The Journal of Experimental Biology 213, 2889-2895

doi:10.1242/jeb.042705

Tarsal taste neuron activity and proboscis extension reflex in response to sugars and amino acids in *Helicoverpa armigera* (Hübner)

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Accepted 6 May 2010

SUMMARY

In adult female *Helicoverpa armigera* (Hübner), the fifth tarsomere of the prothoracic legs bears 14 gustatory trichoid chemosensilla. These chemosensilla were characterized through electrophysiological experiments by stimulating with sucrose, glucose, fructose, maltose, *myo*-inositol and 20 common amino acids. In electrophysiological recordings from nine sensilla, responses were obtained to certain compounds tested at 100 mmol l^{-1}, and the response spectra differed from broad to narrow. The four sugars excited the same receptor neuron in sensillum a and sensillum b; sucrose and *myo*-inositol, sucrose and lysine, *myo*-inositol and lysine excited two different receptor neurons respectively in sensillum a; fructose and lysine excited two different receptor neurons in sensillum n. Furthermore, the four sugars, *myo*-inositol and lysine all elicited concentration-dependent electrophysiological responses. These six compounds also induced the proboscis extension reflex (PER) followed by ingestion of the solution when they were applied on the tarsi. Lysine and sucrose caused the strongest electrophysiological responses. However, sucrose had the strongest stimulatory effect on the PER whereas lysine had the weakest. Mixtures of sucrose with the other sugars or with lysine had a similar stimulatory effect on the PER as sucrose alone. The electrophysiological and behavioural responses caused by a range of sucrose concentrations were positively correlated. We conclude that the tarsal gustatory sensilla play an essential role in perceiving sugars available in floral nectar and provide chemosensory information determining feeding behaviour. Tarsal taste-receptor-neuron responses to lysine are implicated in oviposition behaviour.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/213/16/2889/DC1

Key words: amino acids, contact chemosensilla, electrophysiological responses, feeding behaviour, sugar, tarsomere.

INTRODUCTION

Most adult lepidopteran insects feed on floral nectar and honeydew, food sources rich in carbohydrates. These nutrients contribute to female reproductive success (Bauerfeind and Fischer, 2005; O'Brien et al., 2003). Flower nectar is generally thought to be the most important food source (Boggs, 1987; Gilbert and Singer, 1975). Flower nectar contains sugars (mainly sucrose, fructose and glucose), free amino acids, proteins, lipids, antioxidants, organic acids and other substances lacking nutritional value (Baker and Baker, 1975; Baker and Baker, 1982). Previous work has amply documented that feeding behaviour of various herbivorous insects is stimulated either by sugars or by several amino acids (Albert and Parisella, 1988; Bernays and Simpson, 1982; Hirao and Arai, 1990; Romeis and Wäckers, 2000), and some Lepidoptera showed a preference for either sugars or amino acids (Baker and Baker, 1982; Baker and Baker, 1983; Erhardt and Rusterholz, 1998; Rusterholz and Erhardt, 1997; Rusterholz and Erhardt, 2000). Therefore, detecting the sugars and amino acids naturally occurring in nectar is vital for lepidopteran adults.

Contact chemoreceptors, mainly located on appendages such as the proboscis, maxillary and labial palps and on the legs, perceive compounds on and in plant leaves and (extra-) floral nectar (Anderson and Hallberg, 1990; Qiu et al., 1998; Chapman, 2003; Calas et al., 2007; Newland and Yates, 2008). Contact chemosensilla on the legs play a crucial role in perceiving plant compounds after the insect has landed on the plant and subsequently taps or drums the leaf surface with the fore-tarsi of their prothoracic legs (Ma and Schoonhoven, 1973; Gaaboub et al., 2005; Klijnstra and Roessingh, 1986; Maher et al., 2006; Qiu et al., 1998). Previous studies on tarsal chemosensilla mainly focused on their importance in oviposition behaviour (Ma and Schoonhoven, 1973; Ramaswamy et al., 1987; Roessingh et al., 1992; Roessingh et al., 1997; Städler et al., 1995). Several studies showed that individual sugars can be perceived by adult lepidopterans, and stimulation of contact chemosensilla on the tarsi can elicit the proboscis extension reflex (PER) in those species (Kusano and Sato, 1980; Minnich, 1921; Minnich, 1922a; Minnich, 1922b; Ramaswamy, 1987). Amino acids also elicit the PER in some lepidopteran species (Blaney and Simmonds, 1990; Robbins et al., 1965). The contact chemoreceptive function of tarsal chemosensilla in detecting sugars and amino acids has been demonstrated in four noctuid species by Blaney and Simmonds (Blaney and Simmonds, 1990). A recent study showed that tarsal taste sensilla of *Mnesampela privata* were sensitive to some salts, sugars and amino acids (Calas et al., 2009). These results indicated that tarsal sensilla played a role in the assessment of food materials.

