Discrimination of closed shapes by two species of bee, *Apis mellifera* and *Megachile rotundata*

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Summary

In the present study, the performance of two bee species, the honeybee *Apis mellifera* and the leaf-cutter bee *Megachile rotundata*, in discriminating among various closed (convex) shapes was examined systematically for the first time. Bees were trained to each of five different shapes, a disc, a square, a diamond and two different triangles, all of the same area, using fresh bees in each experiment. In subsequent tests, the trained bees were given a choice between the learned shape and each of the other four shapes. Two sets of experiments were conducted with both species. In the first, solid black shapes were presented against a white background, thus providing a high luminance contrast. In the second, the shapes carried a random black-and-white pattern and were presented 5 cm in front of a similar pattern, thus producing motion contrast, rather than luminance contrast, against the background.

The results obtained with the solid shapes reveal that both bee species accomplish the discrimination, although the performance of the honeybee is significantly better than that of the leaf-cutter bee. Furthermore, the effectiveness of the various shapes differs between the two species. However, in neither species is the discrimination performance correlated with the amount of overlap of the black areas contained in the various pairs of shapes, suggesting that, in our experiments, shape discrimination is not based on a template-matching process. We propose that it is based on the use of local parameters situated at the outline of the shape, such as the position of angles or acute points and, in particular, the position and orientation of edges. This conclusion is supported by the finding that bees of both species accomplish the discrimination even with the patterned shapes. These shapes are visible only because of the discontinuity of the speed of image motion perceived at the edge between the shape and the background.

Key words: honeybee, *Apis mellifera*, leaf-cutter bee, *Megachile rotundata*, training, shape discrimination, convex shape, luminance contrast, motion contrast, vision.

Introduction

A closed shape, also termed a ‘convex shape’, is defined as a geometrical figure in which every line connecting two points on the perimeter lies within the area of the figure. Examples are triangles, rectangles or discs. Shapes or patterns that do not meet this condition, such as star shapes, gratings or checkerboards, are said to be ‘disrupted’ or ‘dissected’. Earlier training experiments conducted using patterns presented on a horizontal plane revealed that bees do not discriminate among pairs of closed shapes, but they discriminate well among patterns that differ in the degree of disruption (von Frisch, 1915; Baumgärter, 1928; Hertz, 1929, 1930; Zerrahn, 1934; Wolf and Zerrahn-Wolf, 1935) (for a review, see von Frisch, 1965). On the basis of these findings, it was broadly agreed that the principal parameter used for pattern discrimination is contour density, defined as the ratio between the length of the contours and the area of the pattern. This insight brought an end to the use of closed shapes in studies on shape discrimination for several decades. In fact, a systematic investigation of the capacity of bees to discriminate among convex shapes has never been conducted.

A new era in work on the spatial vision of bees was initiated in the mid 1960s and early 1970s by the results of experiments conducted using patterns presented on vertical planes. Bees were found to discriminate well between shapes, whether closed or disrupted, that did not differ in their contour density but did differ in their alignment in space and thus in the distribution of contrasting areas within the pattern (Wehner and Lindauer, 1966; Wehner, 1971, 1972a,b). It was proposed that, during training, the bee stores a retinotopic (‘photographic’) representation of the rewarded pattern, a so-called template, that is later recognised on the basis of an image-matching process (for reviews, see Wehner, 1981; Heisenberg, 1995;
Effer and Ronacher, 2000). The smaller the amount of overlap of contrasting areas between the stored pattern and the novel pattern, the better the discrimination. The image-matching theory was soon embraced by workers concerned with landmark learning (e.g. Anderson, 1977a; Cartwright and Collett, 1983; Collett, 1992; Zeil, 1993a,b; Collett and Zeil, 1997).

However, not all the results obtained using patterns presented on vertical planes could be explained by postulating image matching. A variety of experiments suggested that, during training, bees extract from the rewarded pattern one or more particular parameters that they later recognise even in novel patterns. Contour density, taken to be the main discrimination cue in the early studies (see above), turned out to be only one of many possible cues.

In various experiments designed to examine the use of either image matching or particular shape parameters by bees, closed shapes were again used sporadically, although without the aim of investigating discrimination among them. Thus, Wehner (1972a,b), Menzel and Lieleke (1983) and Lehrer (1998) used half-discs to examine the role of the distribution of contrasting areas, Wehner and Lindauer (1966), Wehner (1972a,b) and Srinivasan (1994) used rectangles (bars) to investigate the role of contour orientation and Wehner and Flatt (1977) used discs to determine the position of the fixation point. Discs were also used several times to examine the role of size (Schnetter, 1972; Mazokhin-Porschnyakov et al., 1977; Wehner, 1981; Ronacher, 1992).

One attempt to examine discrimination of closed shapes was undertaken by Mazokhin-Porschnyakov (1969a,b), who trained bees to discriminate between a triangle and a square. However, the triangle and the square used in that study were composed of a set of small triangles and a set of small squares, respectively, and were therefore not exactly what could be called closed shapes. Anderson (1972) later showed that the actual parameter used by the bees in the study by Mazokhin-Porschnyakov (1969a,b) was contour density. Ronacher and Duft (1996) trained bees to discriminate between a black disc and a delineated triangle and between a black triangle and a delineated disc (i.e. a ring pattern). By varying the thickness of the annulus in the ring pattern, the authors showed that the cue used by the bees was not the shape of the stimulus, but rather the degree of overlap of areas between the two shapes. Ronacher (1992), investigating the role of size, contrast and shape in the discrimination task, succeeded in training bees to discriminate between a large and a small black disc, between a black and a grey disc and between a black disc and a black triangle. The latter experiment is, to our knowledge, the first successful training experiment using a pair of closed shapes that differed in no other parameter than shape. Bees trained with this pair of shapes preferred the disc to triangles of different sizes and to various star shapes, but not to a diamond (Ronacher, 1992).

The present study constitutes the first systematic investigation of discrimination by bees among various convex shapes. Bees trained to one of five different shapes were tested by giving them a choice between the learned shape and each of the other four shapes. We asked whether the bees accomplished the discrimination and, if they did, whether some shapes were learned better than others. We further asked whether bees used image matching or particular parameters in the discrimination task. We asked these questions to two species of bee, the honeybee *Apis mellifera* and a solitary bee, the leaf-cutter bee *Megachile rotundata*, whose performance in a shape discrimination task has never been studied.

