Pergamon

Journal of Insect Physiology 47 (2001) 509–514

Journal of Insect Physiology

www.elsevier.com/locate/jinsphys

Electrophysiological responses of female *Helicoverpa armigera* (Hübner) (Lepidoptera; Noctuidae) to synthetic host odours

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Received 27 June 2000; accepted 3 July 2000

Abstract

Studies were conducted to investigate the electroantennographic (EAG) responses of adult female *Helicoverpa armigera* to a range of known and putative kairomone components. The studies show that at a given dose the EAG responses elicited by a series of straight-chain aliphatic primary alcohols were not dependent on volatility since butan-1-ol and pentan-1-ol elicited EAG responses that were significantly smaller than those elicited by hexan-1-ol. The amplitudes of responses to hexan-1-ol were found to be dose dependent with a dose of 10^{-1} μmol at source in a non-volatile solvent eliciting the largest response. Similarly, changes in functionality in a range of C_6 straight-chain aliphatic compounds significantly changed the amplitude of response elicited, with aldehydes eliciting smaller responses than the related primary alcohols and saturated compounds eliciting higher responses than related unsaturated compounds. Of the range of nine host plant-produced terpenoids tested, ocimene and β-phellandrene elicited the highest responses and of the six aromatic compounds tested phenylacetaldehyde and benzaldehyde elicited the largest responses, at the doses tested. The significance of these findings for analysis of floral odours by gas chromatography linked to electroantennography as a means of identifying kairomone components attractive to *H. armigera* are discussed.

Keywords: Electrophysiology; *Helicoverpa armigera*; Kairomone; Floral attractants

1. Introduction

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a polyphagous insect of major economic importance throughout the Old World, most notably in cotton (King, 1994). The larvae feed on the green leaves, buds, pods and fruits of their host plants. The flowering stage of the crop is the most preferred phenological state for oviposition by *H. armigera*, although females oviposit on host plants in the absence of flowering parts (Roome, 1975). Each female moth oviposits on average 1000 eggs, although this can range from 500 to 3000. Ovipositional sites on a plant are highly variable but there is a tendency for eggs to be laid on or near flowering plant parts.

Previously considered a pest of secondary importance in India, control has become difficult because of the development of strains resistant to pyrethroid and endosulfan insecticides in Australia (Forrester et al., 1993) and the Indian subcontinent (Armes and Raheja, 1996). To address this problem considerable effort has been invested in the development of transgenic cotton varieties that express *Bacillus thuringiensis* (Bt) endotoxins. However, given that some insect species, notably the diamondback moth, *Plutella xylostella*, have already developed resistance to Bt (Syed and Fauziah, 1996), there still remains a need to develop alternative control strategies.

One option is the control of *H. armigera* by mating disruption using synthetic sex pheromones, but given the migratory nature of adult moths and the fact that only male moths are affected, this approach is unlikely to achieve control. Nevertheless, as female moths are highly attracted to the floral parts of host plants for both ovipositing and nectar feeding, this could be used as the basis for a control strategy. Indeed, Srinivasan et al. (1994) have already shown that the African marigold,

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0022-1910/01/$ - see front matter
PII: S0022-1910(00)00119-0

Tagetes erecta, can be used as a trap crop in tomato, although its use in cotton is limited by a short flowering period (A. Regupathy, personal communication). Problems associated with duration of flowering and the variable attractiveness of flowers over time could be overcome by the development of a synthetic equivalent.

Floral odours are typically composed of blends of compounds (Dobson, 1991) and in order to identify the compounds that elicit attraction from *H. armigera*, a method of screening is required. This, in principle, could be achieved by using gas chromatography linked to electroantennography (EAG) (Moorhouse et al., 1969), a technique developed for the identification of Lepidopterous sex pheromones and successfully adapted for use in identifying a wide range of kairomones (Cork et al., 1990). As a prelude to analysing floral odours by GC-EAG, the current study was undertaken to ascertain whether host plant compounds known to elicit a behavioural response from other Noctuidae could elicit significant EAG responses from female *H. armigera*.

2. Methods and materials

2.1. Insect material

Insects of Indian origin supplied by the International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, were reared at NRI using a semi-synthetic diet and rearing procedures described by Armes et al. (1992). Pupae were sexed at eclosion and separated into plastic boxes (15×10×25 cm). On emergence, adult female moths were provided with a 10% sucrose solution and maintained at 26°C and 60% relative humidity during the reversed 12-h light period and 22°C and 60% relative humidity in the 12-h dark period. All electrophysiological studies were conducted on virgin female moths of between 1 and 3 days old.