Helicoverpa armigera (Hübner) is one of the most important agricultural pests affecting many crops, especially in the Old World. Feeding is required before mating and egg-laying occur in this moth species. The adult moths usually ingest sugars and amino acids in

the form of nectar during both day and night and particularly at dusk (Zalucki et al., 1986). Electrophysiological characteristics of some chemosensilla located on the fifth tarsomere of *H. armigera* have been reported, but specific responses of all the chemosensilla and their relationship with feeding behaviour is unknown. In this study, we focused on the whole set of contact chemosensilla on the fifth tarsomere of the prothoracic leg to try to answer the following questions. (1) What are the electrophysiological response characteristics of tarsal contact chemosensilla when stimulated by a range of sugars and amino acids commonly occurring in natural floral nectar? (2) What is the effect of single sugars and amino acids and their mixtures on feeding behaviour? (3) Do tarsal electrophysiological responses predict feeding behaviour?

MATERIALS AND METHODS

Insects

Helicoverpa armigera were collected in Zhengzhou, Henan province of China. The larvae were reared in the laboratory on an artificial diet, the main components of which were wheat germ and tomato paste. Rearing took place at a temperature of 27±1°C with a photoperiod of 16 h:8 h, L:D. Pupae were sexed and males and females were put into separate cages for eclosion. The adult female *H. armigera* used for experiments were 12–24 hours old since eclosion and were provided with double-distilled water until the experiment.

Chemicals

Myo-inositol and α-D-glucose were from Serva, New York, NY, USA. Potassium chloride was from Beijing Shuanghuan Company (Beijing, China). Sucrose and fructose were from Beijing Huagong Factory (Beijing, China) and maltose from Beijing Dingguo Company (Beijing, China). The amino acids L-alanine (Ala), L-arginine monohydrochloride (Arg), L-asparagine (Asn), L-aspartic acid (Asp), L-cysteine (Cys), L-glutamic acid (Glu), L-glutamine (Gln), glycine (Gly), L-histidine hydrochloride (His), L-isoleucine (Ile), L-leucine (Leu), L-lysine hydrochloride (Lys), L-methionine (Met), L-phenylalanine (Phe), L-proline (Pro), L-serine (Ser), L-threonine (Thr), L-trypophan (Trp), L-tyrosine (Tyr) and L-valine (Val) were purchased from Sigma Chemical Company (St Louis, MO, USA). All the chemicals were of analytical grade.

Scanning electron microscopy

Prothoracic tarsi of female moths were excised using a scalpel. To gain a better view of the chemosensilla, we descaled the tarsal samples gently with sticky tape. The tarsal samples were mounted directly on stainless steel sample buds and sputter-coated with a 10 nm thick layer of gold. Photomicrographs were obtained with a scanning electron microscope (HITACHI S-3000N) in the Institute of Genetics and Developmental Biology, Chinese Academy of Sciences.

Electrophysiological characterization of tarsal contact chemosensilla

The tip-recording technique for insect contact chemosensilla, originally described by Hodgson et al. (Hodgson et al., 1955), modified as described by van Loon (van Loon, 1990) was used for electrophysiological recording. The foreleg of the moth was cut at the proximal region of the tibia and an AgCl-coated silver wire was inserted into the opening and was connected to a copper mini-connector, which served as the recording electrode. A glass capillary filled with the stimulus solution into which an AgCl-coated silver wire was inserted acted as the indifferent electrode. To avoid possible adaptation of the chemosensilla tested, the interval between two successive stimulations was at least 3 min. Prior to each stimulation, a piece of filter paper was used to absorb solution from the tip of the glass capillary containing the stimulus solution to avoid the increase of concentration due to water evaporation from the capillary tip. Between stimulations, the fifth tarsomere was rinsed with double-distilled water and then wiped with absorbent tissue. Action potentials (spikes) generated during the first second after stimulus onset were recorded with the aid of SAPID Tools software, version 16.0 (Smith et al., 1990).

