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A Model for Landmark Learning in the Honey-Bee

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Summary. 1. A single bee is rewarded with sugar for visits to the centre of a circle of eight landmarks.

2. After training, tests are given in which the sugar is removed and the flight path of the bee recorded as it searches for it. The bee persistently searches a small area in the centre of the circle, demonstrating that it has learnt the position of the sugar relative to the landmarks (Fig. 1A, C).

3. In a second test, three landmarks are removed leaving a semi-circle. The bee now searches a small area "inside" the semi-circle (Fig. 1B, D). In its chosen position none of the landmarks match in size, bearing, or angular separation with the values of the landmarks present during training (Fig. 2), showing that a "retinal matching" model of landmark learning does not predict these results.

4. It is suggested that the bee is not measuring the position of individual landmarks but the overall landmark configuration, a "Gestalt" hypothesis first put forward by van Beusekom (1948). It is hypothesised that the bee moves "inside" the semi-circle in an attempt to have landmarks "surrounding" it as it had when collecting sugar from the centre of the circle.

5. The term "sourroundedness", a concept similar to the Gestalt idea of "degree of closure" is given a rigid definition. A term describing landmark average distance and a comparison process are also defined, these terms are incorporated into a computer program.

6. The computer program successfully predicts the results of a series of experiments with various training and testing situations (Figs. 1, 5, 6, 7) and some results found by van Beusekom (1948) with the digger wasp (Fig. 8).

7. The model is compared with a "retinal" model and its behaviour in real world situations discussed. It is concluded that the model, although containing some arbitrary features, represents a possible, rigidly defined and testable model of the landmark learning of the bee.

Introduction

Many hymenoptera are able to use landmarks to find specific locations. Manning (1956) showed that bumble-bees visiting *Cynoglossum officinale* could learn the locations of individual plants. If a particular plant was removed the bee searched in the area where it had previously been located. Individual honey-bees also visit specific small groups of flowers, even when the flowers are growing in dense and continuous crops (Ribbands, 1949). Although navigation by the sun compass can take a bee close to its goal the final small area of flowers it restricts its attention to must be defined by the surrounding landmarks. Lauer and Lindauer (1971) have clearly shown that bees can use landmarks close to the goal to define the position of a sugar source. They showed that the ability to use near distance landmarks is dependent upon the race of the bee, *Apis mellifica carnica* having a greater learning ability than *Apis mellifica ligustica*. It is not known how bees use near distance landmarks to define a particular location, but experiments with other insects have given rise to some theories which may have general application.

Tinbergen (1932) conducted a long series of experiments with the wasp *Philanthus triangulum* in which he manipulated a circle of objects marking the entrance to the nest. He showed that the wasps oriented themselves neither to a specific number of objects, nor to the exact shape of the circle, but to a "visual stimulus complex". This idea was developed by van Beusekom (1948). He was able to establish that the properties of individual landmarks are not of as great importance as the overall configuration of the landmark constellation. The wasp can still find its way even when landmarks are added or removed provided that the landmarks present retain the same overall configuration as the original constellation. These observations led van Beusekom to believe that a set of landmarks is perceived as a "Gestalt", that is as a whole shape or configuration which can be recognised independently of the precise location, number or type of landmarks comprising it.

Recent experiments with a dipteran, the hoverfly *Eristalis*, have produced a different kind of theory. Collett and Land (1975) show that the hoverfly can return from a distance to its "home" – a stable, mid-air hovering position defined by visual cues. They propose that "the fly has a representation of the spatial position of its home in terms of the visual image on its retina when it hovers there. Thus the home is defined in terms of an essentially two dimensional picture: the sizes, forms and relative positions of landmarks imaged on its retina .... if the fly is displaced from its home it can find its way back by obeying relatively simple rules which make the fly move in such a way that the retinal image is transformed to what it is when the fly is at home" (p. 79). These rules are easy enough to understand when only one landmark is being used by the fly; if the retinal image is smaller than its remembered image then the fly moves towards the marker and if it is bigger it moves away. The problem becomes more difficult when the home is defined by many markers; matching the retinal image and the remembered image may now be very difficult. If the fly is in a position where its view of the landmarks puts them in a completely different order on its retina from the order in its remembered image then very complex rules may have to operate for it to work out how it should move in order to improve the fit.

