The Relation Between Pattern and Landmark Vision of the Honeybee (Apis mellifera)

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This is an exploratory study which takes advantage of a new method to study the difference between discrimination of patterns and the use of landmarks by honeybees. The experiments examine the transfer of black and white cues between two-dimensional patterns that are seen ahead by the bees, and lateral landmarks on the walls of tunnels through which they fly, and vice versa. The Y-choice apparatus, in which freely flying bees choose one of two targets from a fixed distance, was modified by adding, in each arm, a white paper tunnel followed by a transparent baffle, which controls the range at which the bees' choices are made. The results reveal that: (a) Bees can use both the distribution of black areas and the orientation of edges that they see on the side walls as they pass. So far as they were tested, the same visual features are used in landmarks as in targets. (b) The bees can immediately transfer the cues learned on tunnels to corresponding patterns on the targets, i.e. transfer forwards along their flight path, but not in the reverse direction. (c) New landmarks are learned in a few visits, sometimes even in one visit, but orientation cues on tunnels and targets take about 2 h to learn. (d) When trained on targets, they will not at first use the same cues on unfamiliar landmarks, but they rapidly learn to insert a new landmark into their flight path. The conclusion is that learning landmark locations and discriminating 2D patterns subtending < 45° in forward vision have different mechanisms.

Honeybee  Landmarks  Insect vision  Pattern  Food  Search

INTRODUCTION

The difficulty of separating landmark and pattern vision is highlighted by Tinbergen's famous experiment on the digger wasp, Philanthus, which has been repeatedly quoted in books and reviews. While a female wasp was within her burrow in the ground, Tinbergen (1932) placed a circle of pine cones around the entrance. When the wasp emerged, she briefly surveyed the scene before departing. During her absence the circle of cones was moved a little way along the ground. The wasp, on her return, aimed directly at the centre of the pine cones, demonstrating that she had formed a representation of the scene which enabled her to pin-point the nest entrance. An important point is that the wasp did not need an extended learning period. One key question is whether the wasp has a representation of the circle of pine cones as a pattern or as a group of landmarks, or both, or possibly in some other form peculiar to bees. Apart from the demonstration that bees use the position and range of a bar at the side to locate a reward hole (Lehrer, 1990), there are no relevant experiments, but as can be seen from recent discussions (Gould, 1998; Goodman and Fisher, 1991; Huber et al., 1994; Lehrer, 1994), the question of how the bees guide themselves visually runs through numerous studies of insect vision.

In the past, the experiments involved bees flying past landmarks to targets to obtain a food reward. I use the word "landmark" in the sense that bees fly past a landmark and orient themselves relative to several landmarks at different large angles. In contrast, they fly towards a "target" in forward vision as if that is their destination. In the traditional view of bee vision, at the desired destination, the landmarks lie in different directions at expected angles relative to each other, and the bees make the best fit that they can to an internal spatial representation (Anderson, 1977). A natural landmark is usually at a particular place on the horizon and need not have much two-dimensional (2D) structure or shape. In contrast, a pattern is traditionally a 2D target, and it has features such as length of edges, average orientation, disruption, or symmetry. In targets subtending less than 45° at the choice point, these features are detected in the tar-
get as a whole by 2D global filters for orientation and radial symmetry irrespective of location, and in larger targets by the relative positions of dark and light areas laid out in two dimensions (Horridge, 1996a, b). The pine cones in Tinbergen's experiment can be regarded as a 2D pattern for the approaching *Philanthus* or as landmarks when the wasp arrives near the nest entrance.

It is a familiar fact that bees take many visits before they associate a 2D black and white pattern with a food source. To make them look for and learn a pattern, its location must be regularly shuffled. Even after they learn to look for it and discriminate it irrespective of location, they continue to improve their performance. Over the course of two hours, 20–30 visits is a typical number to establish a pattern discrimination. On the other hand, if they find a stationary food source the bees learn its location in relation to local landmarks in that one visit, and will return again for more sugar solution in a few minutes. Tinbergen's *Philanthus* wasp, in the above example, learned the positions of the pine cones in a single survey. The present experiments were designed, among other objectives, to see whether this obvious difference in rate of learning is replicated in a controlled experimental apparatus.

Numerous experiments since the pioneering work of von Frisch (1914) have shown that bees are able to use both distant and local landmarks in the sense of the word used here, and quite different experiments using different techniques have shown that they can also be trained to discriminate between different 2D black and white patterns presented on a vertical surface towards which they fly to obtain a food reward (review, Wehner, 1981). As bees may act in different ways in different situations, it is important to note that in all the experiments they are flying towards a food reward, so data for other situations, e.g. recognizing the hive, may not be relevant.

