J Comp Physiol A (1998) 183: 737–744

ORIGINAL PAPER

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Tactile learning in the honeybee

Accepted: 17 September 1998

Abstract Free-flying bees were conditioned on a vertical wall to a vertical tactile pattern consisting of parallel lines of grooves and elevations. The asymptote of the learning curve is reached after approximately 25 rewards. Bees can discriminate the conditioned vertical pattern from a horizontal or diagonal alternative. Angle discrimination is apparent only for relatively coarse tactile cues. The proboscis extension response of fixed bees was used to condition bees to a vertical tactile pattern which was presented to the antennae. The learning curve reaches an asymptote after 4 rewards. After 7 unrewarded extinction trials the conditioned responses are reduced to 50%. Bees show best discrimination for patterns whose edges they can scan with their antennae. The animals show a high degree of generalization by responding to an object irrespective of the trained pattern. Under laboratory conditions fixed bees can discriminate the angles and spatial wavelengths of fine tactile patterns consisting of parallel grooves. Bees can also discriminate forms and sizes of tactile patterns. They do not discriminate between different types of edges and between positive and negative forms.

Key words Insect · Honeybee · Learning · Tactile · Antenna

Introduction

During foraging honeybees can rapidly learn odours, colours, visual shapes and landmarks. For many decades the learning capacity of bees has been used to analyse the processing of sensory information by this insect (for a recent review see Menzel and Müller 1996). Learning experiments under laboratory conditions have been targeted mainly at analysing the discrimination of odours (Vareschi and Kaissling 1970) and the neural processes involved in olfactory learning and memory formation (Erber et al. 1980; Erber 1981; Menzel et al. 1994). In these experiments classical conditioning of the proboscis extension reaction (PER) was used. An odour, the conditioned stimulus, is presented to the bee, then the antennae are stimulated with sucrose solution which elicits the PER. This reflex response is then quickly reinforced by feeding the bee with a drop of sucrose solution. After one to three pairings the animals respond to the presentation of the conditioned odour alone with proboscis extension (for an animation of olfactory conditioning see Erber 1997). This conditioning paradigm has been used successfully for many years to analyse the physiological mechanisms underlying olfactory learning (Hammer 1997).

Although the learning of olfactory and visual signals has been analysed in great detail, there is only very limited knowledge about tactile learning in the bee. Martin (1965) was able to train bees to discriminate between different gratings and holes. For his experiments he used a relatively large maze in which each alternative arm had a length of 10 cm. Experiments on compound conditioning using tactile and olfactory cues demonstrated that bees strongly prefer the olfactory cues when they are confronted with a choice situation between odour and large-scale tactile stimuli (Martin 1965). Tactile stimuli are of importance for bees during all life stages from the larva to the adult bee (Kevan 1987). Foraging bees can learn to associate relatively coarse tactile cues with a reward (Mühlen 1987). Fine-scale textural discrimination was demonstrated convincingly by Kevan and Lane (1985) who used flower petals for training free-flying bees in a small Y-maze and tethered bees in the laboratory. These experiments suggested for the first time that bees might use fine-scale textural tactile information to identify nectar sources.

Recently, it was shown in laboratory experiments that bees display tactile motor learning with the antennae

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(Erber et al. 1997). In these experiments the animals scanned an object within reach of their antennae for several minutes. After removing the object, antennal movements were directed at the location where the object had been positioned before. Bees can also be conditioned to associate an object within the reach of the antennae with a reward and they can distinguish between objects presented to the right or left antenna (Erber et al. 1997). Bees can learn to asscociate a tactile cue with a reward in three to four trials, unrewarded motor learning takes much longer, usually about 10–30 min.

The acquisition of tactile information with the antennae is a complex process involving active movements of the antennae (Martin and Lindauer 1966; Erber et al. 1993) and many different types of mechanoreceptors on the antennae (Esslen and Kaissling 1976; Eichmüller and Schäfer 1995). The antennal motorsystem which controls the acquisition of tactile information consists of six different muscles (Snodgrass 1956). Two of them are located in the scape and enable movements of the pedicellus and flagellum. Four other muscles within the head capsule enable rotatory movements of the scape. The six muscles are innervated by 15 motoneurons which have their dendritic projections in the dorsal lobe of the deutocerebrum where they overlap with projections of mechanoreceptors from the ipsilateral antenna (Maronde 1991; Kloppenburg 1995).

Bees can be conditioned to distinguish between the fine textural patterns of flower petals (Kevan and Lane 1985). These findings together with those on tactile motor learning and tactile conditioning (Erber et al. 1997) suggest that bees have tactile spatial memory. The tactile parameters which bees use during learning and discrimination are unknown. Using tactile conditioning, we analysed some basic parameters of tactile discrimination, like the orientation and wavelength of a regular pattern, the form, the size and other features of objects.