This theory is clearly of a different kind from that proposed by van Beusekom. Here we deal not with the overall configuration of landmark constellations but with the precise bearings, sizes and angular separations of individual landmarks. In the experiments to follow, the results will be discussed in terms of both kinds of theory.

Methods

A single honey-bee (*Apis mellifica*) is trained to visit a sugar source whose position is marked by a set of landmarks. After training, a series of tests is carried out; in each test the sugar is removed and the flight path of the bee recorded as it searches for it. The bee is found to persistently search certain small areas, their location shows where the bee thinks the sugar should be in relation to the landmarks. If the arrangement of the landmarks is altered after training, then during the test the bee is found to search in new areas. These changes tell us how the bee tries to match its view of the new landmark arrangement to its memory of the landmark arrangement present during training. From the positions it chooses it is possible to guess at the parameters of the landmark constellation that it is measuring.

Apparatus. The experiments were conducted in a room 15 m from the bee hive. The bee could enter the room through a large window. Adjacent to the window, a chamber had been enclosed by hanging large, white, cotton sheets from the ceiling of the laboratory. A pair of white sheets also hung across the window, they overlapped in the centre but were separated sufficiently to allow bees to fly between them and into the chamber. The hanging sheets prevented any view of the external world but permitted sunlight to diffuse through giving an even light. A large white board (2 m) level with the bottom of the window formed the base of the chamber. On this board were placed a set of landmarks and a source of sugar. The landmarks were tall cylinders (40 mm diameter, 500 mm high) painted matt black to contrast sharply with the white surroundings of the chamber. The source of sugar was a small drop of 2 M sucrose solution (3 mm diameter) formed around the tip of a hypodermic needle. The needle projected through the board from below and was connected to a vessel containing sucrose solution which replenished the drop as the bee drank from it.

The behaviour of the bee inside the chamber was observed by means of a camera attached to the ceiling. The camera pointed straight down from the centre of the ceiling providing a view of the whole experimental area upon a video monitor and allowing records to be made on videotape.

Training. A single bee, marked with a spot of paint on its thorax, was allowed to visit the sugar source. One particular training constellation of landmarks was used with each individual bee. The position of the source remained fixed with respect to the landmark constellation but the whole arrangement of sugar source and landmarks was moved at regular intervals. The bee appeared to learn the position of the sugar source very rapidly as after only a few visits it flew directly to it. On average the bee returned to the experimental chamber every three to five minutes throughout the hours of daylight. After a three day training period, tests began.

Testing. The sugar source and the landmark beacons were removed and the board was cleaned with hot water and absolute alcohol. Some or all of the beacons were then replaced but without the sugar source. When the bee entered the room it flew among the beacons searching for the sugar. Its flightpath was recorded on videotape for a period of two minutes and then the sugar source and the training constellation of landmarks were restored. The bee was then allowed to go on visiting the sugar source until the next test thirty minutes later.

Results

The flight path of the bee was transcribed from the videotape recordings to give results like those shown in Figure 1A, B. Each figure shows the flight path from one test, the results from a series of tests were added together to find the average frequency with which the bee visited different areas. The flight path records were added by projecting a grid containing 20 mm squares onto them and recording the number of times each square was crossed. To simplify the display of results the square crossing values were then divided into categories and enclosed by contour lines (see Fig. 1C, D), shaded areas show the most frequently visited areas.

In the first situation to be considered, the bee was trained to visit the centre of a circle of eight landmarks. When it was tested on a circle identical to that present during training (Fig. 1A, C) the most frequently visited region was a small area in the centre of the circle, this demonstrated that the bee had learnt the position of the sugar relative to the landmarks. When the circle was changed into a semi-circle (Fig. 1B) by removing three of the landmarks, the bee still concentrated its search in a small area (Fig. 1D) even though its only previous experience had been of the circle of landmarks. Interestingly, this area was not in the centre of the circle of which the semi-circle was a part, but much further "inside" the semi-circle.

It must be remembered that these observations were derived from a television camera looking down upon the landmarks and the flying bee. The bee, however, was not looking down upon the landmarks but was flying among them, the beacons were 500 mm high while the bee rarely flew more than 50 mm above the ground. We can depict the view seen by the bee by diagrams like those shown in Figure 2. At the top is shown the view of the training constellation from the centre of the circle, the eight landmarks are spaced at equal intervals around the bee and all have the same retinal size.