Considerable evidence suggests that bees see landmarks and patterns differently, but the difference has not been identified. In the literature there are repeated accounts that landmarks are relied upon by the bees to bring them to a goal, but when their goal has been moved they arrive at the expected place and fail to recognize it, even though it may be less than a metre away. For example, in our experiments, when a feeder that they frequently visit is moved 20 cm they may fail to see it, but when another bee lands on it, they immediately turn and land beside the other bee, as if they use the other bee as a visual trigger stimulus but cannot recognize the feeder. They learn the place but not the pattern. On the other hand, when a landmark is moved, the bees frequently recognize it and are led astray.

An obvious difference between landmarks and patterns is that the former are strung out in a line along the horizon, separated as far as possible from each other to maximize the accuracy of triangulation. Landmarks can certainly be distinguished by colour (Cheng et al., 1986), angular size (Cartwright and Collett, 1983), range (Lehrer et al., 1988) and by their angular directions relative to each other (Anderson, 1977; Collett, 1992, 1993). The wide field of view of the compound eye along the horizon could be an adaptation to vision of landmarks. As bees rely on landmarks at every flight to and from the hive but learn to recognize two-dimensional patterns only slowly when there is no alternative, we could justifiably expect that the most exquisite discriminations are evident for landmarks, not for patterns. Whether bees can use orientation cues to distinguish landmarks from each other has still to be tested (see below). In fact, we might well ask why flying bees need to discriminate orientation at all when a combination of odour, colour vision and detectors for flower shapes (Horridge, 1994; Lehrer et al., 1995; Horridge and Zhang, 1995) are adequate.

As mentioned above, landmarks can be learned in one visit but patterns take much longer. This difference is presumably because 2D patterns require much more spatial processing of features than landmarks to be useful. The maximum number of combinations in a pattern increases as (number of states each unit area may assume) raised to the power (number of unit areas that combine), so enormous numbers of possible combinations are soon reached in quite small 2D patterns if all possibilities are to be distinguished. Recent work has shown that when bees discriminate patterns subtending angles larger than 100°, they rely mainly on the locations of black areas along the line of the perimeter of the pattern, strung out as widely as possible as if they are landmarks, as one way to avoid processing all the 2D features in the pattern (Horridge, 1994, 1996b). This finding led directly to the present study, which extends the target periphery to the side walls of the apparatus. As another way to avoid distinguishing all the combinations of features, in forward vision of targets subtending up to 45° at the choice point, bees use a group of large-field filters in parallel which take a global measure of the pattern as a whole (Horridge, 1994, 1996a).

Another potential relationship between landmarks and patterns is that as the bees fly along, the patterns ahead are converted over time to landmarks at the side, and it has already been proposed that at each place along the way the visual system is primed to look out for the next expected landmark (Collett et al., 1993). Time enters into the use of landmarks, whereas in experiments on pattern vision the bees learn to associate the food source with a stationary 2D pattern ahead.

In their use of landmarks, bees return for a reward to a position that makes the best fit with artificial landmarks (Anderson, 1977). For example (Cartwright and Collett, 1983), three black vertical cylinders were arranged around the reward. When the cylinders were moved, the bees looked for the reward at a place from which the landmarks most resembled the remembered arrangement as seen from the goal. A difficulty with this view is that the bee has not yet received the images on its retina until it is facing the same way as before and nearly at the goal. The more accurate the remembered image the greater is the problem of finding a match. The difficulty at any
particular moment is resolved if the bee has learned a succession of cues along the way. In fact, a recent study in which the bees learn to pass through a sequence of chambers, shows that they learn to take the appropriate direction at successive points along their route according to the location where they find themselves, and that they are then primed for the next landmark (Collett et al., 1993). So, we might expect that as the bee flies along the patterns ahead are transformed into landmarks at the side. If so, the bees should transfer easily from patterns back to corresponding landmarks. This expectation, however does not fit the observed behaviour for two reasons. When the bees learn the layout of landmarks at a new food site, they back away and oscillate from side to side in flight, making a visual survey which rapidly establishes, in reverse, their return track to the goal (Lehrer, 1991). Superficially, this behaviour facilitates the learning of local landmarks while the target still lies in view ahead. However, in this "turn-back-and-look" behaviour there is evidence that the pattern of the object fixated upon is not learned at all, only the relative positions of the local landmarks, for, as said above, the bee returns to the right place but does not necessarily recognize the goal. Secondly, we are familiar with the fact that patterns take some time to learn while landmarks are learned very quickly, so there is already some distinction between vision of landmarks and patterns. The intention is to explore the relation between vision of local landmarks and the discrimination of related patterns by a variety of experiments to clarify some of these questions.