Material and methods

Conditioning of free flying bees

The test apparatus was a white cube with side lengths of 80 cm which was placed on a turntable under a roof approximately 100 m away from the hive. Conditioning and testing of a single bee was performed by using the four vertical walls of the cube. Two opposite walls were used for conditioning and the two other walls for testing in order to keep the patterns on the test-walls free from scent marks (schematic drawing Fig. 1A). The tactile cues were fixed on discs with a diameter of 5 cm. Two discs which were 40 cm apart and which had alternative tactile cues were offered to the bees during conditioning and testing. In most experiments computer band cable consisting of parallel insulated cores was used as the tactile cue. The tactile pattern had a spatial wavelength of 1.2 mm with grooves which were 0.375 mm deep and 0.3 mm wide. The cable was painted black to reduce visual contrast of the pattern. The bees could land on these discs and enter a small tube with an inner diameter of 6 mm and a length of 16 mm in the centre of the disc. The angle of the tactile cues could be changed by turning the discs. By turning the cube on the turntable either a conditioning wall or a test wall could be offered to the bee.

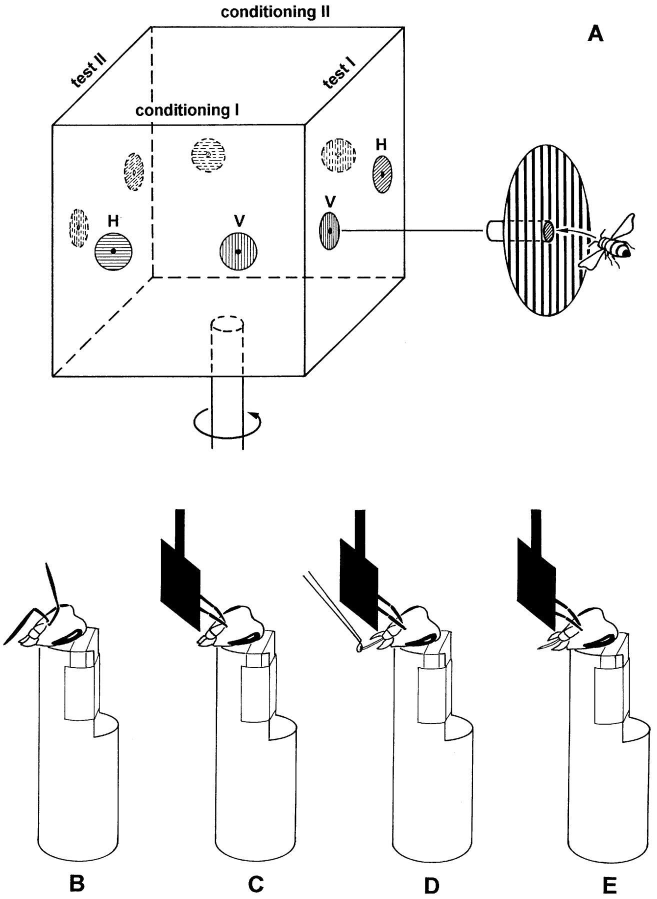

Fig. 1A–E Conditioning and testing of free-flying bees and bees under laboratory conditions. **A** Schematic drawing of the test cube (80 cm × 80 cm × 80 cm) used for conditioning and testing of free-flying bees. Two of the four walls were used for conditioning and the other two walls for testing. On each wall a vertical and a horizontal pattern was offered to the bee. The bees could enter small tubes in the centre of the discs. The animals were conditioned to the vertical pattern. The two conditioning walls were changed in random order between conditioning trials. The bees were tested using the two testing walls which were changed every minute (for further details see text). **B–E** Schematic drawing of conditioning and testing in the laboratory using the proboscis extension reflex: **B** the bee was fixed in a tube; **C** during conditioning the bee first scanned the tactile pattern with both antennae for approximately 3 s; **D** after scanning the pattern for 3 s proboscis extension was elicited by touching the antennae with 30% sucrose solution. Proboscis extension was rewarded with a small drop of sucrose solution; **E** 5 min after a conditioning trial the bee was tested by presenting the tactile pattern. Proboscis extension was recorded as a positive conditioned response

The experiments were performed with single, individually marked bees. A feeder near the apparatus was used to feed a foraging group of bees. A newly recruited bee was marked and trained to find food on the test wall in the centre of a black disc which had no tactile cues. The foraging group was meanwhile caught and kept in a box. After three visits to the apparatus the spontaneous choice behaviour of the bee was tested by presenting it with a vertical and a horizontal tactile pattern on one of the test walls (Fig. 1A, test I and II). The number of approaches toward the discs, the number of landings and the duration of stay on the discs were recorded. In a series of pilot experiments we found that the duration of stay on the two discs is an unambigous and reliable measure of the behavioural changes ocurring during learning. Although the approaches and the landings were recorded in all experiments, we present only the duration of stay on the alternatives in this paper.