Solutions of sucrose, glucose, fructose, maltose, *myo*-inositol and the 20 amino acids dissolved in 0.01 mmol l^{-1} KCl solution in double-distilled water were used as stimulants in the electrophysiological experiments. Each stimulant solution, at a concentration of 100 mmol l^{-1} was used to stimulate all 14 chemosensilla on the ventrolateral surface of the left side of the fifth tarsomere. The chemosensilla from which electrophysiological responses to a compound were registered were subsequently stimulated with a series of ascending concentrations (0.1, 1, 10 and 100 mmol l^{-1}) of those solutions to explore dose–response characteristics. For each stimulant and sensillum responsive to it, a minimum of 10 individual moths from three to five different rearing batches were studied. A solution of 0.01 mmol l^{-1} KCl served as the control stimulus. All the stimulants and control solutions were stored at 4°C.

Identification of the neurons activated in a chemosensillum

Some tarsal chemosensilla such as F5a, F5b, F5d and F5n responded to more than one stimulant. In order to identify whether the same or different receptor neurons in the same sensillum were activated by two stimulants, we first stimulated the sensillum with solutions of each compound separately and then with a mixture of the two. Mixtures of sucrose and fructose, sucrose and *myo*-inositol, sucrose and Lys, *myo*-inositol and Lys, glucose and maltose, fructose and Lys were tested. For both the solutions of the single compounds and the binary mixtures, the concentration of the compounds was 10 mmol l^{-1} except for Lys it was 1 mmol l^{-1}. The control solution was 0.01 mmol l^{-1} KCl and these trials were repeated five times.

Behavioural experiments – proboscis extension reflex

A clear plastic cylinder (diameter 9 cm, height 12 cm) was placed vertically in a Petri dish with a piece of filter paper at the bottom and a second Petri dish to cover the top of the cylinder. An individual female moth was released into the cylinder to allow it to fly until it landed on the aluminium coil bottom surface. Upon landing either the test or control solution was applied to both the forelegs of the moth with a 100 µl syringe, making sure that both tarsi were fully immersed in the solution. It was observed whether the PER was induced within 30 s after the tarsi contacted the solution. If the PER was performed, the duration of proboscis extension was recorded with a stopwatch, and the moth was gently taken out after the proboscis was retracted. We observed but did not find any moth that touched the stimulant solution with its antennae during the trial.

For both control and test solutions, 30 individual moths originating from the same rearing batch and in similar physiological condition (2–3 days after eclosion and satiated with double distilled water until the trial) were used as one group and three rearing batches separated in time by 3 days were used for replications. When a moth did not exhibit the PER within 30 s after tarsal contact with a stimulus solution, the solution was considered to lack a feeding-stimulatory effect. We tested the following solutions: (a) 0.1, 1, 10, 100 mmol l^{-1} sucrose; (b) 100 mmol l^{-1} glucose; (c) 100 mmol l^{-1} fructose; (d) 100 mmol l^{-1} maltose; (e) 100 mmol l^{-1} myo-inositol; (f) 100 mmol l^{-1} Lys; (g) a mixture of the four sugars each at 25 mmol l^{-1}; (h) a mixture of 1 mmol l^{-1} sucrose and

0.02 mmol l^{-1} Lys; (i) a mixture of 10 mmol l^{-1} sucrose and 0.02 mmol l^{-1} Lys. The control solution was 0.01 mmol l^{-1} KCl.

Data analysis

Electrophysiological responses were quantified by counting the number of action potentials in the first second after stimulus onset, using SAPID Tools (version 16.0) (Smith et al., 1990). Behavioural data were first corrected using Abbott's formula, arcsine root transformed and analysed by one-way ANOVA, followed by paired-sample *t*-tests. Statistical analysis was done using SPSS 17.0 software.

RESULTS

Distribution and nomenclature of tarsal chemosensilla

Two clusters of 14 trichoid chemosensilla could be identified on the fifth tarsomere of female moths from the scanning electron photomicrograph (Fig. 1A). The chemosensilla were shorter than other cuticular extensions on the tarsi and had a blunt tip. Fig. 1B is a schematic drawing of Fig. 1A showing the distribution of the 14 chemosensilla on one side of the tarsomere labelled with their prefix F5 (fifth tarsomere of the female tarsus) and alphabetical codes from a (proximal) to n (distal). Over 100 female moths were examined under the light microscope and in every case the number of sensilla on one side was 14.

Electrophysiological responses to sugars, sugar alcohol and amino acids

Among the 14 chemosensilla, nine (F5a-F5d, F5i, F5k, F5l, F5m and F5n) showed responses to certain test compounds at 100 mmol l^{-1}, but with different response spectra; F5a and F5b exhibited the broadest and F5d the narrowest spectra. F5a, F5b, F5d, F5k and F5n showed much stronger responses to one or two stimulants than the other chemosensilla (one-way ANOVA, $P<0.05$). Sensilla F5e, F5f, F5g, F5h and F5j had no response to any of the stimulants (see Fig. S1 in supplementary material). Representative electrophysiological recordings are shown in Fig. S2 in supplementary material.