**MATERIALS AND METHODS**

All experiments were done with the Y-choice chamber (Srinivasan and Lehrer, 1988), modified by the addition of the tunnels and baffles and ventilation for the extraction of odour (Fig. 1). The apparatus was used under an outside shelter with the targets facing bright daylight. The walls of this apparatus are of white card, the roof is of transparent Perspex. The baffles have been added so that the angle subtended by the target can be controlled, and they bring the added advantage of facilitating sharp decisions about the success or failure of the bees' choices. The baffles are of transparent "Artisicane Drawfilm" 0.13 mm thick set in a frame 1 cm wide between the tunnel and the target. The hole at the centre of the baffle is 8 cm in diameter and the bees can also exit by walking under the baffle. They never learn to enter this way, but always fly through the central opening without touching it. To create a situation in the Y-choice apparatus in which the bees fly past experimentally manipulated targets as if they were landmarks, the bees were obliged to fly through one of two short tunnels before they reached a baffle. Each tunnel was a cylinder 30 cm in diameter and 12 cm long, made to fit into the Y-choice apparatus. One tunnel was placed in each arm (Fig. 1).

Honeybees from a local hive select one of the two targets by looking into and exploring the tunnels while in flight in the central chamber. They soon learn to fly into the tunnels and look at a target through a baffle. The inside walls of the tunnels carry cues that are visible to the lateral eyes of the bees flying through. The criterion for scoring the bees as correct or not is when the bee first passes through the hole in the baffle, so they can explore both tunnels during training and in tests on tunnels without scoring an error. The targets, 25 cm dia., subtend an angle of 45° at the bee's eye when the baffle is at (A) at a distance of 27 cm, and 103° with the baffle at 9 cm at (B) (Figs 1 and 2). Positive targets have a hole 2 cm dia. at their centre for access to the reward chamber and negative ones have a blind tube. Although the positive side is always drawn on the left in the illustrations, the positive target and the reward with it is alternated every 10 min with the negative target to prevent the bees from learning which side to visit. The reward is a fresh aqueous solution of sucrose sufficiently strong to keep the regular bees coming without too many recruits. During the training the bees obtain a reward at every correct choice. The bees are individually marked and a separate record is kept of the performance of each. Most experiments use a fresh group of 8–12 marked bees, which is about the right number to avoid several arriving at the same time, and new recruits are removed.

In all of the experiments, the bees are trained on a pair of tunnels or targets and, after an initial training period of up to 2 h on the targets, their performance is measured in the same situation while training continues. These results are labelled "train and test". The bees that were trained with a pair of tunnels or targets were then tested for periods of only 5 min, with two different tunnels or patterns that they had not seen before, first with the reward on one side and then with the sides reversed. The brief periods of testing last 5 min on each side, and the bees are rewarded on one of the targets on each side. If they are not rewarded, they continue to search inside.

**FIGURE 1.** The Y-choice apparatus modified by the addition of a paper tunnel and a transparent baffle in each arm, and with odours extracted from the chambers adjacent to the targets. The decision of the bees are scored when they pass the baffles, which can be placed at AA' at 27 cm or at BB' at 9 cm from the targets.
the apparatus and seriously confuse new arrivals. Previous work has shown that rewarding during short tests on targets subtending 40°–45° has no effect on the performance of the bees (Horridge and Zhang, 1995) but we discovered in the present work that rewarding during tests has an immediate effect on learning of landmarks. These tests were mainly to discover whether discrimination could be transferred from tunnel to target or vice versa. In most cases a number of different tests were introduced at random in 5 min periods between longer periods of continued training. The test periods are very short compared to the time required to train bees to a 2D pattern, and the bees have time to make only one rewarded visit in any one test period. These results are labelled “test”.

In some of the experiments, the positive and negative targets or tunnels are identical but one is rotated by 45° or 90° relative to the other. This strategy means that the bees have less chance of using differences between images that are not relevant to the experiment, such as differences in disruption or brightness of the pattern, regional layout of the pattern, differences in area of black regions, or the existence of particular detail in one pattern and not in the other. These stimulus pairs allow a further powerful control to be made. Instead of interchanging the positive and negative targets or tunnels every 10 min, they were both rotated by 45° or 90° and the reward was moved to the other side. This strategy acted as a control against differences in odour, brightness or unexpected cues such as dirty marks on the targets, but the result was the same as interchanging the two sides.

Odour left behind by other bees may be an influence when the bees approach closely to the reward hole, but in all experiments their choices are recorded as they pass the baffle before they have that opportunity. As a further precaution against the use of odour as a cue, a small fan at a distance and two pipes 1 cm dia. extracted the air from the lower corners of the chamber containing the pattern (Fig. 1).

Some of the patterns are printed in black on white copying paper of constant quality and then copied on a Xerox machine with standard paper and the same settings; others are made of strips of black card stuck on the same white paper. Previous work has shown that bees can resolve the gratings and bars used here (Srinivasan and Lehrer, 1988). The resolution of the bee’s eye for the equal black and white stripes of a parallel grating is equal for vertical and horizontal gratings, and is adequate to give at least 65% correct choice at a period of 4° per stripe period, which falls to 50% at 3° per period, measured with the same Y-choice apparatus with no baffles. Single bars are more easily resolved than gratings of the same bar width, and gratings of period 4° are drawn to scale in Figs 2 and 3.