**Materials and methods**

**The animals and their biology**

**The leaf-cutter bee**

The leaf-cutter bee *Megachile rotundata* (Megachilidae) is a small (approximately 0.9 cm long), solitarily living hymenopteran insect that forages mainly on alfalfa plants (*Medicago sativa*, Fabaceae). The female builds its nest in narrow cavities, 5–10 cm deep, roughly tubular in shape, e.g. defects in the stones of old walls, or under rocks or in deserted nests of mason bees. Starting at the deep end of the tube, the female builds a series of individual cells, lined with pieces of alfalfa leaves, provisioning each cell with pollen and nectar, and laying one egg in it. Once the tube is full, the bee seals it with a thick plug of leaf pieces and starts a new nest, usually in a nearby cavity. After having laid her eggs and sealed the cells, the bee takes no further care of the brood.

To build and provision one cell, *M. rotundata* undertakes approximately 50 foraging trips (Klostermeyer et al., 1973). In the course of the reproductive season, lasting for 3–4 weeks, she lays 25–30 eggs, thus performing a total of 1200–1500 homing trips to her various nests in the course of the breeding season. On every return, the bee must find the nesting site and her own nest there. This homing behaviour is therefore very suitable for investigating the orientation performance of this bee species.

**The honeybee**

The honeybee *Apis mellifera*, which is twice the size of the leaf-cutter bee, is a eusocial (i.e. truly social) insect. The workers take care of their mother’s offspring long after the eggs have been laid and are responsible for the food storage of the whole colony, including winter reserves. The honeybee is not specialised on one particular plant species. To optimise its foraging strategy, it keeps returning to a profitable feeding site for long periods, there visiting a particularly rewarding flower species for as long as it is rewarding. This so-called flower constancy (Grant, 1950; Manning, 1957) requires a good learning capacity for the various cues that flowers display. The honeybee’s visual performance is therefore best examined at the food source, be it a natural or an artificial one.

**Experimental procedures**

Leaf-cutter bees were trained and tested at the nesting site, whereas honeybees were trained and tested at the feeding place. Therefore, the experimental arrangements and the
methods employed, to be described further below, differed between the two species. The shapes used, however, were the same in both cases.

The shapes used

Five different shapes (see insets in the figures), all of the same area (100 cm²), were used: a disc, a square, a diamond (i.e. a square rotated by 45°), a triangle with the vertex pointing upwards (which will be termed ‘triangle-up’) and a triangle with the vertex pointing downwards (‘triangle-down’).

In one set of experiments, the shapes were cut out of black cardboard and were presented against a white background, thus providing a high luminance contrast. In a second set of experiments, the shapes carried a black-and-white random-pixel pattern (pixel size 1 cm) (Fig. 1C) and were presented 5 cm in front of a similarly patterned background, thus producing motion contrast, rather than luminance contrast, against the background. With either the solid or the patterned shapes, bees were trained to one of the shapes, each in turn, and then given a choice between the learned shape and each of the other four shapes.

Experiments with the leaf-cutter bees

In the USA (mainly in Idaho and California), *M. rotundata* is reared in large numbers to act as the main pollinator of the alfalfa crops. To increase the number of foraging bees, artificial nesting material has been developed, consisting of Styrofoam boards, 8 cm thick, in which holes, 6 mm in diameter and 6 cm deep, are drilled in each square centimetre, thus providing the bees with plentiful nesting opportunities (for details, see Campan et al., 1993). The boards are available at any desired size.

The experiments were conducted in a private park near Toulouse (France) in July and August of three consecutive years, 1998, 1999 and 2000. *M. rotundata* were delivered as pupae by a Canadian breeding company (Manitoba). By keeping the pupae at low temperatures, we could delay their development and make them emerge at any time during the months of June, July and August.

A Styrofoam board with an array of 30 × 45 tubes, in which several females were usually already nesting, was attached to the inside back wall of a wooden box, 70 cm deep, whose front (50 cm × 50 cm) was open for the bees to enter. The roof was made of wood for the first 40 cm from the entrance and, for the last 30 cm, the wood was replaced by translucent Plexiglas, allowing natural light to illuminate the nesting board. Four identical boxes separated by 1 m were installed in a row on a metal portico 1 m above the ground, the openings of the boxes facing southwest, thus being exposed to the sun from midday until late afternoon.

The bees were allowed to become familiar with the box for a couple of days until they learned to find their nest making a minimum of errors. Although the bees were not marked individually, each bee could be identified easily by the particular nest that it entered upon arrival. An individual bee flew out and returned 1–3 times in the course of 30 min, depending on the ambient temperature, but also on whether the bee was busy provisioning the nest or was building and sealing cells.

In a second step, the bees nesting in each box were trained to one of the five shapes described above (Fig. 1A, training situation). To this end, a removable vertical wooden partition was inserted in a slit, 40 cm from the entrance of the box, dividing the box in two compartments. On the side facing the entrance, the partition was covered with white Styrofoam in the series with the black shapes and with a random-pixel black-
and-white pattern in the series with the patterned shapes. The partition had a circular hole, 4.4 cm in diameter, cut out of its centre. A polyvinyl chloride tube of the same diameter was inserted into the hole, protruding 5 cm towards the entrance of the box. The shape, with a suitable hole in its centre, was mounted on the front end of the tube, facing the entrance. Bees entering the front compartment had to fly through the centre of the shape to reach the nest compartment. Thus, they were encouraged to learn to associate the shape with the reward (successful arrival at the nesting site).

The five shapes were used one at a time during training, presenting different shapes in different boxes and thus to different bees. In each box, bees were trained to the shape for at least 2 days before discrimination tests were conducted. Prior to a test, the partition used during the training was replaced by another partition with two tubes, 20 cm apart, identical in diameter and level with the initial tube (Fig. 1A, test situation). In the tests, the bees had to choose between the training shape, termed positive, and each of the other four shapes, all of which were novel to the bees. The positive and the novel shape were each mounted on one of the two tubes. A bee flying through the hole associated with the positive shape scored a plus point. When it flew through the alternative hole, it scored a minus point. Thus, every return of every bee scored one point, either a plus or a minus. To prevent the bees from developing a side preference, the left and right positions of the two shapes were interchanged between tubes at time intervals ranging between 15 and 30 min, depending on the level of the activity of the bees.