The chemosensilla with strongest response to sucrose at 100 mmol l^{-1} were F5a and F5b, to glucose F5b and F5d, to fructose F5a and F5n, to maltose F5b and F5k, to *myo*-inositol F5a and to Lys F5a and F5n (see supplementary material Fig. S1). Among the 20 amino acids tested at 100 mmol l^{-1}, only Lys, Phe, Ile, Gly, Tyr, Arg and Pro evoked electrophysiological responses. F5a and F5b were responsive to all these 7 amino acids, F5l responded to Tyr and Pro, F5m to Tyr, Arg and Pro, F5n to Lys and Ile (see supplementary material Figs S1 and S2). Moreover, the four sugars, *myo*-inositol and Lys all evoked concentration-dependent responses (Fig. 2).

Receptor neurons excited in corresponding chemosensilla

Based on the electrophysiological recordings in response to individual compounds and their binary mixtures (see supplementary material Fig. S3), it was established that in F5a, sucrose and fructose activated the same receptor neuron, whereas the mixtures of sucrose and *myo*-inositol, sucrose and Lys, *myo*-inositol and Lys excited two different receptor neurons. Moreover, glucose and maltose activated responses in the same receptor neuron in F5b, but fructose and Lys elicited responses in two different receptor neurons in F5n. It was confirmed that the number of spikes in response to the binary mixture was not higher than the sum of spikes in response to each individual compound (see supplementary material Fig. S4). This proved that at least three neuron types existed in the corresponding tarsal contact chemosensilla.

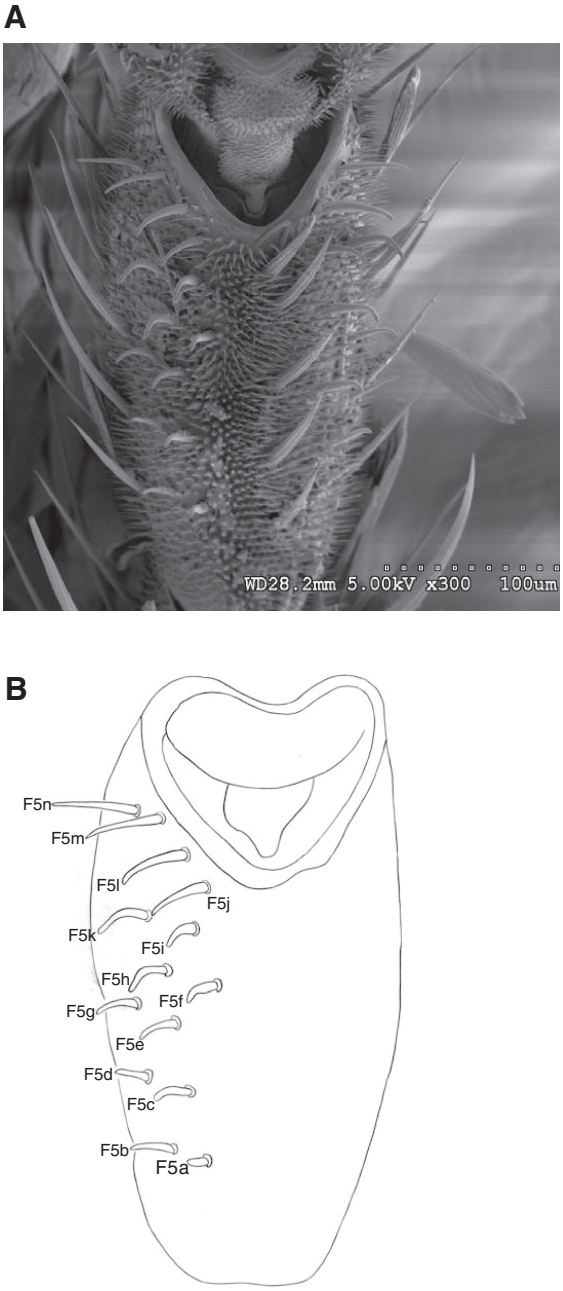

Fig. 1. External morphology and distribution of chemoreceptive hairs on the fifth tarsomere of adult female *H. armigera*. (A) Scanning electron micrograph of the fifth tarsomere. Ventral view. (B) Schematic drawing of the fifth tarsomere showing the 14 contact chemosensilla on one ventrolateral side of the tarsus and their nomenclature. For clarity, other cuticular structures on the fifth tarsomere were omitted.

