of applied research. Several of these compounds have elicited more than 50 % orientation in *Ae. albopictus*, and some odoriferous substances exhibited attractant and repellent or attraction inhibitor properties. The attraction inhibitors function by masking the chemical cues (kairomones) used by mosquitoes for host location, while the less attractive compounds could be used in the development of repellent formulations to reduce the biting menace of target mosquitoes.

Acknowledgments The work received financial grants through the Project-201 (S&T) of Defence Research and Development Establishment, Gwalior. The authors are thankful to the Director, Defence Research and Development Establishment, and Head, Vector Management Division, for their encouragement. We thank all the members of Vector management division for the help in maintenance of the mosquito culture. Lopamudra expresses her gratitude to Defence Research and Development Organisation, New Delhi, for the Junior Research Fellowship during the course of work.

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