During the course of each experiment, the positive shape was tested against each of the other four shapes, presented in random order. An experiment (consisting of training interspersed with discrimination tests) lasted for several days. Every day, bees were rewarded in the training situation for 2–3 h before commencing the discrimination tests of the day. After each test, with the positive shape being presented once to the right and once to the left for an equal time, the training situation was restored, with the positive shape being presented alone in the centre of the partition for 30–60 min before the next test was conducted. An experiment was considered completed when tests with each of the four alternative shapes rendered at least 100 decisions (plus and minus summed). The results are expressed in terms of choice frequency (CF), i.e. the percentage of plus points calculated from the total number of points.

Experiments with the honeybees

The experiments on honeybees were conducted at the Institute of Zoology of the University of Zurich (Switzerland) in the summer of 1999. The bees came from a small sheltered hive placed in one of the many gardens of the Institute, approximately 30 m from the laboratory in which the experiments were conducted. The laboratory had a huge glass front including a wide glass door opening to the garden. The experimental apparatus was placed in the laboratory, 1.5 m away from the door. For each experiment, 6–8 individually marked bees were trained to enter the laboratory and collect sucrose solution from a feeder placed in a dark reward box within the apparatus (Fig. 1B). Two Plexiglas tubes, 40 cm apart, each 20 mm in diameter, connected the front of the apparatus with the reward box. Bees could enter the reward box through only one of the two tubes at a time because the other tube was blocked by a black plug. The plug was inserted 5 mm into the tube, so that bees could land on the tube entrance, although they could not enter the reward box through that tube.

Throughout each experiment, two shapes, one rewarding, termed positive, the other not, termed negative, were presented simultaneously, facing the open door. In the experiments with the black shapes, each shape was glued to the centre of a white (ultraviolet-reflecting) cardboard disc, 22 cm in diameter. A suitably sized hole in the centre of the cardboard disc allowed the shape to be mounted on one of the two tubes. In the experiments using the patterned shapes, a disc, 33 cm in diameter, with a suitable hole in its centre, was affixed to the front wall of the apparatus to serve as background. It carried a black-and-white random pattern identical to that used for the shapes and had a Plexiglas tube inserted in its centre. The shape was mounted on the front end of the tube, the distance between shape and background being 5 cm.

Each of the five shapes served as positive in each of five separate experiments, training a fresh group of bees in each. The negative shape was one of the remaining four shapes, presented in turn during the course of each experiment. The places of the two shapes were interchanged after every 2–3 rewarded visits (on average for all bees) to prevent the bees from developing a preference for the right or left tube.

This method, as opposed to that used for M. rotundata (see above), did not require modification of the apparatus prior to each test, i.e. the training situation served, at the same time, as the test situation. On each visit, each bee’s first choice between the two shapes was recorded. As in the experiments on M. rotundata, each bee scored either one plus point or one minus point on each of its visits to the apparatus.

Unlike in the case of M. rotundata, the criterion for giving a plus or a minus point according to the tube through which the bee entered the reward box could not be used with A. mellifera because the bees could enter through only one of the tubes (that associated with the positive shape). A possible alternative criterion would have been the bee’s first landing on one of the tubes, or touching it, indicating the bee’s intention to enter through that tube. However, observation of the choice behaviour of the bees in a pilot experiment, and in all experiments that followed, showed that this criterion would not be adequate either. Even when a bee touched the positive tube or landed on it immediately upon arrival, it never entered the reward box through that tube upon that very first decision. Not even one exception to this rule was observed during the course of the experiments. Instead, the bee flew between the two tubes several (up to 20) times, inspecting each of the shapes carefully before entering the tube associated with the positive shape. This behaviour suggests that decisions were not made during
the approach flight, i.e. during a phase when the bee saw the two shapes simultaneously, but rather at close range, when the bee could see only one shape at a time. Thus, landing on the tube with the positive shape immediately upon arrival could not be taken to be a correct decision before the bee had had a chance to inspect the alternative shape. Therefore, in the present experiments, a bee scored a plus point only if it entered through the positive tube without having previously touched (or landed on) the tube associated with the negative shape. In other words, if a bee touched, with its antennae or the legs, the tube associated with the negative shape or landed on it, it scored a minus point, even if it had already touched the positive tube or landed on it prior to touching the negative one. Because bees sometimes touched the tube during free flight whilst inspecting the shape, touching the tube with the negative shape scored a minus only if the bee fixated the tube entrance frontally, thus expressing a clear intention to land there.

This method is more conservative than would be a method counting the very first correct landing (or touching) as plus, i.e. the true proportions of correct choices may be higher than the proportions we obtained, but at least we are sure that they are not lower.

At the beginning of each experiment, bees were rewarded at the positive shape for approximately 1 h before scoring began. During the experiment, each of the four negative shapes was presented against the positive one until the total number of visits amounted to at least 150. To exclude the possibility that the discrimination performance of the bees might be influenced by the number of preceding rewarded visits (i.e. after a long training, bees might perform better than at the beginning of the training), in each experiment the two negative shapes that were presented first, i.e. at an early stage of the training, were tested until approximately 80 decisions had been recorded, and were then presented again at the end of the experiment to obtain the final number of decisions. We found no systematic differences between the results of the two sessions. Performance was sometimes better in the second session, but sometimes it was poorer, and in most cases the difference was not dramatic. The results of the two sessions were therefore pooled in all cases. The other two negative shapes, presented in the middle of the experiment, were each tested in a single session until at least 150 visits had been recorded. The results are, again, given as the percentage of plus points (choice frequency, CF).

Typically, a bee visited the apparatus 2–4 times within 15 min. Thus, collecting the data from the honeybees took only approximately a quarter of the time that it took to collect a similar amount of data from the leaf-cutter bees.

**Statistical analyses**

The number of correct choices obtained in each type of test with either *M. rotundata* or *A. mellifera* was compared with the theoretical number of choices expected under random-choice conditions (i.e. $p=q=0.5$) using the $\chi^2$-test. Tests for the significance of differences between results of pairs of independent tests were conducted using 2x2 contingency tables. To compare the overall discrimination performance between sets of results of independent experiments, the Wilcoxon signed-ranks test was used. Whenever regression analyses were performed, the correlation coefficient ($r$) was tested against zero using the $t$-test after Spearman.

**Results**

The results obtained using the two types of patterns will be presented separately. In both cases, the results obtained from the honeybee and those obtained from the leaf-cutter bee are presented side by side.