When the bee was presented with a semi-circle of landmarks it now chose the position where its view was as in Figure 2B. For comparison, two alternative views of the semi-circle from positions which the bee did not choose are shown in Figure 2C and D.

The problem to be solved is now clear: Why does the bee see view 2B (the view from its chosen position in the semi-circle) as more similar to 2A (the view present during training) than either view 2C or 2D or any other view of the semi-circle? As all the information available to the bee when it was at the centre of the circle during training is represented in Figure 2A, it should be possible to find some measure of this landmark arrangement which the bee could remember and which would match to view 2B of the semi-circle better than to any other view.

A hypothesis will now be developed to explain the results of this one experiment, it will then be applied to a series of other experiments and to some of the results of van Beusekom (1948). Firstly, let us consider the models proposed by previous authors. As explained in the introduction the model proposed by Collett and Land (1975) is a "retinal" one, the behaviour of the fly being a result of the mismatch between its current retinal image and its stored image.

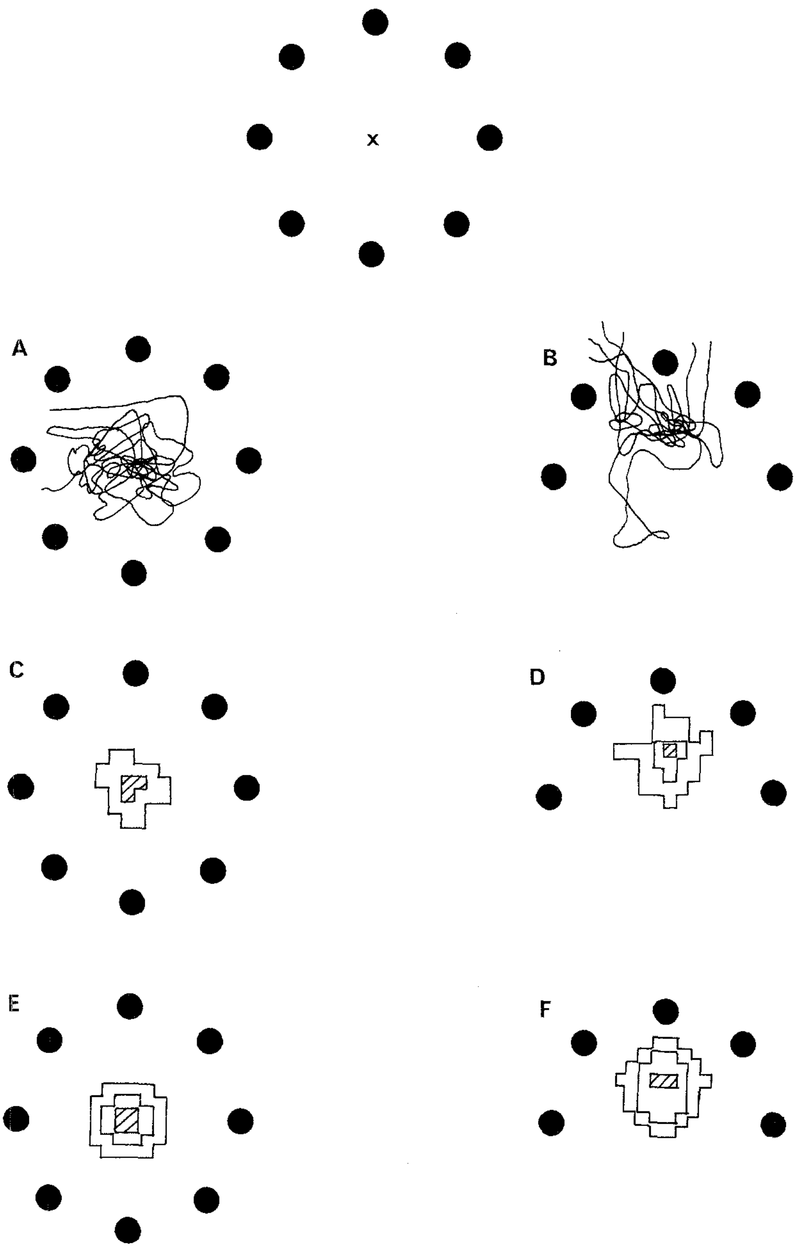

Fig. 1. At the top of the figure is shown the arrangement of landmarks during training, the position of the sugar source is marked with a cross. The diameter of the circle is 360 mm. **A** and **B** Flight paths of the bee during single tests. **C** and **D** The distribution of the bee's flights summed from a set of 4 tests (**C**) and a set of 9 tests (**D**). The shaded regions show where the frequency of square crossing exceeded 90% of the highest frequency found in that test situation. The first contour line encloses the region where frequency of square crossing exceeded 50% of the highest frequency, the second (in **D** only) shows where the frequency exceeded 25%. **F** and G Computer predictions. The area with the highest score is shaded. Contour lines indicate 5% decreases from the highest score