After 1 min the whole cube was turned by 180°. The bee could now approach the other test wall (Fig. 1A, test I or II) on which the location of the vertical and horizontal pattern was reversed. If, for example, the vertical pattern during the 1st min was presented on the left side, it was presented during the 2nd min on the right side. (see Fig. 1A). The test of spontaneous choice preference lasted for 4 min. The cube was turned every minute by 180°; consequently, the location of the patterns changed every minute.

In the experiments we varied a number of tactile parameters, like the spatial frequency of the grooves, the depth of grooves, the height of elevations in the pattern and the colour of the tactile pattern. In order to compare the behavioural effects of these different tactile parameters with each other, the bees were always conditioned to the vertical pattern. The bees first had to land on the vertical pattern, walk to the tube in the centre and enter it. The animals were rewarded inside the tube with a small drop of 30% sucrose solution. The other disc was oriented horizontally, no sucrose was placed in the tube of this alternative. During conditioning the rewarded alternative was placed either right or left by changing between the two reward walls in random order. The bee returned to the hive and was rewarded again after returning to the training apparatus.

In a first series of experiments the learning curve of the bees for vertical tactile cues was measured. The choice behaviour of each bee was tested after 5, 10, 15, 20, and 25 rewards by presenting a vertical and a horizontal disc for 4 min in the same way as described for spontaneous choice behaviour. In a second series of experiments bees were conditioned 25 times to the vertical pattern. Their choice behaviour for the vertical and horizontal pattern was measured after 25 rewards. They were then tested using different tactile and visual alternatives in random order. Between the different tests the bees were rewarded on the vertical pattern. In one test series the vertical pattern was presented against an alternative disc which was oriented diagonally (45°). In a second test series the two alternatives were horizontal and 45°. In the third series the vertical and horizontal discs were covered with transparent adhesive film which eliminated the tactile cues. In the last series of tests two horizontally and vertically striped visual patterns without tactile cues were presented. The patterns had the same spatial frequency as the tactile cues but they had higher visual contrast due to the black and white pattern.

To avoid olfactory cues due to scent marking of the bees, the patterns used for conditioning and testing were cleaned regularly by immersing them in 70% ethanol for several minutes. The patterns used for conditioning were never used for testing the animals.

Conditioning in the laboratory

Pollen- and nectar-collecting bees differ in their learning behaviour for tactile cues (Erber et al. 1998). To reduce this behavioural variance, we used only pollen-collecting bees. The animals were caught by blocking the entrance of the hive with mesh wire. The animals were put in small glass vials and were cooled in the refrigerator until they were immobile. They were then mounted in small metal tubes by fixing them with adhesive tape between head and thorax (Fig. 1B). They were fed a small drop of 30% sucrose. The eyes of the animals were covered with black acrylic paint. The animals were used for the experiments approximately 1 h after mounting.

At the beginning of the experiment the PER to a 30% sucrose stimulus applied to the antennae was tested. Bees which showed this unconditioned response were kept for the following experiments. The patterns or forms which were later used during conditioning or testing were then presented, using a micromanipulator, in random order ventrally to the bees (Fig. 1C). The animals could scan the object with both antennae and spontaneous extension of the proboscis onto the different objects was recorded. Animals which responded with proboscis extension before conditioning to any of the tested patterns or forms were discarded.

First, the conditioned pattern was presented to the bee. After the animal had scanned the pattern intensively with the antennae for approximately 3 s, a drop of 30% sucrose was presented to the antennae which elicited proboscis extension. The bee was then rewarded by offering the sucrose drop for 1–2 s to the proboscis (Fig. 1D). After an intertrial interval of 5 min the bee was conditioned again. The pattern was first presented to the antennae, then conditioned proboscis extension was recorded when it occurred (Fig. 1E), and finally the animal was rewarded again with a small drop of sucrose. In animals which did not show proboscis extension during presentation of the pattern, the antennae were stimulated again with sucrose and proboscis extension in response to the sucrose stimulus was rewarded with a small drop. Bees were conditioned ten times. The responses recorded during conditioning were used to calculate a learning curve. The conditioned object was cleaned after each conditioning trial by immersing it in 70% ethanol and drying it with a cellulose cloth.

After ten conditioning trials different test patterns were presented to the bee in random order. The test patterns, including those with the conditioned pattern were never used during conditioning. To remove possible scent marks, all patterns were cleaned in ethanol before the tests. The animals were conditioned once again between the consecutive tests.

For most laboratory experiments we used small copper plates which were manufactured by a professional engraver. The engraved parallel lines had widths between 150 and 300 μm and depths between 35 and 60 μm (the exact details are presented with the specific experiment). The pattern wavelengths varied in some experiments between 280 μm and 980 μm (the exact details are presented with the specific experiment). In one experiment we used a pattern produced with a copying machine. In this case the pattern was a computer printout which was copied onto transparent film. The black bars of this pattern had a maximum elevation of 23 μm. Different forms were manufactured by using polished copper plates, in one case a form was made from wire with a diameter of 400 μm (the exact details are presented with the specific experiment).