Proboscis extension reflex

All test compounds at 100 mmol l^{-1} triggered a PER (Fig. 3). Sucrose elicited the highest response in terms of numbers of insects exhibiting PER, followed in order by fructose, maltose, glucose, *myo*-inositol and Lys (Fig. 3A). The PER for fructose and maltose were higher than for glucose, *myo*-inositol and Lys (one-way ANOVA, $P<0.05$); the percentages for the last three were similar. Compared with each respective solvent control, all compounds had a significantly higher stimulatory effect (paired-samples *t*-test,

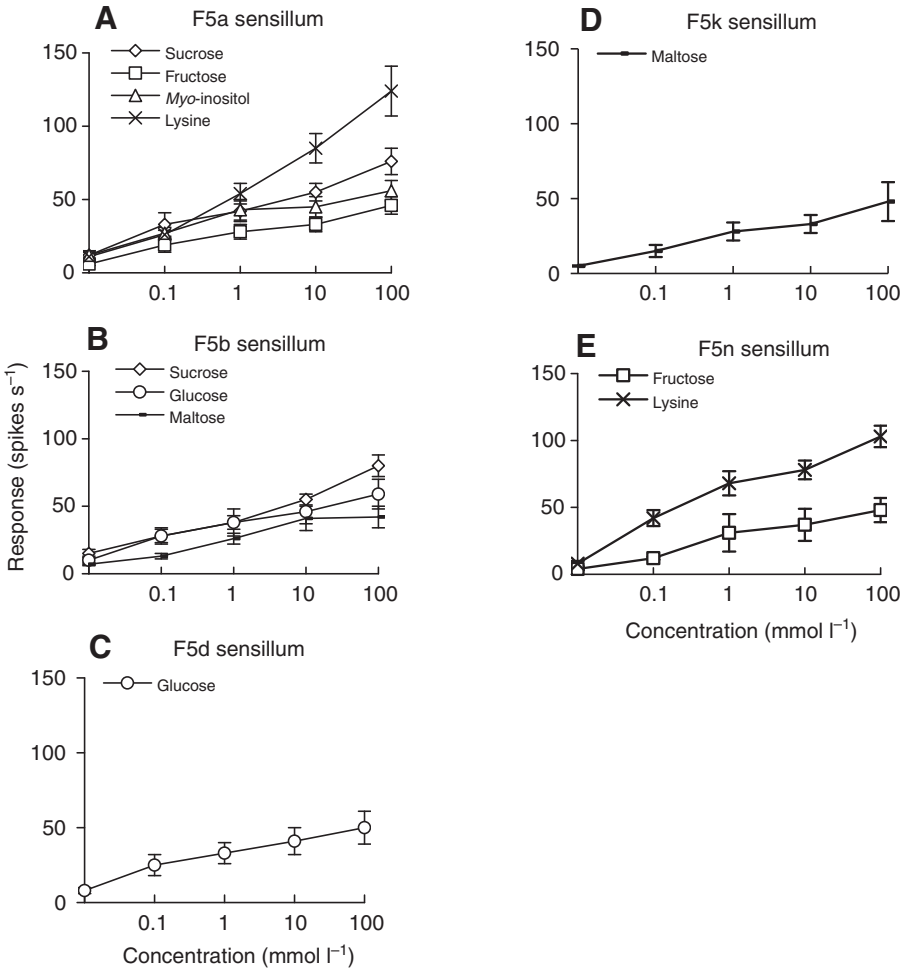

Fig. 2. Dose–response curves of electrophysiological activity in contact chemosensilla on the fifth tarsomere of adult female *H. armigera* in response to different compounds at four concentrations. The response curves of F5a, F5b, F5d, F5k and F5n are shown in A, B, C, D and E, respectively. N=10 for each data point. KCl at 0.01 mmol l^{-1} was used as the control. Errors bars represent s.e.m.

$P<0.01$). Duration of proboscis extension in response to sucrose was similar to that to fructose but significantly higher than that to maltose. Proboscis extension upon tarsal contact with maltose lasted significantly longer than upon contact with Lys. There were no significant differences between the effect of maltose, glucose and *myo*-inositol (paired samples *t*-test, $P>0.05$). All the sugar mixtures and the mixture of sucrose and Lys also triggered a PER (see supplementary material Fig. S5). The percentage of insects exhibiting PER in response to the mixture of four sugars was significantly lower than those for sucrose and fructose alone (one-way ANOVA, $P<0.05$). No significant differences were found between the effect of glucose, maltose and the mixture of four sugars (see Fig. S5A in supplementary material, one-way ANOVA, $P>0.05$). The duration of proboscis extension upon tarsal contact with the mixture of four sugars was significantly lower than that upon contact with sucrose solution (see supplementary material Fig. S5B; one-way ANOVA, $P<0.05$). Both the percentage of insects exhibiting PER and the duration of proboscis extension, were the same for the mixture of sucrose and Lys as for sucrose alone (see supplementary material Fig. S6; paired-samples *t*-test, $P>0.05$).