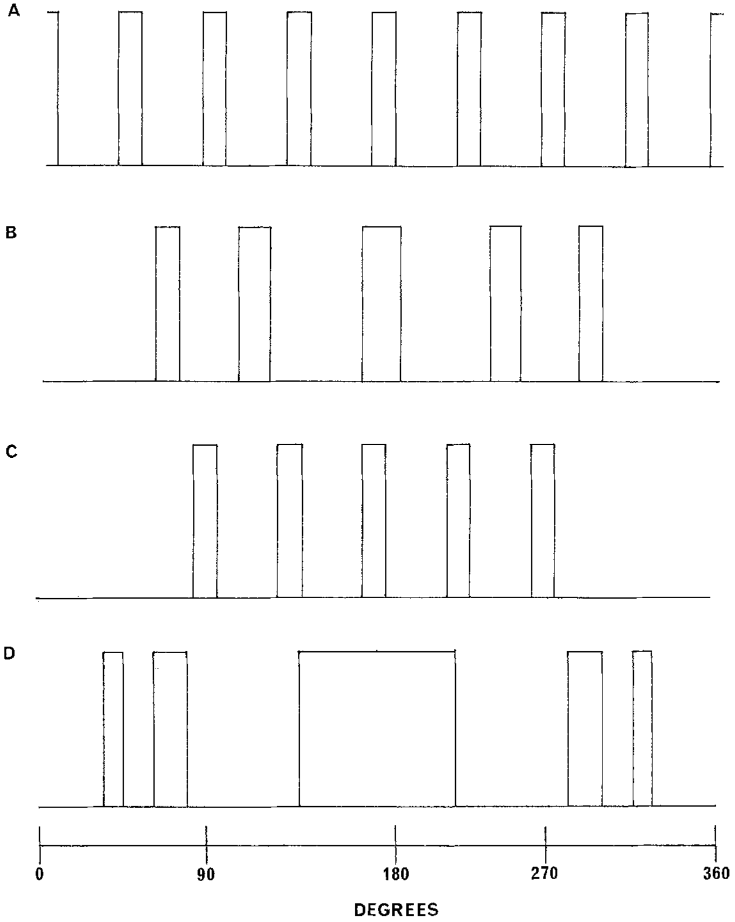

Fig. 2. A View of the training arrangement of landmarks from the sugar source. **B** View of the semi-circle from the bee's preferred position. **C** View of the semi-circle from the centre of the circle of which the semi-circle is a part. **D** View of the semi-circle from a position 10 mm in front of the central landmark

If we compare Figure 2A and B it can be seen that the bee chooses a location in the semi-circle in which not a single landmark has a retinal size, angular bearing or angular separation corresponding with those seen from the sugar source during training. Had it instead chosen the centre of the circle of which the semi-circle is a part (Fig. 2C) the view of the five landmarks present would have corresponded exactly in their retinal sizes, distances and angular bearings with any five of the landmarks present during training. As it did not choose this position it would seem certain that the bee uses mechanisms other than the simple matching of individual landmark positions.

When we consider van Beusekom's (1948) hypothesis, that the overall configuration of the landmarks is important rather than the position of individual landmarks, then we are better able to understand the behaviour of the bee.