The groups of bees make 10–20 visits in each period of 10 min. The number of correct choices, and the total number of choices, are counted in each period. The fraction of correct choices for 8–12 periods of 10 min each, together with the standard deviation and the total number of choices, are tested by the χ² test for a difference from 0.5, then the results are converted to percentages. Further details are given in van Hateren et al. (1990). Each pair of patterns is illustrated in the figures with the percentage choice and their statistical significance, if this is in doubt. Performance is defined as the average percentage of correct choices, and some of the important results are those where the bees cannot discriminate.

RESULTS

A tunnel with 4 bars, discriminated from itself rotated by 45°

In this experiment four black bars 12 cm long and 4 cm wide are located longitudinally at equal intervals of 90° on the inside of the two tunnels but they differ in position. The tunnels are identical but one is rotated by 45° relative to the other every 10 min when the reward is moved to the other side (Fig. 1). The bees fly through a tunnel before they reach a baffle and are scored. During the training, the targets on the end walls around the reward were blank white paper, but the bees were used to heading towards the central hole leading to the reward.

This experiment is designed to test whether the bees discriminate the positions of the bars in the tunnels. After only an hour of training, the result was 83.1 ± 2.6% correct, n = 205, P < 0.0001. The bees fly along the axis of the cylinder without fixating on the bars on the sides. There is no doubt that learning is faster and more effective than when they learn a 2D cross pattern subtending 100° seen straight ahead. A repetition of this experiment with the positive and negative tunnels reversed [Fig. 2(a)], including some continued training periods between the following tests, gave the result 85.4 ± 1.5%, n = 498, P < 0.0001.

The tunnels were now removed and the trained bees were tested with targets for periods of 5 min on each side. The targets have 4 bars in the same positions relative to each other as in the tunnels [Fig. 2(b)]. From previous work, it is known that bees learn to discriminate these two targets, with 80% correct, when the baffle is at 0 cm and the targets subtend > 100° at the choice point (Horridge, 1996b). Despite the fact that these targets normally take about 2 h to learn, the bees transfer their discrimination to the targets from the bars in the tunnels at once, with 73.8 ± 2.7% correct choices, n = 253. This result suggests that the bees look ahead and see in front of them the familiar combination of bars that they would anticipate on entering the tunnels.

As a control, in tests alternating with the above, the trained bees were tested on the targets with the baffles at 27 cm, making an angle of 45° subtended at the choice point [Fig. 2(c)]. The result, 52.4 ± 3.9%, n = 292, shows that as usual (Srinivasan et al., 1994; Horridge and Zhang, 1995) the flying bees fail to discriminate the crosses at this range, but this is not a problem of resolution of the pattern as shown by Fig. 2(d). The bees fail
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(a) Train and test on tunnel

\[ 83.4\% \pm 1.3\%, \quad N = 498, \quad p < 0.00001 \]

(b) Test on target at 9 cm

\[ 73.8\% \pm 2.7\%, \quad N = 253, \quad p < 0.00001 \]

(c) Test on target at 27 cm

\[ 52.4\% \pm 3.9\%, \quad N = 292, \quad p > 0.5 \]

(d) Resolution of bee’s eye 4° period

FIGURE 2. (a) The two training tunnels have each four horizontal bars but one is rotated 45° relative to the other. The bees learn this situation very well. (b) They then transfer their discrimination to targets of two crosses at 45° to each other, with the baffle at 9 cm. (c) With the baffle at 27 cm the bees cannot discriminate these targets, but this is not due to a lack of resolution of the eye, as shown by (d) a grating of period 4°.

because in forward vision they have no mechanism for discriminating the rotation of right angled crosses that subtend less than 45° at the choice point (Horridge, 1996a).

Vertical and horizontal gratings in the tunnels

This experiment tests whether bees flying through the tunnels can discriminate the orientations of coarse gratings that they pass, and whether they can subsequently transfer the strong orientation cue to a target directly ahead. The positive tunnel had 3 circumferential black rings of period 6 cm and the negative one had a longitudinal grating of 15 periods of stripes each 6 cm long [Fig. 3(a)]. The two tunnels are orthogonal, and it was necessary to change them over together with the reward every 10 min. During the training periods there was no pattern on the targets except the central hole. The baffles were at 9 cm throughout the experiments.