2.2. Electroantennography (EAG)

EAG preparations were made as described by Cork et al. (1990). Insects were immobilised on their dorsal surface in a notch in a block of plasticine and restrained with a strip of polystyrene held in place with pins. The exposed antennae were fixed on the plasticine, with ventral surface uppermost, using U-shaped copper wires (10×0.5 mm diameter). Glass microelectrodes (50×2 mm diameter, Clark Electromedical Instruments Ltd., UK) filled with ringer solution (Roelofs and Comeau, 1971) were fixed onto micromanipulators (Leica, UK) where they were in electrical contact with a high impedance (10^7 Ω) microamplifier in the DC mode (Grass P60, USA) via an Ag/AgCl junction. The recording electrode was inserted into the distal end of an antennal flagellum and the indifferent electrode into the basal scape of the same antenna. Unfiltered EAG responses were digitised using a Nelson 600 interface (sampling rate 16.6 Hz), displayed and processed on a PC using TurboChrom software (Version 4.0, Perkin Elmer, UK). EAG responses were quantified by comparison with a −1 mV calibration signal from the amplifier.

2.3. Test compounds

Chemicals tested were selected on the basis of a bibliographic search for host-plant-derived compounds identified as attractants of Noctuidae in general and Heliothidae in particular. Chemicals were obtained from Aldrich Chemical Company (Gillingham, UK) and used without further purification. Thus, all compounds were at least 98% chemically and isomerically pure except limonene, linalool, α-pinene and β-pinene, which were racemic mixtures of enantiomers, and ocimene, which was a mixture of (*Z*)- and (*E*)-isomers. Solutions of test compounds were prepared in molar equivalents in a non-volatile, polar solvent, diethyl phthalate, and stored at −20°C. Aliquots (5 μl) of test solutions were presented to the EAG preparation adsorbed onto filter paper (6×10 mm, Whatman No. 1) in a Pasteur pipette.

2.4. Olfactory stimulation system

Pasteur pipettes containing test samples were positioned 25 mm above the midpoint of the antennal preparation and the compound released in a 3-s pulse of nitrogen (500 ml/min) over the antenna, with a delay of 57 s between samples during which time the EAG preparation was left in the laboratory air. The laboratory was well ventilated with a complete air change every 5 min. Each sample was tested four times with solvent blanks presented before and after each sample. Each series of samples was repeated in a randomised order with five different EAG preparations.

EAG responses were corrected for solvent and other background effects by subtracting the averaged EAG responses of the solvent responses recorded before and after each sample as described previously (Dickens, 1984; Visser, 1979). Thus, corrected EAG response $=R_C-\{(R^S_{C-1}-R^S_{C+1})/2\}$, where R_C is a single EAG response elicited by a compound, R^S_{C-1} is the response to the solvent before the test compound and R^S_{C+1} is the response to the solvent after the test compound. If the sample response was the second of four replicates it was corrected by using the average of the second replicates of each of the four solvent responses before and after the sample. Corrected EAG responses were statistically analysed by analysis of variance (ANOVA). If treatment means were significantly different at the 5% level or lower they were compared by Duncan's multiple range test (DMRT) (Duncan, 1955).

3. Results

3.1. Reproducibility of responses

The first replicate of each sample tested was found to elicit a significantly higher EAG response than the other three replicates, averaging −0.81, −0.66, −0.62 and −0.59 mV for replicates one through to four respectively for the whole data set. Since background responses also showed a similar distribution of responses, EAG responses were corrected using the same replicate number for samples and solvent controls. The reasons for this gradual reduction in EAG response from a single sample were uncertain but might suggest incomplete recovery of the EAG preparation between exposures, decrease in the responsiveness of the preparation, or decrease in the effectiveness of the stimulus (fewer molecules). This issue was not investigated further since it was the relative EAG response that was under consideration in the study and not the absolute EAG response.