**Black shapes on a white background (luminance contrast)**

The discrimination performance

*M. rotundata* preferred the positive shape to the novel shape in 18 out of the 20 tests (Fig. 2A–E, black columns), CFs being significantly different from 50% in 11 of these 18 tests. *A. mellifera* preferred the positive shape to the negative one in all 20 tests (hatched columns), discrimination being highly significant in all cases. The overall performance of *A. mellifera* is significantly better than that of *M. rotundata* ($P<0.001$, Wilcoxon signed-ranks test). Fig. 2 reveals, in addition, qualitative differences between the two species: some of the pairs of shapes that *A. mellifera* discriminates best belong to pairs for which *M. rotundata* displays the poorest discrimination performance and vice versa.

**The effectiveness of the shapes**

To visualise the qualitative differences between the results of the two species, we calculated the mean values of the CFs obtained for each shape in the four tests in which it served as positive. Because, with both species, each positive shape was tested against the same set of alternative shapes (excluding itself), we consider the mean CF to constitute a measure of the bees’ success in learning the positive shape or, equivalently, to reflect the degree of effectiveness of the shape. When the mean CF values are arranged in descending order of magnitude (Fig. 3A,B), it becomes evident that the hierarchy of the shapes with respect to their effectiveness differs between the two species with the exception of the diamond, which is learned best by both. For *A. mellifera*, however, only the difference between the diamond and the triangle-down is statistically significant ($P<0.01$). The differences between the diamond and the triangle-up and between the diamond and the disc are just non-significant (0.05<$P<0.1$), and all other shapes do not differ significantly in the CFs obtained. For *M. rotundata*, however, we found statistically significant differences between the diamond and the square ($P<0.001$), the diamond and the disc ($P<0.001$), the triangle-up and the disc ($P<0.05$) and the triangle-up and the square ($P<0.05$). The differences between the triangle-down and the disc and between the triangle-down and the triangle-up are just non-significant (0.05<$P<0.1$). We conclude that the two species differ in that the various shapes are roughly equally effective for the honeybee, whereas they are not for the leaf-cutter bee.
Spontaneous shape preferences

One possibility to explain these differences would be to consider some species-specific spontaneous preferences for particular shapes. It has been shown repeatedly that two stimuli are discriminated better when the more attractive of the two has acted as the rewarding one than when the less attractive one has (Zerrahn, 1934; Hertz, 1935; Menzel and Lieke, 1983; Ronacher, 1992; Giurfa et al., 1996; Lehrer, 1998). This is because, in the former case, the spontaneous preference is superimposed on the learned association between the pattern and the reward, whereas in the latter case it is subtracted from the learning effect. Therefore, a comparison between the results of reciprocal training experiments constitutes a reliable criterion for judging the presence or absence of spontaneous preferences.

Because each positive shape was tested against each of the other four shapes, the 20 CFs obtained involve 10 pairs of shapes tested against each other reciprocally in two different training experiments. With the exception of only two pairs of shapes in A. mellifera (triangle-down/diamond and triangle-up/square) and only one pair in M. rotundata (diamond/disc), the results of reciprocal tests do not differ statistically. We conclude that our results are not a consequence of some spontaneous shape preferences on the part of the bees.

Template learning or parameter extraction?

Another possible explanation for the difference found in the performance of the two species might be that they differ in the strategy that they employ in the task. For example, one species might base the discrimination on the comparison of areas (template matching) and the other on particular shape parameters (see Introduction). To examine this possibility, we analysed, for each of the two species, the correlation between the CFs obtained in the tests and the amount of overlapping areas contained in the pairs of test shapes. A significant correlation between the two sets of values would indicate the use of an image-matching process in the present discrimination task. Note that, because all the shapes possess the same area, for each pair of shapes the amount of non-overlapping areas between the template and one of the shapes is identical to that between the template and the other shape. Therefore, one type of regression analysis is sufficient to examine this question (see Dill and Heisenberg, 1995; Ronacher and Duft, 1996).

The regression lines obtained (Fig. 4A,B) reveal a slight tendency for the CFs to decrease with increasing amount of area overlap. However, in neither species is the correlation significant ($P=0.63$ for A. mellifera and $P=0.30$ for M. rotundata), suggesting that bees do not store a template of the
shape area in the present task, but rather some parameter(s) situated at the edges of the shape.

The edges of the shapes used in our study possess several parameters that are suitable to serve as discrimination cues: the presence or absence of angles (see Ronacher, 1992), the number of angles (see Mazokhin-Porshnyakov, 1969a), the contour density (contour length), the average (predominant) orientation of contours (see Srinivasan et al., 1994) and the orientation of individual edges (see Srinivasan 1994; Horridge, 1998). What is the role of these various parameters in the present discrimination task?

The presence (absence) of angles and the number of angles

To judge the role of the presence or absence of angles or acute points, we compared the CFs obtained in the tests in which the disc constituted one of the test shapes with the results of the tests in which the disc was not involved. If the absence of angles served for the discrimination, then the mean CF obtained in the eight tests in which the disc was one of two alternative test shapes would be expected to be higher than the CFs obtained in the remaining 12 tests, because the disc differs from all the other shapes in possessing no angles. For A. mellifera, the mean CF obtained in the tests with the disc was 76.7 %, and that in the tests without the disc was 76.6 %. For M. rotundata, the corresponding values were 56.4 % and 62.2 %, respectively. The latter two values differ significantly (P<0.001), the difference, however, being in favour of the tests in which the disc was absent. These findings suggest that, in the honeybee, the presence or absence of angles is no more effective than are other parameters, and in the leaf-cutter bee it is less effective than are the other parameters.

The number of angles plays no role either: bees of both species discriminate well between the two triangles, as well as between the square and the diamond, which do not differ in the number of angles.

Contour length

Although all shapes were equal in area, they differed in the length of outline and therefore in the ratio between contour length and area (contour density, see Introduction). The finding that the two pairs of shapes that possess identical perimeters, namely the diamond and the square, and the two triangles, are discriminated well renders the use of this parameter rather unlikely. We nevertheless analysed, for each species, the correlation between the CFs obtained in the tests and the differences in contour length among the various pairs of test shapes (not illustrated). For neither species did we find a significant correlation between the two sets of values (A. mellifera, P<0.23; M. rotundata, P=0.68). We conclude that contour length plays no role in the present discrimination task.