Results

Conditioning of free-flying bees

In a first series of experiments we tested the tactile cues which were used by Mühlen (1987) for conditioning bees in a walking maze. The two discs were covered with abrasive paper of different grain size (conditioned to grain 80, tested against grain 180). We confirmed the results of Mühlen (1987). Free-flying bees can also distinguish tactile cues of different grain size. The duration of stay on the rewarded pattern differed significantly from the alternative after five conditionings ($P < 0.05$, one-tailed t-test). In a second experimental series we used engraved metal discs as tactile patterns. These patterns were similar to those used in the following laboratory experiments. They consisted of parallel grooves which were approximately 170 μm wide and 40 μm deep, the patterns had a spatial wavelength of 500 μm. To avoid visual cues, the discs were coloured dark by treatment in a pickling bath. The bees were conditioned to a vertical pattern and tested against a horizontal pattern. The animals did not show significant learning during 25 conditioning trials with these tactile cues. After these experiments we decided to use a relatively coarse pattern made from computer band cable.

The learning curve for a group of bees conditioned to a vertical pattern and tested against a horizontal pattern is shown in Fig. 2A. In the tests after ten or more rewards the animals spend significantly more time on the vertical pattern compared to the horizontal pattern. For the vertical pattern the duration of stay was significantly different from the spontaneous behaviour for all tests after the fifth reward ($P < 0.01$; one-tailed t-test). No significant changes of behaviour in the course of conditioning were found for the unrewarded horizontal pattern ($P > 0.05$; one-tailed t-test).

The choice behaviour of bees for different patterns was tested in a separate group conditioned with 25 rewards to the vertical tactile pattern (Fig. 2B). The animals discriminated the rewarded vertical pattern from a horizontal or diagonal pattern. Animals which had been rewarded on the vertical pattern did not show a preference for the diagonal pattern against a horizontal pattern. The animals also did not discriminate vertical from horizontal when the tactile pattern was covered with a transparent film or when a visual black and white pattern with the same spatial frequency was presented vertically and horizontally. We conclude from these experiments that free-flying bees can learn to discriminate relatively coarse tactile patterns which differ in the angle of orientation.

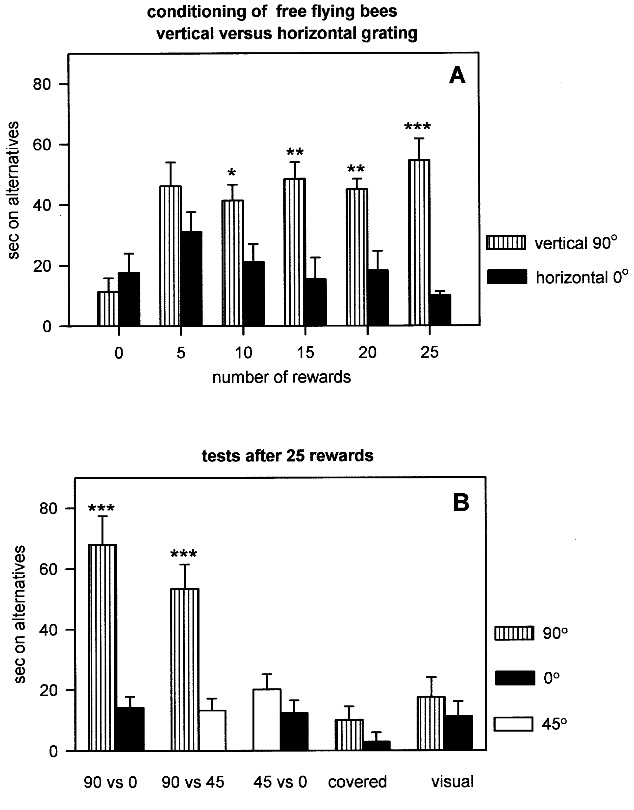

Fig. 2A, B Conditioning of free-flying bees to a vertical tactile pattern. **A** The learning curve for 25 conditioning trials to a vertical pattern. The duration of stay of the animals on the rewarded vertical pattern and on an alternative horizontal pattern was tested before (0) and after different numbers of conditioning trials. The graphs show means and SEM (standard error of the mean). The *stars* indicate significant differences between the durations on the vertical and horizontal discs ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; one-tailed t-test). Abscissa: learning trials; ordinate: time on the discs during the 4 min of test; eight bees were tested. **B** The choice behaviour of bees after 25 conditioning trials on a vertical pattern. All symbols as in **A.** *90 vs 0* vertical pattern tested against a horizontal pattern; *90 vs 45* vertical pattern tested against a diagonal pattern; *45 vs 0* diagonal pattern tested against a horizontal pattern; *covered* vertical and horizontal pattern covered with a transparent film which eliminates the tactile cues; *visual* visual vertical and horizontal black and white pattern with the same spatial wavelength as the tactile pattern; ten bees were tested