Relationship between the electrophysiological and behavioural responses

When adult females were stimulated with sucrose, fructose or maltose, both the percentage of insects exhibiting PER and duration of proboscis extension increased as the electrophysiological response intensity strengthened, however, this was not the case with glucose (Fig. 4A,B). The firing rate of the sucrose-sensitive receptor neuron and the duration of proboscis extension increased when the sucrose concentration was raised (Fig. 4C). This validated that the electrophysiological and behavioural responses to sucrose were positively correlated.

DISCUSSION

In lepidopteran insects, the tarsus is subdivided into five tarsomeres. The most distal part of the tarsus, the fifth tarsomere bears more contact chemosensilla than the four more proximal tarsomeres. It is most flexible and is the first to contact the landing surface. Our microscopy results demonstrated that there were 14 contact chemosensilla on each ventrolateral side of the fifth tarsomere of *H. armigera*, and the majority of them responded to sugars and amino acids, with response spectra ranging from broad to narrow. It seems that the proximal and distal chemosensilla such as F5a, F5b, F5k and F5n were more sensitive to the sugars and amino acids tested.

Electrophysiological response spectra of tarsal chemosensilla

There have been several earlier studies on electrophysiological responses of tarsal chemosensilla in moths. Ramaswamy (Ramaswamy, 1987) found that tarsal chemosensilla of *H. virescens* responded to sucrose, glucose and fructose. Similarly, Blaney and Simmonds (Blaney and Simmonds, 1990) reported that some tarsal chemosensilla in four noctuid species including *H. armigera* also

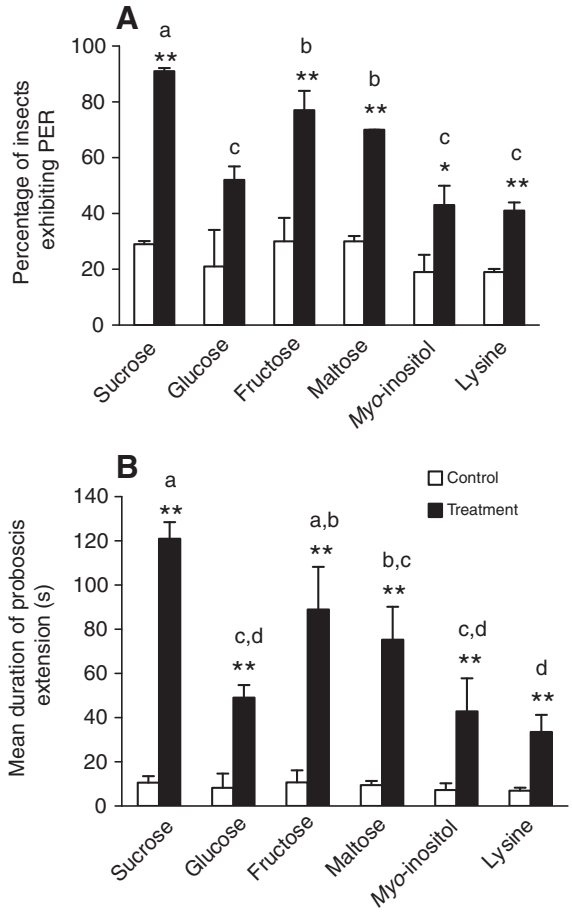

Fig. 3. Proboscis extension reflex (PER) in adult female *H. armigera* upon tarsal stimulation by 100 mmol l^{-1} solutions of sucrose, glucose, fructose, maltose, myo-inositol and lysine. (A) Percentage of insects exhibiting PER. (B) Mean duration of proboscis extension. In both A and B, bars having no letters in common differ significantly; *P<0.05; **P<0.01; The trial was repeated three times on three different batches of 30 moths; N=90 moths. Control solution was KCl 0.01 mmol l^{-1}. Errors bars represent s.e.m.