One parameter that van Beusekom drew particular attention to was the "degree of closure of the figure". A circle of landmarks is a "closed" figure; when the bee is inside the circle we can say that it is completely "surrounded" by landmarks. If the bee learns the degree of "closure" present during training then, when confronted with a semi-circle, it may move "inside" it in an attempt to close the figure around it, i.e., to reproduce the degree of "surroundedness" it experienced when collecting sugar from the centre of the circle. It can be seen by comparing Figure 2B and C that the angular spread of the landmarks across the bees retina has increased from 192 degrees to 238 degrees as the bee has moved inside the semi-circle to its preferred position. However, if the bee recorded only a measure of "surroundedness" it should choose, in the semi-circle, to move right up against the central landmark as this would close the landmarks around it even further (compare Fig. 2D and B). Also, as all points inside a circle would be completely "surrounded" by landmarks this parameter alone would not enable the bee to find the centre of the circle. Some kind of landmark distance measure must be added to that of closure or surroundedness to make this explanation adequate. If the bee learnt, in the centre of the circle, that it was completely surrounded by landmarks and that they were at an average distance r, the radius of the circle, then it would on later visits be able to find the centre of the circle. It chosen position in the semi-circle would then be a resultant of the tendency to move further into the semi-circle to produce the same degree of of surroundedness as present during training, and a tendency to move out of the semi-circle to prevent the average distance of landmarks being too different from that present during training. We might thus say that the bee chooses its final position in the semi-circle by saying "there were landmarks all around me but I wasn't very near to any of them".

This hypothesis will be made into a testable model by giving rigid definitions to the concepts of "surroundedness" and "average distance". A comparison process will also be defined so that it will be possible to measure the degree of fit between the view of the training constellation from the sugar source and views of the test constellations from different positions around them. The definitions will be incorporated into a computer program so that precise predictions can be made and tested for a series of training and test situations.

The Concept of "Surroundedness". A measure is proposed which can record the pattern of surroundedness. There may be many different ways of defining surroundedness so this definition has an element of arbitrariness, it is derived from the commonsense observation that to be surrounded is to have something to the left of you, something to the right of you, something in front and something behind.

To implement this statement the visual world of the bee is divided up into sectors and the pattern of surroundedness is described by the sectors which are occupied by landmarks. It was found to be sufficient to use only four sectors, each of angle 90 degrees, as shown in Figure 3. In Figure 3A we see the bee in a position and orientation where one landmark lies in each sector, here the bee would be said to have a pattern of surroundedness in which

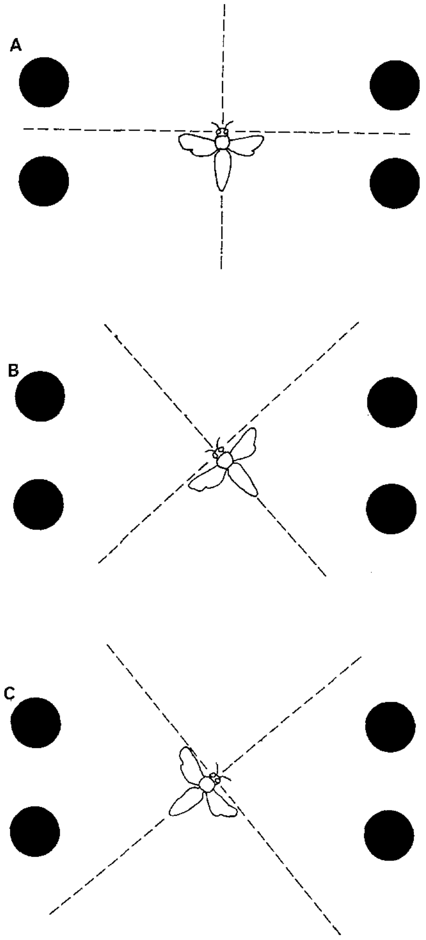

Fig. 3. The visual world of the bee divided up into sectors

all sectors are occupied. This can be expressed as:

Sector number:	1	2	3	4
Occupancy:	1	1	1	1

where the value 1 implies that a sector is occupied by any number of landmarks and the value 0 that it is unoccupied.

When a bee is in the position shown in Figure 3, it would rarely happen to be oriented in just such a way that the sector boundaries fall in between two closely spaced landmarks (Fig. 3A), on a chance basis we would expect the bee to be more frequently oriented so that only two sectors are occupied, as in Figure 3B and C.

Here, starting at the bees front right sector and proceeding clockwise, the sector occupancy is as follows:

for Figure 3B	0	1	0	1
for Figure 3C	1	0	1	0

These descriptions are circular and they begin at an arbitrarily selected sector. If we consider only their sequential form, i.e., their pattern, the two descriptions above are identical both being of the general form:

0 1 0 1 0 1 ... etc.