Conditioning of fixed bees in the laboratory

General characteristics

A honeybee that is fixed in a small tube can be conditioned to respond with proboscis extension to a small plate with a vertical tactile pattern. Mean learning and extinction curves are shown in Fig. 3A. After the first reward the number of conditioned responses to the tactile cue is significantly different from spontaneous choice ($P < 0.001$; Fisher exact probability test). The learning curve shows saturation after four rewards. The asymptote of the learning curve is dependent on the properties of the conditioned object and on the time of the year. The highest conditioned response probabilities were found in autumn and the lowest in late winter when the animals were kept in a flight room. The dependence of the learning asymptote on the properties of the conditioned pattern will be discussed below. After ten rewards the bees were tested consecutively without further reward. The extinction curve (Fig. 3A) demonstrates that the conditioned responses decline. After seven unrewarded tests the responses are reduced to approximately 50% of the asymptote after ten rewards.

Bees conditioned to a small vertical pattern discriminate this cue from a horizontal pattern and a smooth plate (Fig. 3B). The size of the pattern and the depth of the grooves in the pattern have an influence on the asymptote of the learning curve. The animals learn a pattern best when they are able to scan also the edges of the pattern with their antennae. A small plate of 4 mm × 3 mm leads to significantly better conditioned responses than a larger plate of 10 mm × 10 mm (Fig. 3B). A tactile pattern with grooves that are 35–60 μm deep is learned significantly better than is a pattern printed on a transparent film and with regular elevations of 23 μm (Fig. 3B). Also the discrimination between vertical and horizontal is dependent on the size and the type of the pattern. The experiments in Fig. 3B demonstrate that the animals show some generalization to the different patterns by responding after conditioning also to the unrewarded alternatives.

Discrimination of angles and spatial wavelengths

Bees were first conditioned with ten rewards to a vertical pattern. The proboscis responses to the conditioned

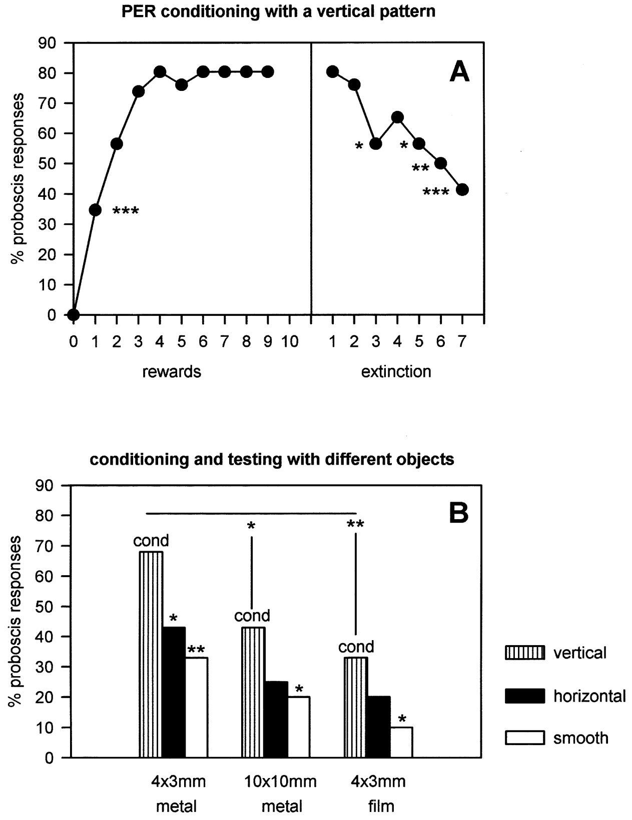

Fig. 3A, B Conditioning to a vertical pattern and testing of bees using the proboscis extension reflex. **A** The learning and extinction curves for 46 pollen foraging bees conditioned to a vertical pattern. On the *left side* the percentage of proboscis extensions (ordinate) is shown over the number of rewards. Before each reward the pattern was presented to the bee and proboscis extension was recorded (see Fig. 1E). On the *right side* the extinction of the conditioned response over seven consecutive tests without reward is shown. The *stars* in the left panel indicate significant differences of the conditioned proboscis response compared to spontaneous behaviour. The *stars* in the right panel indicate significant differences between the first and consecutive extinction trials ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$; one-tailed Fischer exact probability test). **B** Conditioning and testing using different tactile patterns. *4 × 3 mm metal* 40 bees were conditioned ten times using a 4 mm × 3 mm plate with vertical parallel grooves, the wavelength of the pattern was 600 µm, the grooves were 300 µm wide and 35–60 µm deep. The horizontal pattern had the same spatial parameters, the smooth pattern was a polished plate. *10 × 10 mm metal* 40 bees were conditioned ten times using a 10 mm × 10 mm plate with a pattern identical to that of the 4 mm × 3 mm plate. *4 × 3 mm film* 40 bees were conditioned ten times using a 4 mm × 3 mm plate with a regular vertical black and white pattern printed with a copying machine onto transparent film. The pattern had a spatial wavelength of 510 µm, the black lines were 250 µm wide and had an elevation of 23 µm. The horizontal pattern had the same spatial parameters, the smooth pattern was the plain transparent film. The *stars above the columns* indicate significant response differences between the conditioned pattern and the alternative patterns; *the stars at the top of the drawing* indicate significant differences between the conditioned 4 mm × 3 mm vertical metal pattern and the other conditioned patterns ($*P < 0.05$; $**P < 0.01$; one-tailed Fisher exact probability test)