3.2. EAG responses to a range of straight-chain aliphatic alcohols with different chain lengths

Many plant volatiles have been found to contain straight-chain aliphatic alcohols. So the effect on EAG response of varying the carbon chain length of a range of saturated straight-chain alcohols was tested from C_4 to C_{12}. The results (Table 1) showed that all the compounds tested elicited significant EAG responses above background except dodecan-1-ol. EAG responses were not proportional to volatility since hexan-1-ol elicited significantly larger responses than either butan-1-ol or pentan-1-ol at the dose tested, although it is conceivable that the lower EAG activities elicited by the longer chain alcohols could be due at least in part to their lower volatilities.

Table 1
EAG responses elicited by synthetic compounds from female *H. armigera*

Compound[a]	Average EAG[b] (mV)	Standard error	DMRT
Butan-1-ol	−0.30	±0.09	d
Pentan-1-ol	−0.77	±0.05	b
Hexan-1-ol	−1.28	±0.06	a
Heptan-1-ol	−0.50	±0.06	c
Octan-1-ol	−0.45	±0.06	cd
Dodecan-1-ol	−0.07	±0.02	e
(*E*)-2-Hexenyl acetate	−0.59	±0.09	a
(*E*)-2-Hexenal	−0.80	±0.08	ab
Hexanal	−0.85	±0.13	abc
(*Z*)-3-Hexen-1-ol	−1.00	±0.11	bcd
(*E*)-2-Hexen-1-ol	−1.06	±0.05	bcde
(*E*)-3-Hexen-1-ol	−1.12	±0.12	cde
Hexyl acetate	−1.13	±0.10	cde
(*Z*)-2-Hexen-1-ol	−1.16	±0.09	de
Hexan-3-ol	−1.17	±0.07	de
Hexan-1-ol	−1.32	±0.09	ef
Hexan-2-ol	−1.47	±0.14	f
Linalool	−0.24	±0.05	a
α-Pinene	−0.26	±0.09	a
Myrcene	−0.28	±0.11	a
β-Pinene	−0.29	±0.06	a
Limonene	−0.33	±0.04	a
1,8-Cineol	−0.36	±0.08	a
Ocimene	−0.57	±0.08	b
β-Phellandrene	−0.59	±0.06	b
β-Caryophyllene	−0.35	±0.53	a
Acetophenone	−0.39	±0.10	a
Methyl salicylate	−0.40	±0.05	a
Benzyl alcohol	−0.52	±0.07	ab
2-Phenylethanol	−0.62	±0.11	ab
Phenylacetaldehyde	−0.73	±0.10	b
Benzaldehyde	−0.74	±0.09	b

[a] Dose 5×10^{-2} μmol in 5 μl of diethylphthalate.
[b] EAG responses are averages of four replicates taken from each of five EAG preparations and corrected for the average of background responses before and after the sample replicate.

3.3. Effect of dose on the EAG response to hexan-1-ol

In order to test whether the EAG responses were dose dependent a range of doses of hexan-1-ol was tested against female EAG preparations. The results (Fig. 1) showed a typical sigmoid shape with 10^{-1} μmol eliciting the highest response and 10^{-4} and 3.33×10^{-3} μmol eliciting responses that were not significantly different from background. On the basis of this result other compounds were tested at a dose of 5×10^{-2} μmol.

3.4. EAG responses to a range of straight-chain aliphatic compounds with C_6 chain length

Eleven C_6 straight-chain aliphatic compounds were tested at a dose of 5×10^{-2} μmol. Since the number of molecules per aliquot was fixed and the relative volatility of the compounds tested similar, EAG responses might be expected to vary solely on the basis of antennal sensitivity to each compound. The compounds tested elicited EAG responses that were significantly above background and some were significantly different from the others ($P<0.001$, $F_{11,\,228}=16.15$) (Table 1). Hexanal, (*E*)-2-hexenal and (*E*)-2-hexenyl acetate elicited the lowest responses, −0.85, −0.80, and −0.59 mV, respectively, while the related saturated alcohols, hexan-1-ol and hexan-2-ol, elicited the highest responses, −1.32 and −1.47 mV respectively.