The role of average (predominant) contour orientation

The average orientation of contours, when it results in a particular predominant orientation, has been found to play a role in shape discrimination (e.g. Srinivasan, 1994; Srinivasan et al., 1994; Horridge, 2000). In our experiments, the disc, with perfect radial symmetry, and the square and the diamond, each with four planes of symmetry, possess no predominant contour orientation. They are nevertheless discriminated well from one another by both bee species. The two bilaterally symmetrical triangles possess a slight predominance of the horizontal contour orientation, but they are nevertheless discriminated well from each other, showing that the predominant orientation had no great effect on discrimination performance. However, the triangles are discriminated better from the other shapes by M. rotundata than they are by A.
mellifera (P<0.01) (see Fig. 3). Thus, we can at most conclude that, for the honeybee, shapes that possess a bilateral symmetry, such as triangles, are less effective than are shapes that possess a higher degree of symmetry (see also Lehrer et al., 1995), whereas in the leaf-cutter bee bilateral symmetry is more effective. However, a more systematic investigation of this parameter is needed.

It seems, therefore, that the only parameter whose effectiveness in the present discrimination task is beyond any doubt is the spatial orientation of individual edges.

Hints from the flight behaviour of bees

The significance of the edges was manifest in the flight behaviour of A. mellifera in a very conspicuous manner. The two alternative shapes were inspected particularly intensively in those parts of the shape that differed. Thus, the disc was inspected particularly closely in those parts where the alternative shape had angles or acute points. With the pair triangle-up/diamond, bees inspected the shapes mainly in the lower part, where the diamond displays an angle, but the triangle does not, whereas with the pair triangle-down/diamond inspection mainly occurred in the upper part of the shapes. The attraction that acute points exert on bees has already been reported by Free (1970) and Anderson (1977b).

However, it is mainly with respect to the effectiveness of contour orientation that the honeybees’ flight behaviour provides valuable hints. Earlier studies have shown that honeybees flying in front of patterns presented on a vertical plane (Lehrer et al., 1985) or above patterns presented on a horizontal plane (Lehrer and Srinivasan, 1994), tend to follow, in free flight, the contours contained in the pattern, a behaviour we termed scanning. In our present experiments, A. mellifera tended to scan mainly those contours whose direction differed between the two shapes. When the two triangles or the square and the diamond were presented against each other, the bees scanned all the contours contained in each of the two alternative shapes. But when the diamond was presented against the triangle-down, the bees flew mainly along the upper horizontal edge of the triangle and along the two oblique upper edges of the diamond. Similarly, when the diamond was presented against the triangle-up, mainly the lower contours of the two shapes were scanned. We plan to quantify this flight behaviour by means of video recordings.

In M. rotundata, neither scanning of contours nor searching for missing angles or acute points was observed. We believe that the leaf-cutter bee was able to compare each pair of shapes, presented only 20 cm apart, simultaneously during its approach flight and therefore it needed no closer inspection. This conclusion is corroborated by two recent observations (R.

![Fig. 5. (A–E) The same as in Fig. 2, but using patterned shapes placed in front of a patterned background, thus presenting the bees with motion contrast, rather than with luminance contrast. Black columns, Megachile rotundata; hatched columns, Apis mellifera. Asterisks denote the level of significance against random-choice expectation (CF=50%, dashed lines) (χ²-tests). ***P<0.001; **P<0.025; *P<0.05. NS, not significance. Numbers above columns denote the total number of choices.](image-url)
Campan, unpublished observations): (i) *M. rotundata* does scan contours when it is required to come near the surface of the target to make the decision, and (ii) when honeybees are trained using the same apparatus as the one we used here for *M. rotundata*, they neither shuttle between the two shapes as they did in the present study (see Materials and methods) nor do they scan the contours of the shapes.

**Patterned shapes and patterned background (motion contrast)**

This series of experiments served to test the hypothesis expressed above that bees accomplish the discrimination by using shape parameters located at the edges of the shape. Patterned shapes produce no luminance contrast against a similarly patterned background and are therefore invisible even when shape and background differ strongly in texture density (i.e., pixel size) (Srinivasan et al., 1990). However, when the shape is nearer to the observer than is the background, it moves faster than does the background when the observer moves, thus giving rise to relative motion (motion contrast) between shape and background. It has already been shown that the abrupt change in motion speed occurring at the edge enables the detection of otherwise invisible edges and thus object/ground discrimination (Srinivasan et al., 1990; Lehrer and Srinivasan, 1994). It is conceivable that motion contrast provides information not only on the presence of an edge but also on some of its features. By using this information, bees might be able to discriminate among different shapes without the need to recognise the shape as a whole.

**The discrimination performance**

The results of these experiments (Fig. 5A–E) show that shape discrimination based on motion contrast occurs in both bee species. In *M. rotundata* (black columns), 14 out of the 20 tests rendered CFs that differed significantly from the random-choice expectation of 50%. With *A. mellifera* (hatched columns), all 20 tests rendered highly significant discrimination. As in the experiments using the solid shapes (see Fig. 2), the results obtained for the honeybee were significantly better than those obtained for the leaf-cutter bee (*P*<0.001).

**The effectiveness of the shapes**

By analogy with Fig. 3, we established, for both species, the hierarchy of the effectiveness of the five shapes on the basis of the average CF obtained for each shape when it served as positive in the tests against all other shapes (Fig. 6A,B, hatched columns). In the honeybee, the CFs obtained for the individual shapes differ statistically between the triangle-up and the square (*P*=0.05), the triangle-up and the diamond (*P*<0.001) and the triangle-down and the diamond (*P*<0.001). The difference between the diamond and the disc was just-non-significant (0.05<*P*<0.1). In the leaf-cutter bee, significant differences in the CFs are found between the diamond and the square (*P*<0.01), the diamond and the disc (*P*<0.001) and the triangle-down and the disc (*P*<0.001). For the pair triangle-down/square, the difference was just-non-significant (*P*<0.1). We conclude that, with the patterned shapes, the shapes differ in their effectiveness in both *M. rotundata* and *A. mellifera*.

For the sake of comparison, the results obtained with the solid black shapes (see Fig. 3) are also shown in Fig. 6 (black columns). For *M. rotundata*, the hierarchy of the shapes is very similar between the two sets of experiments. In the honeybee, however, the hierarchy obtained with the patterned shapes is reversed compared with that obtained with the black shapes. Thus, the honeybee, but not the leaf-cutter bee, seems to use different shape parameters in the two different tasks. This conclusion is supported by the finding that the performance of *M. rotundata* does not differ statistically between the two sets of experiments (*P*=0.14, Wilcoxon signed-ranks test), whereas *A. mellifera* performs much better with the motion-contrast shapes than with the luminance-contrast shapes (*P*<0.001). However, even with the patterned shapes, the honeybee scans the contours (see above), showing that it perceives the edges and probably uses their spatial orientation in the discrimination task.