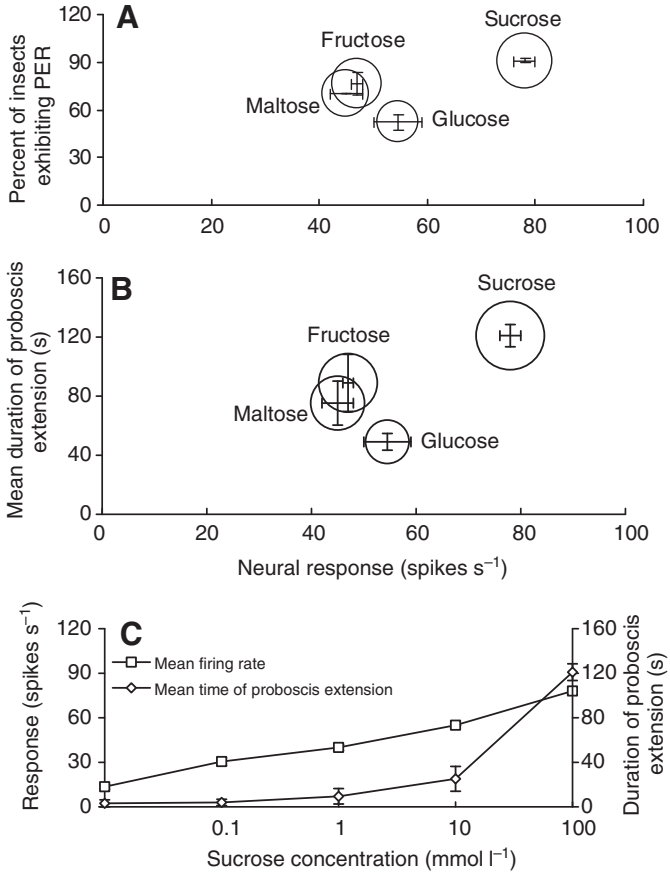

Fig. 4. Relationship between electrophysiological response and behavioural response in adult female *H. armigera* upon stimulation with sucrose, glucose, fructose and maltose. (A) Plot of electrophysiological response against percentage of individuals exhibiting a proboscis extension reflex (PER) upon stimulation with a 100 mmol l^{-1} solution of the individual sugars. (B) Plot of electrophysiological response against mean duration of proboscis extension upon stimulation with a 100 mmol l^{-1} solution of the individual sugars. (C) Plot of electrophysiological response against behavioural response (mean duration of proboscis extension on contacting sucrose solution) on stimulation with four concentrations of sucrose. Control solution was 0.01 mmol l^{-1} KCl. Errors bars represent s.e.m.

responded to these three sugars and the amino acids, Ala, Phe, Leu and Lys. A recent study by Calas et al. (Calas et al., 2009) showed that tarsal chemosensilla responded to sucrose, glucose, fructose and the amino acids, Ala and Ser. We studied the full set of chemosensilla on the fifth tarsomere of *H. armigera* stimulated with four sugars, one sugar alcohol and 20 amino acids, and we found that the response spectra of some tarsal chemosensilla were broad and that of others more narrow. Taste neurons in five out of the 14 sensilla were not excited by any of the 25 compounds tested. F5a and F5b responded to the four sugars, *myo*-inositol and seven amino acids, but responded most strongly to sucrose and Lys. It seems that the response spectrum of tarsal gustatory cells to sucrose, glucose and fructose is similar in different moth species, but that of the amino-acid-sensitive receptor neurons is diverse.

In the majority of insect gustatory sensilla studied, there are four contact-chemosensory neurons, one responds to sugars, one to inorganic salts, one to behaviourally deterrent compounds, and one to water or amino acids (Bernays and Chapman, 1994). In our work, besides the sugar- and amino-acid-sensitive cells, an inositol cell was identified in both F5a and F5b, which has also been reported for *Spodoptera littoralis* (Blaney and Simmonds, 1990). Moreover, considering that the four sugars excited the same receptor neurons in corresponding sensilla, it may be quite possible that different sugars interacted with different receptor proteins expressed by the respective cell. This interpretation is supported by Kusano and Sato (Kusano and Sato, 1980) who observed a relationship between sugar chemical structure and the sensitivity of the tarsal chemoreceptors in the butterfly *Pieris rapae crucivora* Boisduval.

The four sugars, *myo*-inositol and Lys induced concentration-dependent responses; however, the dose–response curves did not reach a plateau. This may be due to the fact that the highest concentration of the stimulants tested was below the saturating dose. The concentration of sugars and amino acids occurring in floral nectars varies substantially, with the total concentration of sugars varying from about 118 mg ml^{-1} to 723 mg ml^{-1} of nectar (in sucrose equivalents this corresponds to with 0.35–2.11 mol l^{-1}). The total concentrations of nectar amino acids varies from about 5.45 μg ml^{-1} nectar to 2693 μg ml^{-1} nectar, both of which are much lower and more variable than that of sugars (Gottsberger et al., 1984).