3.5. EAG responses elicited by a range of mono- and diterpenoids

EAG responses elicited by some of the nine terpenoids were significantly different from the others ($P<0.001$,

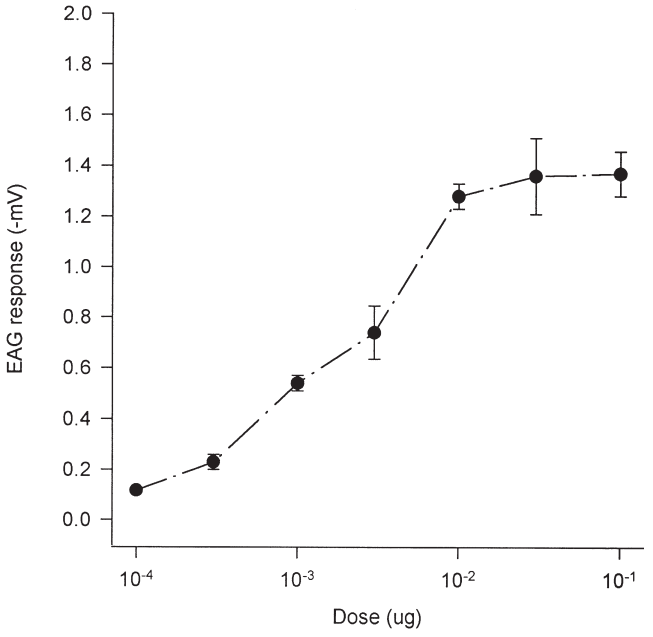

Fig. 1. Electroantennographic responses of female *H. armigera* to a range of doses of hexan-1-ol (mean±S.E., n=20).

$F_{9,\ 190}$=6.13). Comparison of the means by DMRT showed that the responses elicited by ocimene and β-phellandrene were significantly larger than those elicited by the other monoterpenoids, β-caryophyllene, limonene, linalool, myrcene, α-pinene, β-pinene and 1,8-cineol and the diterpenoid, β-caryophyllene, at the doses tested (Table 1).

3.6. EAG responses elicited by a range of aromatic compounds

Six aromatic compounds were tested and some were found to elicit EAG responses significantly different from the others ($P<0.001$, $F_{6,\ 133}$=9.72). Comparison of the EAG responses by DMRT showed that phenylacetaldehyde and benzaldehyde elicited EAG responses that were significantly larger than acetophenone and methyl salicylate. However, responses elicited from benzyl alcohol and 2-phenylethanol were not significantly different from any of the other compounds at the doses tested (Table 1).

4. Discussion

Primary aliphatic alcohols were found to elicit significant EAG responses from virgin female *H. Armigera*. The amplitude of responses varied with carbon chain length of the compound, with the C_6 compound hexan-1-ol eliciting the largest responses. Punter and Menco (1981) found a linear relationship between carbon chain length and saturated vapour pressure for *n*-aliphatic alcohols. Thus, the predominance of the response to hexan-1-ol was not due only to volatility but to a higher sensitivity of the antenna to hexan-1-ol than the other shorter-chain aliphatic alcohols tested. It appears that many insects are more responsive to C_6 straight-chain compounds and to a lesser extent to C_5-, C_7- and C_8 straight-chain compounds, irrespective of the terminal functional groups (Visser, 1979; Kozlowski and Visser, 1981; Dickens, 1984; Light et al., 1988).

Responses elicited by hexan-1-ol were dose dependent, giving rise to a typical sigmoid dose–response curve. Chemical functionality influenced the amplitude of response elicited, with C_6 straight-carbon chain acetates and aldehydes eliciting lower-amplitude responses than the related alcohols. Given that aldehydes are more volatile than the corresponding alcohol, the responses were not related to changes in relative volatility. Similarly, the unsaturated compounds tested elicited smaller EAG responses than related saturated compounds. This result was similar to that found by Guerin and Städler (1982) in a study of three phytophagous Diptera, but contrasted with data reported from other pest species where unsaturated compounds were shown to elicit significantly higher electrophysiological responses than related saturated compounds (Visser, 1983, 1986; Light et al., 1988). The compounds tested are commonly referred to as components of ‘green leaf volatiles’ and are typically released by damaged plants in a range of ratios (Buttery, 1981; Visser, 1983, 1986). Thus, the absolute amplitude of responses elicited by each of these compounds for a given dose may not necessarily be behaviourally important but the fact that they are detected by *H. armigera* receptor neurones may be. It remains to be seen whether the EAG responses were generated by plant odour specific receptor neurones as found in related Noctuidae (Anderson et al., 1995) or by generalists.