**Image matching**

In these experiments, we had not expected to find a correlation between the test results and the amounts by which the areas of the pairs of test shapes overlapped, because a moving image is not likely to be stored retinotopically. Indeed, for *Apis mellifera*, there is no correlation between the two sets of values (*P*=0.34) (Fig. 7A). Quite unexpectedly, however, in *M. rotundata*, the CFs are correlated with the amount of overlapping areas (*P*=0.033) (Fig. 7B). We will propose a possible explanation of this finding in the Discussion.

**Contour density**

As in the experiments with the solid shapes, we find no correlation between the CFs obtained in the tests and the

![Fig. 6](image-url)

Fig. 6. (A,B) Mean choice frequency (CF) (ordinate) for each positive shape (abscissa) calculated from the results of all tests against the four other shapes (hatched columns). (A) *Apis mellifera*; (B) *Megachile rotundata*. Note the different scales on the ordinates. For the sake of comparison, the results of the tests using solid shapes (see Fig. 3) are also shown (black columns).
amounts by which the pairs of test shapes differ in their contour length ($P=0.69$ for *Apis mellifera*, and $P=0.92$ for *M. rotundata*) (not illustrated).

**Spontaneous shape preferences**

As a criterion for a possible influence of spontaneous shape preferences, we again used the comparison between results of reciprocal experiments. Of the 10 pairs of reciprocal tests, only one pair of shapes (triangle-down/square) rendered significantly asymmetrical results in *Apis mellifera*, and for *M. rotundata* this was the case with only two pairs of shapes (triangle-up/disc and triangle-up/diamond). We again conclude that spontaneous preferences do not participate in the choice behaviour of the bees.

**The role of average (predominant) contour orientation**

In *M. rotundata*, the role of average contour orientation seems to be as weak as that observed with the solid shapes (Fig. 6B). In *A. mellifera*, however (Fig. 6A), the two triangles are now much more effective than they were in the former experiments. Thus, when motion cues are involved, the honeybee is capable of using a particular predominant contour orientation (in this case horizontal) as a discrimination cue (see also Srinivasan, 1994; Srinivasan et al., 1994).

**Discussion**

The present study constitutes the first investigation of shape discrimination in a solitary bee, demonstrating the capacity of the leaf-cutter bee *M. rotundata* to discriminate among various pairs of closed (convex) shapes. For the honeybee, our results demonstrate an unexpectedly good performance in the present discrimination task. Earlier workers have denied bees the capacity to discriminate among closed shapes (see Introduction), a finding that was, at that time, easy to explain on the basis of the idea that such shapes differ neither in figural quality nor in figural intensity as defined by Hertz (1933).

Another new result is the finding that bees of both species discriminate between pairs of closed shapes even when luminance contrast is excluded by using patterned shapes placed against a similarly patterned background. In this situation, there are two ways in which bees could separate the shape from the background. One is by exploiting the difference in texture density: the pixels on the shape appear at a larger visual angle than the pixels on the more distant background. This possibility can be ruled out on the basis of earlier results showing that even large differences in texture density between object and background provide no cue for shape detection (Srinivasan et al., 1990). The other possibility is by using motion contrast: the shape, being nearer that the background, moves faster than does the background. The honeybee’s use of motion cues has been demonstrated in several visual tasks (for reviews, see Lehrer, 1994, 1997a). However, evidence for the use of motion contrast in the task of shape discrimination is provided here for the first time.

An earlier attempt to train honeybees to discriminate between pairs of patterned shapes placed in front of a patterned background (Zhang and Srinivasan, 1994) failed. However, bees did learn to discriminate between the shapes when they had been pre-trained with the same two shapes in a black-and-white arrangement, i.e. with luminance contrast (two-step training) (Zhang and Srinivasan, 1994). The authors’ failure to train bees directly to the motion-contrast shapes as we have done might be due to the fact that, in those experiments, the bees’ decisions were recorded at a distance of 30 cm from the targets, at which the amount of relative motion between shape and background was smaller than in our experiments. Another possible explanation for the discrepancy would be the fact that in their experiments the positive and negative shapes were similar with respect to the parameters present at the edges. The rewarding and non-rewarding shapes were either two bars that differed in their spatial orientation by $90^\circ$ or a disc and a ring. The two bars both possessed the same two (perpendicular) orientations of edges, and the disc and the ring both possessed exclusively circular contours. In our experiments, all shapes differed from one another with respect to the positions and orientation of edges, and our results show that this is indeed the main parameter used in the present discrimination task.

**The role of pattern presentation**

In the earlier studies on pattern discrimination by the bee (see Introduction), only a few closed shapes were used, mainly with the aim of investigating the bee’s discrimination between them and dissected shapes. Most of those studies used patterns presented on a horizontal plane, so that bees could approach them from any direction. Under these conditions, parameters that require constant spatial relationships between pattern and eye, such as the position and orientation of edges, and the distribution of contrasting areas within the pattern, cannot be used for discrimination unless patterns are memorised in a rotation-invariant manner. We know, however, from many studies that they are not (e.g. Wehner, 1972a,b; Wehner and Flatt, 1977; Menzel and Lieke, 1983; Srinivasan and Lehrer, 1988).

The mode of pattern presentation is, however, not always
crucial in a discrimination task. Thus, contour density is a very effective parameter even when patterns are presented in a vertical plane (e.g. Wehner, 1981; Lehrer, 1997b), and several shape parameters that have been shown to be effective using vertical patterns are also used for discrimination when shapes are presented on horizontal planes, e.g. the size of the shape (Schnetter, 1972; Wehner, 1981; Ronacher, 1992), its contrast against the background (Mazokhin-Porshnyakov, 1969a,b; Ronacher, 1992), the presence or absence of acute points (Mazokhin-Porshnyakov, 1969a; Ronacher, 1992) and the number of acute points (Mazokhin-Porschynakov and Vishnevskaya, 1965). The perception of these parameters, as for that of contour density, does not require a constant relationship between the object and the eye.