Stimulants inducing proboscis extension reflex followed by feeding

Although sucrose, fructose, maltose and glucose at 100 mmol l^{-1} all induced the PER and feeding behaviour in *H. armigera*, sucrose and fructose were the best stimulants of the four sugars. Moreover, a mixture of the four sugars had no stronger stimulatory effect than sucrose or fructose alone at equal concentrations. Concerning the stimulatory effect of sucrose and fructose, Blaney and Simmonds (Blaney and Simmonds, 1990) found that sucrose and fructose could trigger the PER in adult female *S. littoralis*, *S. frugiperda*, *H. armigera* and *H. virescens*. Romeis and Wäckers (Romeis and Wäckers, 2000) also indicated that in *Pieris brassicae* L. (Lepidoptera: Pieridae), of the ten sugars tested only sucrose and fructose elicited a feeding response. These findings point to the importance of sucrose and fructose in triggering feeding behaviour of lepidopteran adults. However, stimulation of tarsal sensilla in *Papilio xuthus* (Lepidoptera: Papilionidae) with sucrose (as high as 1000 mmol l^{-1}) did not trigger food-sucking behaviour although some tarsal trichoid sensilla were sucrose-sensitive (Inoue et al., 2008).

In previous studies of *H. virescens*, sucrose at 1000 mmol l^{-1} induced 100% PER when the tarsi or antennae were stimulated (Jorgensen et al., 2006; Ramaswamy, 1987). In our study, the percentage of insects exhibiting PER in response to sucrose at 100 mmol l^{-1} was about 91%. It is probable that sucrose acts as a general phagostimulant in lepidopteran species. Moreover, we found that sucrose had a higher stimulatory effect than fructose, followed by maltose and glucose, similar to the findings for the cabbage butterfly, *Pieris rapae crucivora* (Kusano, 1963). We also found that Lys had a relatively weak stimulatory effect on the PER when compared with sugars. Different stimulatory effects of sugars and amino acids might result from varied gustatory sensitivity to individual nectar sugars and amino acids in different Lepidoptera, as suggested by Romeis and Wäckers (Romeis and Wäckers, 2000). Differences in nutritive quality of the sugars and amino acids may lead to different stimulatory effects.

Relationship between electrophysiological and behavioural responses

We confirmed that firing rates of tarsal receptor taste neurons and the PER of *H. armigera* to sucrose, fructose and maltose were positively correlated. Sucrose produced the highest firing rate and the strongest behavioural response. Furthermore, the electrophysiological and behavioural responses of *H. armigera* to a series of sucrose concentrations were positively correlated, and we expect such a correlation to exist also for glucose, fructose and maltose. Feeding behaviour of the moth can thus be predicted from electrophysiological responses to sugars.

Of the compounds tested apart from the sugars, Lys evoked the strongest electrophysiological response, but excited a different receptor neuron and had a weak stimulatory effect on the PER in *H. armigera*. We also found that mixtures of sucrose and Lys had no synergistic effect on the PER. Possibly, Lys and other amino acids have different functions, such as stimulating oviposition, which has been reported in some other insects (Mevi-Schütz and Erhardt, 2005; Thompson, 2006). Moreover, a crucial role for assessing amino acids before oviposition has been reported (Wäckers et al., 2007). It is also possible that certain amino acids may modulate the input of sugars and provide the moth with the potential to select nutritionally more appropriate plants (Robbins et al., 1965; Wolbarsht and Hanson, 1967).

In conclusion, on the fifth tarsomere of adult female *H. armigera*, there are chemosensilla electrophysiologically sensitive to sucrose, glucose, fructose, maltose, *myo*-inositol and seven out of the 20 common amino acids. Their response spectra range from broad to narrow. The four sugars, *myo*-inositol and Lys have a stimulatory effect on feeding. The feeding behaviour of the adult females is correlated with the electrophysiological responses of tarsal chemosensilla to sugars. Some amino acids such as Lys induce strong electrophysiological responses by activating a taste receptor neuron different from the sugar receptor neuron in the tarsal chemosensilla, but are weak feeding stimulants. The role of amino acids in food and host-plant selection of adult *H. armigera* deserves further study.

ACKNOWLEDGEMENTS

We thank Ling-Qiao Huang for assistance in preparing the experiments, Yun-Hua Yan in rearing the moths, Yan-Bao Tian in scanning electron photomicrography, Zhi-Yuan Yao and Li-Hong Dang in drawing the tarsal sketch. This work was supported by the National Basic Research Program of China (grant no. 2006CB102006) and the National Natural Science Foundation of China (grant no. 30925026, 30621003) and Public Welfare Project from the Ministry of Agriculture, China (grant no. 200803006).

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