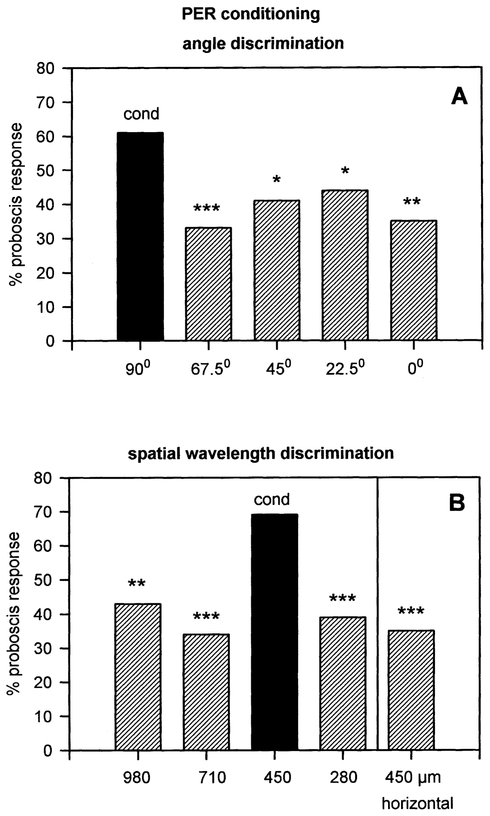

Fig. 4A, B Angle and spatial wavelength discrimination in bees conditioned using the proboscis extension reflex. In each experiment (**A, B**) 80 bees were conditioned ten times using a 4 mm × 3 mm plate with an engraved vertical pattern which had a spatial wavelength of 450 µm, the parallel grooves were 150–190 µm wide and 30–40 µm deep. The *stars* indicate significant response differences between the conditioned pattern and the tested alternatives ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$ one-tailed Fisher exact probability test). **A** Testing of different angles of the pattern after conditioning to the vertical pattern. All the patterns had identical spatial parameters, the tilted patterns were engraved, as the conditioned pattern, on a 4 mm × 3 mm plate. **B** Testing different spatial patterns and a horizontal pattern after conditioning to a vertical pattern. The wavelengths of the patterns are indicated. The grooves in the patterns had the same width and depth as the conditioned pattern. For comparison a horizontal pattern with spatial parameters identical to the conditioned pattern was also tested

pattern and other patterns which differed in angle were tested in random order. Figure 4A shows that the animals discriminated between the conditioned vertical pattern and patterns that are tilted by 22.5° or more.

Bees could also discriminate different spatial wavelengths of the tactile pattern (Fig. 4B). Discrimination of different wavelengths is similar to the discrimination between a vertical and a horizontal pattern. Both experimental series shown in Fig. 4 demonstrate that the animals also respond to the unrewarded alternatives. These generalizing responses amount to approximately 50% of the reactions to the conditioned pattern.

Discrimination of forms and size

Bees were conditioned ten times to a filled triangular form with a smooth surface. It was the objective of these experiments to test whether bees can discriminate between different forms. Figure 5A shows that the animals