In the present study, size and contrast were not tested, but we already know that these parameters are used for discrimination even when patterns are presented on a vertical plane (Wehner, 1981; Ronacher and Duft, 1996). The absence or presence of angles and their number, however, seem to play no role in the present task. This is probably because other parameters, which could not be used in the horizontal plane, such as the positions and orientation of edges, are now much more effective.

**Template matching versus parameter extraction**

Although template matching and parameter extraction may be active in parallel (see Ronacher and Duft, 1996), most studies on shape discrimination have demonstrated the use of either one or the other. In the honeybee, for example, Gould (1985) found the exclusive use of the template mechanism, whereas Effer and Ronacher (2000) demonstrated the exclusive use of particular shape parameters. Similarly, in the fruit fly *Drosophila*, Dill and Heisenberg (1995) demonstrated the exclusive use of image matching, whereas Ernst and Heisenberg (1999) demonstrated its capacity to exploit several shape parameters in a discrimination task. Whether the former or the latter mechanism is active in an experiment seems to depend on the training method and on the visual stimuli used (see also Ronacher, 1998). In our present experiments with the patterned shapes, for example, bees could use only those cues that they were able either to infer from image motion or to extract in spite of image motion.

Experimentally, bees can be prevented from forming a template during training by randomising the distribution of contrasting areas contained in the training patterns (Mazokhin-Porshnyakov, 1969a,b; Van Hateren et al., 1990; Srinivasan et al., 1994; Horridge, 1997, 2000). In our study, however, we did nothing of the kind. With the solid shapes, the bees were free to memorise the position and extent of the black areas and to use the amount of overlap to discriminate the positive shape from each of the other shapes. The results of the correlation analyses (Fig. 4) show, however, that the bees have not stored a template of the shape area. They must, therefore, have used parameters situated at the circumference of the shape.

Bees could memorize the positions of orientated edges in two ways. One is to store edges retinotopically, in which case the use of edges and the use of areas would not differ in principal. However, although this mechanism might work well with the solid shapes, it would not be expected to work with the motion-contrast shapes, because retinotopic recognition of the edges, as for the recognition of the distribution of areas, requires that the image be stationary at the eye.

Another possibility would be to store edge orientation in a translation-invariant manner. With closed shapes, translation invariance might be achieved by memorising the mutual spatial relationships among the differently oriented edges displayed by the shape. This mechanism is expected to work well whether the edges belong to a solid or to a patterned shape.

The correlation found in *M. rotundata* between the CFs and the amount of overlapping areas in the experiments with the patterned shapes (see Fig. 7B) might be explained along these lines. The leaf-cutter bee had to choose between two shapes presented rather close together. Thus, in contrast to the honeybee, it must have perceived the whole perimeter of the shape and was able to learn about the mutual relationships among the various edge elements. This information could be used by the bee to form some concept about the area of the shape. The insect’s capacity to infer some properties of the area from shape elements situated at the periphery has also been demonstrated in *Drosophila* (Ernst and Heisenberg, 1999). The fly was shown to determine the centre of gravity lying within the empty area between two horizontal bars separated by some distance.

The orientation of an individual edge is likely to be a more convenient cue to learn than are the mutual relationships among the various edge elements. Thus, with the solid shapes, the strong influence of the high luminance contrast might explain the absence of correlation between the CFs and the amount of area overlap in both bee species. High-contrast edges are inherently attractive to insects (for a review, see Campan, 1997). The strong attraction that edges exert on foraging bees, documented by Srinivasan et al. (1990) and Lehrer and Srinivasan (1993) using video recordings, has already been reported by Hertz (1930) and Free (1970).

**The role of image motion**

On the basis of their findings on the chromatic properties of the landing behaviour of bees, Lehrer et al. (1990) proposed that edge detection is based on motion of the edge at the eye even when luminance-contrast shapes are used, and thus also in the case of our solid shapes. Although bees seem to discriminate the orientation of edges even when image motion is excluded (Srinivasan et al., 1994), image motion is very likely to be exploited for shape discrimination under natural conditions. Freely moving animals can infer the orientation of an edge from the direction of its motion at the eye. For example, freely flying honeybees discriminate very well between two oblique bars, one rotated by 90° with respect to the other (Van Hateren et al., 1990; Srinivasan et al., 1994). *Drosophila*, in contrast, flying tethered within a rotating cylinder, do not discriminate between the same pair of bars (Ernst and Heisenberg, 1999), which might be because, in that
situation, motion could only occur in the horizontal direction. Therefore, both bars produced horizontal image motion and were indiscernible to the fly.

Indeed, the question of how animals that are continuously in motion can form a stationary template that is not space-invariant has often been addressed. For pattern recognition at close range, Wehner and Flatt (1977) have proposed a fixation phase at the decision point, during which the image of the pattern is stationary relative to the eye (see also Horridge, 1999). For landmark orientation, the so-called snapshot theory has been proposed, according to which bees store and retrieve images during short flight phases in which the image is, again, stationary relative to the eye (Cartwright and Collett, 1983; Collett, 1992; Zeil, 1993a; Collett and Lehrer, 1993; Zeil et al., 1996). Another similar mechanism would be to arrive from a constant direction (Collett and Baron, 1994) or along a constant route (Zeil, 1993b; Collett and Rees, 1997; Collett and Zeil, 1997) so as to view the target from a constant perspective that would allow retinotopic storage and retrieval of the image.

It would be idle, of course, to argue that, to accomplish shape discrimination, it would probably be easier to exploit image motion than to employ all kinds of sophisticated tricks to avoid such motion (see Campan et al., 1967; Horridge, 1988; Fauria and Campan, 1998).

The role of various eye regions

Several earlier experiments on spatial vision in the honeybee revealed that shape recognition and discrimination are better in the lower frontal eye region than in other frontal eye regions (e.g. Wehner, 1972b; Lehrer, 1998, 1999). In the present study, four pairs of shapes differed from each other exclusively in either the lower or the upper visual field: each of the two triangles combined with either the square or the diamond. Because each pair was trained reciprocally, there are four tests involving the upper visual field and four tests involving the lower one. With both the solid black shapes and the patterned shapes and in both A. mellifera and M. rotundata, the two categories of test rendered practically identical mean CF values. Thus, the lower visual field has no priority over the upper one in the present task, which supports the idea that discrimination in this case is based on cues present at the edges. In natural orientation tasks, the most useful and omnipresent edge, namely the horizon, never projects on the ventral eye region.