After 2 h of initial training, the result was 79.1 ± 2.9%, \( n = 186, \quad P < 0.0001 \). The tunnels were then removed and the trained bees were tested with two targets, first on one side for 5 min and then on the other side, between 10 min periods of continued training on each side. The baffles were kept at 9 cm for the tests. In one series of tests, the targets were plane gratings of period 6 cm, one horizontal and the other vertical, to see whether the bees retained an orientation cue [Fig. 3(b)]. The result of these tests was 63.4 ± 4.4%, \( n = 120, \quad P < 0.005 \), in favour of the horizontal grating which shows unexpectedly that the bees rely more on the top or bottom of the tunnel than the sides. In the other tests one target was a pattern of three concentric circles of period 4 cm and the other was a pattern of 8 black and 8 white equal sectors [Fig. 3(c)]. The result was 63.5 ± 4.3%, \( n = 121, \quad P < 0.005 \), showing that the trained bees immediately transfer this discrimination forwards along their path.

Transfer of sectors and circles from targets to tunnels

These experiments are designed to test whether the bees can transfer their discrimination of a target backwards to a corresponding pattern on the tunnel walls as they approach. A new group of bees was trained on randomized targets of 2, 3, or 4 concentric circles (which were also reversed in contrast at alternate presentations) as the positive target, and randomized sector patterns (of 4, 6, 8 or 12 sectors) as the negative target. Only some of these are shown in Fig. 4(a). The baffles were at 27 cm to ensure that the bees learn the distant appearance of the target, which subtends 45° at the choice point. After 2 h of training on the targets the result was 81.1 ± 2.9%, \( n = 131, \quad P < 0.005 \), confirming earlier work that the performance is high on this task (Horridge and Zhang, 1995).

The targets were now removed and replaced by a pair of tunnels, and the trained bees were tested in three situations. In the first, the tunnels carried the circular and longitudinal gratings as previously used [Fig. 4(b)]. In the second, the tunnels carried one set of equally spaced parallel horizontal bars and one set of parallel vertical ones with the bars at each side of the flight line [Fig. 4(c)]. In the third test the sets of bars in the tunnels were above and below the flight line [Fig. 4(d)]. These three tests were repeated in this order five times for 5 min on each side between periods of continued training. The result of the first, with the gratings on the tunnels, was 82.4 ± 3.3%, \( n = 110 \) with the preference towards the circular grating. The result of the second, with bars at the sides, was 88.2 ± 3.1%, \( n = 110 \), and the result of the third, with the bars above and below, was 89.9 ± 2.9%, \( n = 110 \), in both cases with a preference towards the bar orientation corresponding to the target of circles. The performance in the tests is better than that in the training, which shows that the bees in the tests rapidly improve their use of the cues on the tunnels.

When first presented with an unfamiliar tunnel when they expect a target, the bees initially refuse to continue. They do not spontaneously transfer what they have learned from the target to the tunnel. They turn and go back repeatedly to their last familiar landmark at the entrance to the apparatus and make their run again. In doing so, they do not necessarily pass the negative baffle and so do not make an error. Finally, they pass through a baffle, apparently at random, or they follow another bee, but then if successful they rapidly recognize the new landmarks, even after a single visit. The protocols of the individual bees show that they all learn by the third visit. Although the initial choices after the change were ran-
dom, they achieve a rapid recognition so that over the 100 or so choices required for a statistical test they do better than with the original targets [Fig. 4(c,d)]. Brief tests on patterns have little effect on the bees' preferences but tests on landmarks have an immediate effect. The bees are able to fit a new landmark into what they already know much faster than they learn a new pattern.

**Oblique bars in the tunnels**

This experiment tests whether bees flying through the tunnels can use the orientation of single bars that they pass, and whether they can transfer the orientation of the bar at the side to a target directly ahead.

One tunnel had 7 pairs of black bars sloping upwards towards the reward, and the other (the negative one) had 2 pairs of similar bars sloping downwards (Fig. 5). The two sides of a tunnel are mirror images, and one tunnel is identical with the other rotated by 180°. In fact, to change sides both tunnels were simply rotated by 180° and the reward moved to the other side. There was no pattern on the targets during the training periods, except the central hole. The baffles were at 9 cm throughout the experiments.

After 2 h of initial training, the result on the tunnels was 77.4 ± 3.4%, n = 148, P < 0.0001. The tunnels were then removed and the bees were tested with two targets, first on one side for 5 min and then on the other side, between 10 min periods of further training on each side. The targets were chevron patterns of two pairs of oblique bars in the same relative positions as they had been on the side walls of the tunnels, but now projected ahead around the reward hole [Fig. 5(b)]. As the bees approach, the targets bear some resemblance to the insides of the tunnels that the bees had previously learned. The question is whether the bees transfer the orientations from the inside of the tunnels to the targets ahead. The result was 70.5 ± 2.9%, n = 234, showing clearly that they recognize the cues. In the periods of continued training between tests, in aggregate, the result was 76.9 ± 2.4%, n = 322. This result suggests that they now recognize the orientations at the front that had previously become familiar as they flew past, and that they adapt rapidly to the new locations of the cues as patterns, although patterns normally take longer to learn.
test periods were samples of the same crosses [Fig. 5(c)]. At times, but not all the time, the bees turn sideways to look at the crosses as they fly through the tunnels, and they can approach them closely.