In contrast to the aliphatic compounds tested, all the aromatic aldehydes tested elicited larger EAG responses than the corresponding alcohols. Many of these compounds are known attractants of Lepidoptera, notably a blend of benzaldehyde, phenylacetaldehyde, 2-phenylethanol and benzyl alcohol, the four major volatile components emitted from flowers of *Abelia grandiflora* (Haynes et al., 1991) that is attractive to the cabbage looper moth, *Trichoplusia ni*. Heath et al. (1992) later showed that phenylacetaldehyde alone elicited the same response from *T. ni* as a blend of benzaldehyde, benzyl acetate and phenylacetaldehyde extracted from flowers of the night-blooming jessamine, *Cestrum nocturnum*. Furthermore, benzaldehyde is a common component of male scent gland secretions in noctuids (Aplin and Birch, 1970). Given that these compounds elicited significant EAG responses from female *H. armigera*, it is not inconceivable that they would also elicit a behavioural response. Indeed, Pawar et al. (1983) found that phenyl-

acetaldehyde, identified from maize silks and tassels (Cantelo and Jacobson, 1979), was attractive to *Helicoverpa zea*, *H. armigera* and *Ostrinia nubilalis*.

Methyl salicylate and acetophenone, volatiles from lucerne and red clover, elicited significant EAG responses from *H. armigera*, as they did from *Bruchophagus roddi* (Hymenoptera: Eurytomidae), a monophagous pest of lucerne (Light et al., 1992). Given that many leguminosae are host plants of *H. armigera* (King, 1994), these compounds may also elicit a behavioural response.

1,8-Cineole, β-caryophyllene, β-phellandrene and linalool are among the compounds that are thought to contribute most to tomato leaf odour (Buttery et al., 1987) and β-caryophyllene is a major component of the volatiles released from several Compositae (Buttery et al., 1978). However, these compounds, together with the other diterpenoids tested, elicited some of the smallest EAG responses recorded from *H. armigera*. This would again suggest that while EAG responses can be elicited from female *H. armigera* to a range of compounds, the behavioural significance of the compounds cannot be implied directly from the amplitude of the EAG responses elicited. Rather, the identification of EAG-activity confirmed only that the insect could detect the compound under test. It is also conceivable that the use of racemic compounds may have inadvertently resulted in smaller EAG responses than expected, if the insect could only respond electrophysiologically to one enantiomer. However, since plant-derived volatiles do not necessarily contain single enantiomers of compounds or the same enantiomer as other plants species, the use of pure enantiomers for screening compounds by electrophysiology is not necessarily advantageous.

The presumption that host volatiles are important prerequisites for oviposition of polyphagous insects such as *Heliothis virescens* in cotton has been queried by Ramaswamy (1988), although this does not necessarily rule out their potential importance in feeding or mating (Hendrikse and Vos-Bunnemeyer, 1987; Raina, 1988; Rembold et al., 1991). Indeed, the sensitivity that female *H. armigera* have shown to a range of host volatiles in this study would suggest that they may have a role to play in mediating host recognition and acceptance. For instance, Mitchell et al. (1991) found that female *H. virescens* were attracted by methylene chloride washes of host plants, including cotton, tobacco and a weed species, *Desmodium tortuosum*, in a wind tunnel bioassay. Similarly, it is conceivable that the observed rejection of potential host plants in the field by *H. virescens* (Ramaswamy, 1988) could have been mediated by the release of herbivore-induced volatile emissions. Such compounds might indicate that a crop is unsuitable for further oviposition by gravid female moths, especially as some of the compounds released in response to larval feeding on cotton are thought to be attractive to parasitoids (McCall et al., 1994).

Since known attractants of Noctuidae have been shown to elicit EAG responses from female *H. armigera* in this study, it would suggest that linked GC-EAG analysis may well be a useful means of screening behaviourally active plant extracts for compounds that contribute to observed behaviour. Indeed this has already been demonstrated by Gabel et al. (1992) who were able to identify compounds attractive to *Lobesia botrana* on the basis of linked GC-EAG analyses of steam distillates of *Tanacetum vulgare*. Given the promising results obtained in this study, preliminary linked GC-EAG analyses are now under way to identify floral odours that attract *H. armigera* to some of its preferred hosts, notably *T. erecta*, and the results of this work will be published elsewhere. Nevertheless, it remains to be seen whether kairomones based on these compounds will be sufficiently attractive and specific in the field (Pawar et al., 1983) to form the basis of population monitoring or control technologies (Wood, 1991).

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