The leaf-cutter bee versus the honeybee

In the present discrimination task, the performance of the honeybee was found to differ from that of the leaf-cutter bee both quantitatively and qualitatively. The quantitative differences are easy to explain on the basis of the different behavioral contexts in which we studied the performance of the bees (homing in M. rotundata versus foraging in Apis mellifera), which required different experimental conditions. In M. rotundata, we exploited nest-finding (homing) behavior, a task in which the visual cues needed are not just those that mark the goal (nest) itself but also those that guide the animal to the location of the nest. Previous work on homing Megachilidae bees showed that the bee is guided mainly by the positions of straight edges relative to the nest’s location (Fauria and Campan, 1998). In our experiments, the straight edges of the cube-shaped box probably served as useful marks. Indeed, in the test, when the partition that offered two shapes was present, arriving bees aimed first at the centre of the wall where, during training, the entrance to the nesting site used to be. This observation suggests that the position of the opening was more important to the bees than was the shape presented there. A. mellifera, however, were trained and tested at the feeding site, where the rewarding shape was the goal itself rather than a landmark on the way to the reward.

Another reason for the better performance of A. mellifera compared with M. rotundata lies in the training procedures employed. The honeybees were trained using a differential training method, i.e. presenting them with two targets, one rewarding, the other not. To train the leaf-cutter bees, only one shape was used. Thus, the honeybees were encouraged to use the parameters by which the two shapes differed from each other, whereas the leaf-cutter bees were not. Using a differential training method, honeybees have already been successfully trained to use a variety of parameters, such as the number of angles (Mazokhin-Porshnyakov, 1969a,b), the size of the shape (Srinivasan et al., 1994; Horridge, 2000) and bilateral versus radial symmetry (Giurfa et al., 1996).

However, several visual cues have been shown to be learned even without the support of differential training. For example, bees learn the colour of a shape (von Frisch, 1915; Daumer, 1956; Menzel, 1967) and the orientation of contours (Wehner, 1971, 1972a,b; Menzel and Lieke, 1983) even in the absence of a non-rewarding stimulus. Furthermore, even when differential training is used, extracting a particular parameter from the rewarding stimulus does not always depend on whether the rewarding and non-rewarding stimuli differ in that parameter. Thus, the colour and the type of contrast are extracted from the rewarding stimulus irrespective of the pattern that is used as non-rewarding (Ronacher, 1992), and this also holds true when dissectedness (Hertz, 1929, 1930; Ronacher, 1992) and edge orientation (Lehrer, 1998) are considered. Thus, even under our experimental conditions, the leaf-cutter bee is free to extract from the positive shape the parameters that are useful in the shape discrimination task.

Although the differential training is expected to have improved the level of learning in the honeybee compared with that of the leaf-cutter bee, it cannot account for the qualitative differences found between the performances of the two species. Neither within a species nor between the two species are the various shapes equally effective, although all shapes were equally attractive to the bees, as revealed by comparing the outcome of reciprocal experiments, and despite the fact that, within a species, the experimental procedure treated all
five shapes equally. The results suggest that some shape parameters are assigned more weight than are others and that the two species weigh the different parameters differently.

Of course, some of the shape parameters are not mutually independent. The presence or absence of angles is based on the presence or absence of straight contours, the number of angles determines the number of straight edges and the positions of angles determine the positions and the spatial orientation of the edges. Nevertheless, the considerations presented above allow us to draw the conclusion that the main parameter used for discriminating closed shapes is the orientation of individual contours. The differences in the effectiveness of the shapes between the two species suggest that they evaluate different orientations differently.

Another criterion by which the two species differ from each other is the dependence of their performance on the type of contrast used. In the experiments using the patterned shapes, both species must have used motion cues to accomplish the discrimination because these shapes offered no other cues. For each of the two species, the experimental procedure was the same as in the experiments using the solid shapes. In *M. rotundata*, the discrimination performance in these experiments, and also the hierarchy of the effectiveness of the shapes, was almost the same as in the experiments using the solid shapes. This finding suggests that, in this species, discrimination of the motion-contrast shapes and that of the luminance-contrast shapes is based on a similar mechanism. Because, with the patterned shapes, only motion cues could be used, the performance of *M. rotundata* must have been based on motion cues even in the experiments with the solid shapes (see also Campan et al., 1976; Fauria and Campan, 1998). *A. mellifera*, in contrast, performed significantly better with the motion-contrast shapes than it did with the luminance-contrast shapes, and the hierarchy of the shapes differed strongly between the two sets of results. These findings suggest that the honeybee uses distinct mechanisms to cope with the two different tasks. A possible explanation of these particularly striking differences between the performances of *A. mellifera* and *M. rotundata* would be that we are dealing with two species that, on the evolutionary scale, possess two different levels of processing capacity, the honeybee being more advanced, and therefore more sophisticated in its performance, than the leafcutter bee. A similar argument was proposed by Dill and Heisenberg (1995) in a discussion of the difference between the capacities of *Drosophila melanogaster* and *Apis mellifera* in their shape discrimination performance. In that study, the fly was found to employ exclusively image matching and was therefore taken to possess a less advanced capacity for the processing of shapes than the honeybee, whose ability to extract particular shape parameters has already been well documented. In our experiments, both species of bee used particular shape parameters, but *M. rotundata* seems to have derived these parameters exclusively from image motion, irrespective of the type of contrast provided by the shapes, whereas *A. mellifera* seems to have extracted motion cues only from the motion-contrast shapes, but not from the luminance-contrast shapes. In other words, in the leafcutter bee, but not in the honeybee, motion perception dominates the behaviour even when luminance contrast is present. This idea is in accordance with earlier results investigating landmark learning in the solitary bee *Osmia cornuta* (Fauria and Campan, 1998).

In evolutionary terms, motion vision is probably the first visual capacity to have developed. Even the most primitive eyes enable motion and its direction to be perceived, and this is more crucial for the animal’s survival than is spatial resolution. The simplest mechanism to use in any visual task would therefore be to evaluate cues derived from image motion. When the effective parameter is the orientation of edges, as seems to have been the case in our experiments, then motion cues are sufficient for accomplishing the discrimination, because the orientation of an edge can be inferred from the direction in which its image moves. We wish to thank Nabil Yousef and Ron Bittner for providing the *Megachile* bees and Hans-Ulrich Thomas for providing and maintaining the experimental beekeeper. Thanks are due to three anonymous referees for very valuable comments on a previous version of the manuscript.

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