We shall only consider the sequential form of sector occupancy patterns. The computer is programmed so that it recognises sequences with the same form but different starting places as being the same, it does this by a simple repetitive process described later. The landmark distribution is thus described by a pattern in a circular array of sector occupancy.

Average Distance of Landmarks. In each sector the average distance from the bee is recorded. The circular array now acquires a second line, so that for Figure 3A, where all the landmarks are at the same distance x from the bee, the view of the landmarks is described as:

Occupancy:	1	1	1	1
Distance:	x	x	x	x

Comparison Process

The above definitions can be used to produce a description of a set of landmarks as they are seen from any particular position and orientation. A comparison process will now be described which can compare, and calculate the degree of fit, between a view of a test constellation of landmarks and the bee's memory of the training constellation as viewed from the sugar source.

Comparison of the two views takes place by taking the two arrays they generate and matching them sector by sector. If sectors match precisely then a score of 1 is given, if they mismatch completely a score of 0, and if they match in occupancy but not in distance then a score of 1 is reduced according to the size of the distance difference until a minimum score of 0 is reached. An example will make this clear.

Let us assume the bee learns to visit a sugar source at x in Figure 4A. It will record the landmarks as the following array:

Occupancy:	1	1	0	0
Distance:	a	a	–	–

Now, if the bee encountered the landmarks shown in Figure 4B and it was in the position and orientation shown, it would record the array:

Occupancy:	1	0	1	0
Distance:	b	–	b	–

Matching this array to that stored during training:

First Sector: The sectors match in both being occupied by landmarks, but the landmarks are at different distance. *Score = 1–k (difference in distance).*

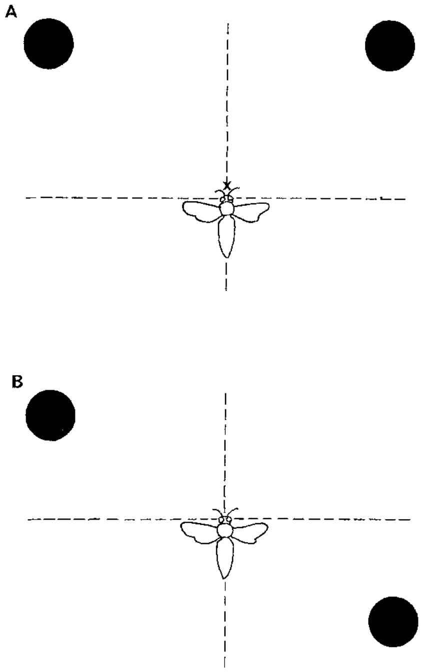

Fig. 4. A A training situation with two landmarks at distance a from the bee. The position of the sugar source is marked with a cross.
B A test situation with two landmarks at distance b from the bee

Second Sector: A landmark is present in the training array but not in the test array, so the sectors completely mismatch. *Score* = *0.*

Third Sector: A landmark is present in the test array but not in the training array, again a total mismatch. *Score* = *0.*

Fourth Sector: Neither array contains a landmark in this sector so they match perfectly. *Score* = *1.*

Total matching score = 1–k (Distance difference) + 0 + 0 + 1.

The value of the constant k determines the size of an effect of a mismatch in distance upon a match in occupancy, i.e., where a landmark occupies the correct sector but is at the wrong distance. The value of k will be determined from the results of the first experiment.

It was pointed out above that the arrays are regarded as circular sequences of occupancy and average distance without particular starting places. When matching two arrays the process is begun at an arbitrary sector and the sectors matched one by one as described above. The whole process is then repeated beginning at the same position in the training array but at one sector further along in the test array, i.e., the test array is rotated against the training array, until the best fit is found. This rotation is necessary so that two arrays having the same sequential form beginning at different sectors will be recognised as the same.

Note that rotating the array, the bee's model of the world, is not the same as rotating the bee. In certain cases, different orientations of the bee can result in different models of the same landmark situations (compare Fig. 3A with B or C).

The model can be summarised by listing the operations performed by the computer in calculating the average matching score for a particular position. The position of the bee and landmarks and the array characteristics of the training constellation as seen from the sugar source are input onto the computer.