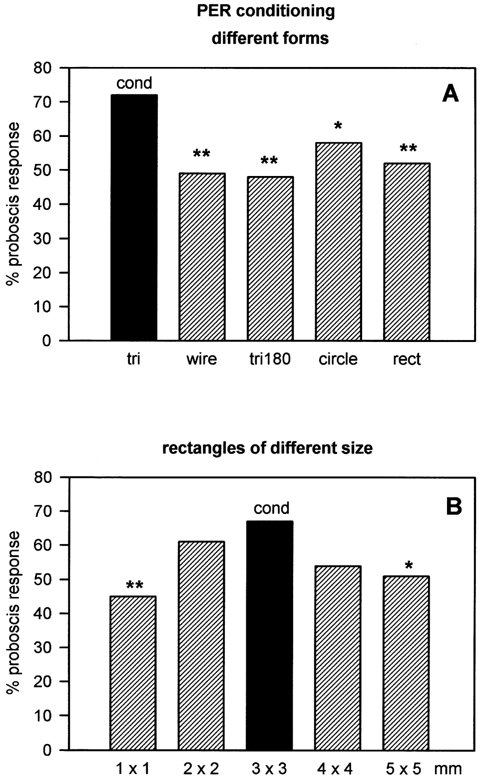

Fig. 5A, B Form and size discrimination in bees conditioned using the proboscis extension reflex. The *stars* indicate significant differences between the conditioned pattern and the tested alternatives, all symbols as in Fig. 4. **A** Discrimination of different forms. 85 bees were conditioned ten times to a smooth equilateral metal triangle with 2 mm side length, the triangle pointed upward. *wire* an equilateral triangle made of 400-μm wire with a side length of 3 mm; *tri 180* a smooth equilateral metal triangle with 2 mm side lengths pointing downward (turned by 180°); *circle* a smooth metal circle with a diameter of 3 mm; *rect* a smooth metal 5 mm × 3 mm rectangle (width × height). **B** Discrimination of squares with different sizes. 69 bees were conditioned ten times to a smooth square of 3 mm × 3 mm. Squares with the indicated sizes were tested

discriminated the conditioned triangle from an open triangle made of wire, from an inverted filled triangle, from a circle and from a larger rectangle.

In another series of experiments bees were conditioned to a square of 3 mm × 3 mm and tested after ten rewards with squares that were larger or smaller. The results of these experiments show that they can discriminate the conditioned form from squares which are considerably larger or smaller (Fig. 5B).

Discrimination of edges, positive and negative forms

The previous experiments have shown that bees can discriminate between different sizes and forms. In the following experiments it was tested whether or not the animals can discriminate between different types of edges. Bees were conditioned ten times to an equilateral triangle with side lengths of 4 mm. The triangle had a smooth surface and three grooves on each of the three sides. Each groove was 300 μm wide and 300–500 μm deep. The animals were then tested by presenting them a triangle without grooves along the edges and a triangle with five grooves on each of the sides. They did not discriminate the conditioned form from the other two triangles ($P > 0.5$; one-sided Fisher exact probability test, 66 animals tested).

In another series of experiments 32 animals were conditioned to an equilateral triangle with side lengths of 4 mm. The triangle had a smooth surface (positive form). After ten conditionings this conditioned form and an alternative triangular form were tested. The alternative was a triangle which had the same size but was cut out from a 8 mm × 8 mm plate whose edges the bees could not scan with their antennae (negative form). Another group of 35 bees was conditioned to the negative form and was tested using the positive form. Both experiments demonstrated that the animals did not show significant differences of their proboscis responses between the conditioned and the alternative form ($P > 0.5$; one-sided Fisher exact probability test, for the two experiments combined with 67 animals).

Discussion

Honeybees can learn tactile cues very rapidly and they can discriminate between the tactile characteristics of surfaces. The velocity of tactile learning and the accuracy of discrimination is higher under laboratory conditions than with free-flying bees. Free-flying bees need about 15 learning trials to reach an asymptote of the learning curve, demonstrating that under free-flying conditions tactile learning is slower than olfactory or colour learning and faster than visual form learning (for a review see Menzel and Müller 1996). In the laboratory the characteristics of acquisition and extinction during tactile learning are very similar to odour learning under these conditions (Menzel and Müller 1996). The discrepancies between free-flying and fixed bees are probably explained by the different modes of acquisition of tactile information. Free-flying bees use their antennae and tarsal mechanoreceptors, they land and walk on the patterns which are presented on a vertical wall. They have to associate the orientation of the pattern with the gravity vector. On the other hand, bees in the laboratory have their eyes covered, the patterns are presented always in the same spatial location and they scan the patterns only with the antennae. Under these conditions other sensory cues which can interfere with tactile learning (Martin 1965) are excluded. The fine tactile discrimination of bees found under laboratory conditions by Kevan and Lane (1985) is probably due to the reduction of other sensory inputs which could interfere with tactile signals.

Bees can distinguish different angles of orientation of a tactile pattern. Under laboratory conditions the animals clearly discriminate a pattern that is tilted by 22.5° against the conditioned vertical pattern. The minimum angle of discrimination has not yet been determined for tactile patterns, but our results demonstrate that the performance of tactile angle discrimination is similar to visual angle discrimination of free flying bees (Wehner 1967, 1981; Srinivasan 1994). Also, the discrimination of different tactile wavelengths in the laboratory is remarkable. The animals can significantly discriminate a trained wavelength λ from alternatives whose wavelengths are approximately λ/2 smaller or greater. Similarly, in experiments with free-flying bees significant visual discrimination of regular radial patterns was found for patterns which differed by λ/2 (Wehner 1981).