After two hours of training the result was $81.1 \pm 2.4\%$, $n = 273$. Tests with the vertical and oblique crosses on the targets and the baffles at 9 cm [Fig. 5(d)], gave the result $62.8 \pm 3.7\%$, $n = 170$, $P < 0.001$, showing that they have learnt a cue of some kind during their training, but not as much as they learn from simple oriented bars.

Experiments without the tunnels

Transfer between targets and landmarks at the baffles. A new group of bees was trained to targets of regular black and white stripes of period 12°, as seen from the 8 cm openings in the baffles placed at 27 cm [Fig. 6 and Fig. 7(a)]. The targets therefore subtend 45° at the choice point. The positive target had vertical stripes and the negative one, horizontal ones. The bees learn this task.

Transfer of right-angled crosses from tunnel to target

In this experiment, the whole cross was placed in a vertical or oblique orientation on the inside wall of the tunnel during the training periods, and the targets in the

FIGURE 5. Transfer between a cue on the tunnels to a corresponding cue on the targets. (a) The bees learn to discriminate the two diagonal stripes on each side of the walls of the tunnels. (b) They then transfer this orientation cue when tested on targets with the corresponding patterns, with the baffles at 9 cm. (c) With a new group of bees, the positive tunnel has on each side a cross with a vertical stem, the negative target has an oblique cross. (d) Tests on corresponding targets with the baffles at 9 cm show that the bees pick up sufficient cues.

FIGURE 6. The arrangement of the apparatus for testing with targets and bars at the baffles, as in Fig. 7.

FIGURE 7. The lack of transfer of orientation cues in either direction between targets and freely hanging landmarks. (a) The bees were trained on two targets with vertical (positive) and horizontal (negative) gratings, with the baffles at 27 cm. (b) The targets were then removed and the bees were tested with two bars 2 cm by 12 cm hanging freely at the orifices in the baffles. The bees first refused to fly between these bars, and they fail to recognize the orientation cue. (c) When they are trained on the freely hanging bars, they learn their orientations rapidly and well. (d) A new group of bees were trained with the bars and the targets, but (e) when tested on the targets alone they are lost.
very well in 2 h of training, to give a result of 85.4 ± 2.5%, n = 201.

The targets were then removed and two black bars 2 × 12 cm were placed at the opening of each baffle. The bars were of black cardboard hanging freely in space at the baffle. At one baffle there was a vertical bar on each side of the opening; at the other there was one horizontal bar over and another bar below the opening [Figs. 6 and 7(b)]. The test was to see whether the bees trained to discriminate the vertical grating would now select the correct opening between the vertical bars.

The result was clear. The bees spent a long time in the choice chamber, hovering and turning this way and that, but they passed the bars only with great hesitation. There were 15 individually marked bees: of these 7 refused to fly between the bars at all. In two periods of 5 min, the bees that would pass through were correct 11 times out of 21 choices. Clearly they did not spontaneously transfer the orientation from the targets to the bars between which they had to fly.

However, the same bees learned the new situation very quickly. After half an hour of training, with only the bars at the baffles and no targets [Fig. 7(c)], the bees had made an average of only 8.4 visits each. They were then scored while training continued. The result was 75.8 ± 4.0%, n = 87, P < 0.0001. By this time it was realized that the rapid learning and high scores are typical of learning the use of landmarks, in this case the mere presence of the bars at the side or above, whereas learning to head towards two-dimensional patterns is a slower process.

Next, a new group of bees were trained to targets of regular gratings together with pairs of bars 12 × 2 cm of the same orientations presented simultaneously at the openings of the baffles. A horizontal positive grating was coupled with a pair of horizontal bars at its baffle [Fig. 7(d)]. The bees learned this situation quickly. Over two hours of training from scratch, with the usual reversals of the bars at the baffles and the gratings on the targets every 10 min, the average performance was 74.9 ± 3.3% correct, n = 172.

The bars were then removed from the openings of the baffles and the bees were tested on just the target gratings for 5 min periods (each way) alternated with continued periods of training [Fig. 7(e)]. The result was 49.9 ± 6.2% correct, n = 66, showing that the bees are incapable of discriminating the target without the bars. They have learned the orientation of the bars that they have to fly between, but not the same orientations of coarse gratings subtending 45° which have been visible throughout the learning period at the goal at a distance of 27 cm in front of them. Meanwhile in the periods between tests with the bars present, the performance was 78.5 ± 3.9% n = 109. These experiments show that the bees have sufficient cues from the bars that act as landmarks at the baffles, where they are first needed, and being sufficiently informed they do not learn the orientations at the reward in front of them. The situation is comparable to that found repeatedly, when bees learn to come to a place but fail to recognize the goal if it is moved.