1. Calculate the angular bearings and distances of each of the landmarks from the bee.
2. Divide the surroundings of the bee into four 90 degree sectors, starting the first sector at an arbitrary bearing.
3. Find which sectors have landmarks in them and which do not, recording the result in the first row of a circular array.
4. Record the average distance of landmarks in occupied sectors in the second row of the array.
5. Match the new array to the training array as described above. These first five steps give a matching score for a particular orientation of the bee, the next step calculates an average matching score for a position over a range of orientations.
6. The above procedures 2 to 5 are repeated, but with the orientation of the bee, i.e., the starting position of the first sector, rotated 10 degrees. This operation is repeated until a complete range of orientations has been considered and then the average matching score is calculated for this position.

These procedures above give a measure of the degree of fit between the bee's memory of a training situation and its view, from a particular position, of a test set of landmarks. The procedures are now repeated for many different positions around each test constellation of landmarks, the positions being chosen to be in the centres of the grid squares used in measuring the bee's frequency of square crossing. A contour map is then drawn showing the distribution of average matching score values. The area with the highest matching score is marked as a shaded area and contours indicate 5% decreases from the highest value.

We now have two contour maps for each test situation, both derived from the same grid system. One shows the distribution of average matching score values and the other the distribution of the bee's visits. The model can now be tested by seeing if there are any similarities in the pairs of contour maps for each test situation.

If the model is correct it is assumed that there will be some relation between the matching score at a particular location and the amount of time the bee spends there. In particular, it would be expected that the most frequently visited area will be the area with the highest matching score. However, it is not possible to predict the precise frequency of square crossing from particular values of matching score. To do so would require a major addition to the model, a description of how the bee responds to changes in matching score while it is flying around the landmark area. The simplest possibility might be that the bee continues on a straight course until the matching score begins to fall and then makes a turn. In this way, like a *Paramecium* approaching a food source, it would eventually reach and remain trapped in the area with the highest matching score. A second alternative might be that the bee turns until it finds the direction in which the rate of increase of matching score is greatest, i.e., where contours are closest together, and then flies "uphill" until it reaches the peak value of matching score. Several other mechanisms are possible, so for the time being we shall simply see if the distribution of matching score values is in any way related to the distribution of the bee's visits and in particular whether it correctly predicts the area most frequently visited by the bee.

Results from various test situations will now be considered, they will be described in groups according to the arrangements of the landmarks during training.

Training Situation 1. The model has been derived from a consideration of this situation. The bee is trained to collect sugar from the centre of a circle of eight landmarks and later tested on a circle without sugar (Fig. 1A, C) and a semi-circle of five landmarks (Fig. 1B, D). The constant k which determines the importance of differences in landmark average distances against similarities in sector occupancy is derived from this second test situation. The constant k is set so that the area of best fit predicted by the computer coincides with the area most frequently visited by the bee. The results predicted by the computer model using this value (0.2) are shown in Figure 1E and F. The same value of k is now used to predict the results of all the rest of the experiments.

Training Situation 2. The bee was trained to visit the centre of the square of eight landmarks shown at the top of Figure 5. In the centre of the square it is completely surrounded by landmarks and the average distance of landmarks in each sector is the same. In the first test, two sides of the square are removed. The bee now moves in towards the remaining corner (Fig. 5A), this is predicted by the model (Fig. 5B) as in this position the bee can mantain the high degree of surroundedness present in the training situation at the expense of some distortion of its average distance scores.

When two more landmarks are removed, leaving only one corner of the original square, the bee moves still further into the corner (Fig. 5C), as predicted by the model (Fig. 5D). Even though the landmark distances now differ greatly from the training situation the bee has to move into the corner to mantain a high degree of surroundedness.

Now, when one landmark from the opposite corner of the square is added (Fig. 5E), there is a dramatic change in the behaviour, of the bee. This additional

Fig. 5. The training situation is shown at the top of the figure with the sugar source marked by a cross. The width of the square is 360 mm. The left hand column shows the summed results from a set of 4 tests (**A**), 7 tests (**C**), 7 tests (**E**) and 2 tests (**G**). The shaded region shows where the frequency of square crossing exceeded 90% of the highest frequency found in that test situation. The first contour line encloses the region where the frequency of square crossing exceeded 50% of the highest frequency. Computer predictions for each test situation are shown in the right hand column, the area with the highest score is shaded and contour lines indicate 5% decreases from this value