Under laboratory conditions, objects whose edges can be scanned with the antennae are learned and discriminated better than larger objects (Fig. 3B). From the experiments with tactile motor learning we know that edges and surfaces induce different forms of behavioural plasticity in the bees (Erber et al. 1997). In these earlier experiments the animals displayed a preference for the surface and avoidance of the edges after scanning an object for 30 min. A similar two-stage process could be involved in the experiments presented here. We hypothesize that the animals learn two features of a conditioned object: (1) its presence which is signalled by antennal contacts with the edges, and (2) its surface characteristics which are signalled by scanning movements over the object. During the unrewarded tests the animals respond to both features. The mere presence of an object with edges elicits a high rate of responses and thus results in a high degree of generalization. The level of generalization is in the range of 50% for different surface textures and it is approximately 60% for objects which have different forms and identical surfaces. The hypothesis of a two-stage learning process is supported by the finding that larger objects with no detectable edges are not learned as well as smaller objects with edges (Fig. 3B).

Compared to the discrimination of surfaces, the discrimination of different forms or sizes is not very impressive (Fig. 5). We tested size and form differences which were great compared to the dimensions of the antennae, and the resulting behavioural differences were relatively small compared to those for different surfaces. As free-flying bees clearly can discriminate positive and negative visual forms (see Ronacher and Duft 1996), we also expected that bees were able to discriminate negative from positive tactile forms. We also expected that the bees should be able to discriminate equal forms which differ in the contours (grooves) of the edges, a feature that can be discriminated by bees for many visual patterns (for a summary and discussion see Wehner 1981). In both cases our hypotheses proved to be wrong.

We conclude from these findings that tactile discrimination is only partially comparable with the performance of the bees in the visual domain. There are two possible explanations for these discrepancies. Information processing and storage of visual and tactile information might be based on two entirely different mechanisms. Most of our models on pattern recognition were derived from experiments in the visual domain, therefore these models could be inadequate to explain tactile discrimination. At the present time we do not have enough experimental information on tactile discrimination to develop a model for this modality. On the other hand, the differences between visual and tactile discrimination might have been caused by the different experimental approaches for visual and tactile learning. Information is acquired sequentially during tactile learning by scanning an object, but during most visual learning tests the animals can use a large part of the visual field thus enabling parallel signal processing. In experiments with human beings many similarities have been found between tactile and visual recognition when the field of view of the subjects was restricted (Loomis et al. 1991). It remains to be tested if similar correlations between tactile and visual recognition can be found in bees with restricted fields of view. Further experiments in bees are needed to show whether common rules for visual and tactile recognition can be developed and if models which have been developed for visual pattern recognition in insects can be also applied to tactile discrimination (for a recent review see Heisenberg 1995).

Surfaces and edges of an object within the reach of the antennae are scanned by active antennal movements. Edges are touched frequently (ca. 80 contacts/min) with various parts of the flagellum, while surfaces are touched and scanned with the antennal tip (ca. 55 contacts/min; Erber et al. 1997). There is experimental evidence that the sensory plates on the antennal tips are used for identifiying surface structures (Martin and Lindauer 1966; Kevan and Lane 1985). Similarly, in free-flying bees visual patterns are scanned by active movements of the whole animal (for a recent review see Lehrer 1994). It has to be tested if tactile scanning is comparable to visual pattern scanning and if similar strategies are applied in the two modalities.

The contribution of different mechanoreceptive sensilla on the flagellum and of mechanoreceptors in the different antennal segments for tactile pattern discrimination is not clear at the moment. There exist a number of hypotheses on the role of the sensilla on the antennal tip for surface discrimination (Martin and Lindauer 1966; Kevan 1987). These hypotheses can now be tested using the tactile learning paradigm. From preliminary experiments we know already that the discrimination of tactile surfaces is abolished when the antennal tip is covered with paint (S. Schnitt and J. Erber, personal observation). It will be interesting to find if specific mechanoreceptors are used for specific tasks during tactile discrimination. The preparation also offers the possibility to distinguish between active and passive touch by using experiments similar to those on human beings (Vega-Bermudez et al. 1991). In the experiments with human subjects no difference was found between stimulus patterns which were actively touched and those which were moved relative to the finger tips. Experiments using passive touch in the bee might also help to elucidate the neural code used by the nervous system of the bee to signal different surfaces and to compare the results with the hypotheses developed for human subjects (Goodwin 1993). The tactile learning preparation offers a number of new possibilities to analyse not only the processing of information but also to compare the mechanisms of learning and memory for tactile cues with those for other sensory stimuli in the bee.

Acknowledgements This study was supported by the DFG (Sonderforschungsbereich 515). We wish to thank Prof. Robert Page for valuable suggestions concerning the manuscript. The experiments with positive and negative forms and the experiments with different edges were developed after a discussion with Dr. Martin Giurfa on visual discrimination. The drawings in Fig. 1 were kindly produced by W. Roloff.

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