The bees that fly past the baffles go straight towards the holes in the centres of the targets, as they would if the guiding bars were present, but if in error they sometimes turn back when they are close to the negative target. Perhaps they have learned not to fly into a horizontal grating. This result suggests that objects hanging freely in space are treated differently from 2D cues on the tunnel walls, and therefore that the bees have a real sense of separate cues in 3D space on either side of them, as opposed to a 2D cue on a flat sheet in front. This is a question for the future.

_Flying through open circles._ When trained to fly to a target of concentric circles, or a single circle, the bees fly cleanly through the familiar 8 cm circular hole in the baffle, but they refuse to fly through a new aperture of 3 cm or less in diameter surrounded by a circular black annulus 0.5 cm wide. They do not recognize the aperture independent of size, but will fly through an aperture only when it is the size they have learned or larger. After a few minutes of hesitation, while a group of bees gather but do not pass, one bee finally goes through the smaller hole, immediately followed by others that see it. Individually marked bees hesitate only once to fly through a smaller than expected aperture; thereafter they go through without delay if rewarded. The minimum size of the aperture through which they will fly is about 2.0 cm, below which they land on the thin edge and take off again on the other side. When the familiar small aperture is suddenly made larger, the bees pass through without pause. This is in agreement with an unpublished finding that bees trained to any grating will go to one with a larger period but not one with a smaller period.

_Landmarks on the side walls._ The following experiments were designed to compare the discrimination of local landmarks at the side (as defined here) with the known abilities to discriminate orientation and the layout of black areas in 2D targets.

With the baffles at 9 cm, the landmarks were placed at the sides of the extended choice chamber [Fig. 8]. In the first experiment two black bars 18 cm long and 2 cm wide were placed on each side of each arm. The bees were trained with the positive bars at an angle of 20° to the vertical and the negative bars vertical. After 2 h of initial training the average result over the next 140 min was 64.0 ± 2.8%, n = 283, P < 0.0001. With a new group of bees trained to an angle of 30° to the vertical [Fig. 8(b)], the result was better at 71.0 ± 2.7%, n = 274, P < 0.0001. Tests with the angle on the positive side reduced to 15° gave the result 59.4 ± 3.3%, n = 217, P < 0.005 [Fig. 8(c)]. The time required to learn shows that the bars are treated as 2D patterns. The performance of the bees with the bars at various angles is almost exactly as previously found by Wehner (1968) with fixating bees looking at single bars subtending 130° long and more than 5° wide at the point of choice. On this scale, discrimination of orientation appears to be similar.
for landmarks at the side and very large targets straight ahead.

Next, the stripes were replaced with ping pong balls, painted matt black, which were located on each arm with the line between them at 20° to the vertical for the training periods (Fig. 9). The black ping pong balls were a convenient way to control the distribution of black areas in space without orientation of edges. The matt black balls look exactly circular from any direction. The pair of balls on one side leaned in the opposite direction to the pair on the other side, and their arrangement in one arm was the mirror image of that in the other. The four balls in each arm occupy the corners of an imaginary tetrahedron through which the bees must fly. The opposite edges of this tetrahedron are inclined at 40° to each other [Fig. 9(a)]. After an initial training period of 2 h, the result over the next 2 h was 65.4 ± 3.1%, n = 231, P < 0.0001. The time taken to learn is similar to that for 2D patterns. At intervals the trained bees were tested for periods of 5 min with the angle halved to 20° [Fig. 9(b)]. The result was 68.2 ± 3.8%, n = 274, P < 0.0001. Meanwhile, during the continued training periods between tests, with the angle at 40°, the performance was 70.3 ± 2.5%, n = 324, P < 0.0001. Tests with an angle of 10° in the tetrahedron showed that the bees can no longer discriminate [Fig. 9(c)]. In similar tests with targets subtending 130° at the choice point, Wehner (1981) found that changes in the positions of sectors in radial patterns could be discriminated down to about 20°. Once again, the bees do not have to fly towards targets to discriminate orientation or the location of black areas. Landmarks at the side are discriminated just as well as targets ahead, and orientation is learned slowly whether on landmarks or targets.

DISCUSSION

A long history of research on landmark vision of bees (reviews by Wehner, 1981; Collett, 1992) shows that landmarks are recognized by their visual appearance, that the track to the goal is defined by minimal cues from a sequence of landmarks passed along the way, and the location of the goal is recognized by the relative directions and ranges of the local landmarks. The basic assumption is that the retinal image of the landmarks is compared with a crude icon or internal trace of an earlier retinal image in memory. Landmarks are learned in a few visits, or even in one visit. It is assumed that this is an
ancient system that evolved in early arthropods that had to find their way in a territory or to a home in a burrow. If we model it by a spatial mapping (and what else is available?), we create the problem of how the map is adjusted during rotation of the whole animal.

Added to the landmark system is another which deals with smaller 2D images as seen ahead by a group of global filters that are less concerned with the location of individual features. Theories of processing of 2D black and white patterns have advanced several steps beyond a comparison or overlap with a hypothetical icon. The first step was the proposal that bees can discriminate the disruption of a pattern or the ratio of edge length to area irrespective of shape or outline (Zerahm, 1933). The second was the inference that orientation detectors with wide fields and broad angular orientation tuning curves abstract the average orientation over regions of the visual field irrespective of location (van Hateren et al., 1990; Srinivasan et al., 1994). A further step was the inference that bees have innate detectors for radial symmetry (Horridge, 1994) as suggested by their spontaneous preferences for flower-like patterns (Lehrer et al., 1995), their insensitivity to rotation of radially symmetrical patterns and excellent discrimination between radial patterns of different types (Horridge, 1996a) and their excellent performance in learning symmetrical patterns (Horridge and Zhang, 1995). All these discriminations take a couple of hours to learn, involving 20–40 visits, and they allow considerable generalization of the stimulus pattern, i.e., learning from randomized patterns and discrimination of global features irrespective of range and other features.

The results presented here reveal the similarities and differences between targets and landmarks as defined here by the actions of "flying towards" targets and "flying past" landmarks. First, there are no great differences between the kinds of cues the bees use on the sides and similar cues on the periphery of very large targets subtending at least 100° at the choice point (Horridge, 1996b). However, new 2D patterns take longer to learn than new landmarks and orientation discrimination requires 20 or more visits for both targets and landmarks. The conclusion is that learning angular location relative to the direction of looking is quick but learning generalized features via spatial filters is slow. Therefore, when presented with very large targets, the bees learn the periphery quickly and the centre more slowly so that measures of learning speed are difficult to interpret. Also, with landmarks and large targets, brief tests influence what has been learned, so the only meaningful tests with trained bees are those on small targets.

The effect of change is greater for landmarks than for targets. Bees fly through a familiar tunnel without hesitation, but a change in the cues or the removal of the three-dimensional tunnels makes them pause. They have to learn to pass through unfamiliar tunnels or to pass unfamiliar landmarks, but they learn to do so very quickly. This difference is less obvious when they are trained to targets which are then changed. From a distance they easily accept a forced choice between two unfamiliar targets that bear some resemblance to the ones they were trained on, but may turn back when the target subtends more than 100°. The bees always behave as if landmarks are more reliable than 2D patterns. Secondly, the bees readily transfer cues from the tunnel forwards along their path to the targets with similar patterns, but they will not transfer easily from targets to tunnels backwards along their path. They have to learn to do that, but again they learn the new landmarks in a few trials. This asymmetry makes sense in terms of the natural sequence of choices that they make when flying through a familiar environment, in that they spontaneously recognize what lies ahead. In summary, they adapt rapidly to new landmarks but learn patterns slowly and then ignore changes to them.

One of the generalizations that is coming out of these studies relates to the way that flying bees process large moving images full of information. To simplify this huge task the bees have an ancient two-dimensional wide-angle system for rapid memory of location of dark areas (Wehner, 1981, Fig. 59; Horridge, 1996b), which now appears to be the same as landmark vision. This is the system that brings the bee to the right place and eventually to the goal as it zooms in with progressively more local landmarks. Added to this is the other system of filters for average orientation that have large fields and broad tuning curves (Srinivasan et al., 1994), also filters for circular and radial flower-like patterns that are independent of rotation (Horridge and Zhang, 1995). There are also filters for bilateral symmetry irrespective of pattern (Horridge, in press). The outputs of these luminance-contrast filters take time to establish a discrimination and they lose the spatial relations within their fields. Recently it has been suggested that edges detected by chromatic contrast or by colour blind motion contrast (parallax) are also discriminated by the same system, on the evidence that discriminations based on one set of inputs are transferred to targets that require a different set of inputs (Zhang et al., 1995). Very large targets are discriminated by these filters as well as by the locations of contrasts at their edges. As shown by the experiments in Fig. 8, the vision of landmarks can also use orientation as well as colour, range and size, so there is no sharp boundary between the limits of discrimination within 2D targets subtending angles up to about 45° at the point of choice and for landmark vision within scenes subtending angles up to 360° around the horizon.

We are justified in distinguishing between landmark and pattern vision, but solving the mechanism of pattern perception by discovering evidence of filters in visual processing has not helped much in understanding the rapid visual learning of local landmarks, because the latter relies instead on a rapidly consolidated memory of very large angles between contrasts on the eye relative to the direction of looking. There is also an additional and unknown mechanism that allows the bee to turn without confusing the directions of the landmarks, as if
the angles are measured irrespective of location. In contrast to the inference of particular non-spatial filters, we have little data that throws light on the mechanisms of landmark vision within the bee, mainly because appropriate controlled experiments have not been devised.

REFERENCES

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