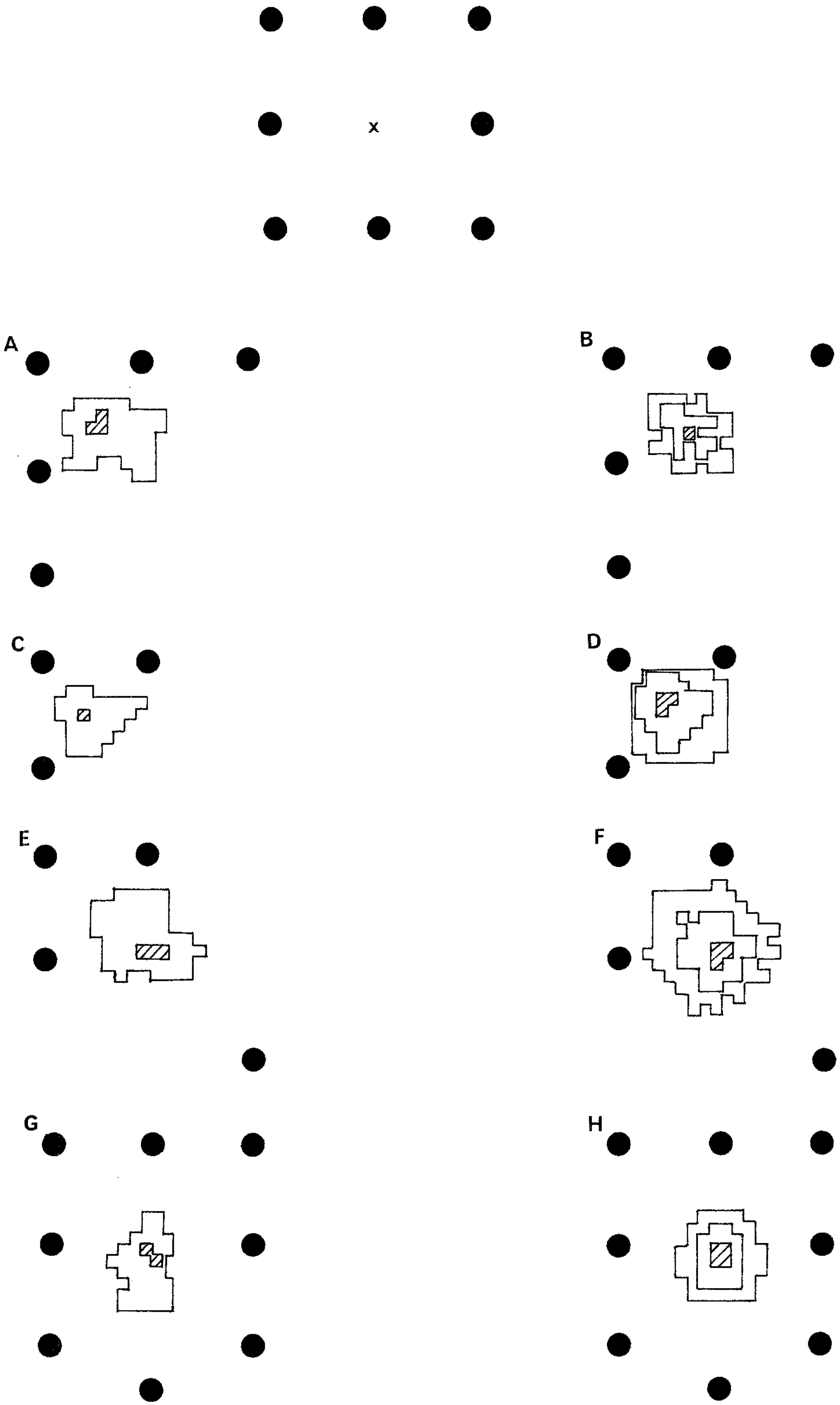

Fig. 5

landmark "pulls" the bee out of the corner, it now visits the centre most frequently but its visits are not distributed symmetrically about the centre but are biased towards the group of three landmarks. This is predicted by the model (Fig. 5F): movement towards the single landmark on the right causes a decrease in both surroundedness and the average distance fit while movement towards the corner of three landmarks causes a decrease only in the distance fit. Thus, although the centre represents the best compromise, the contours are distributed asymmetrically around this peak.

Interestingly, if the one landmark to the right is placed not at the corner of the original square, but an additional 500 mm away from the corner on the same diagonal then it has no effect upon the behaviour of the bee. The bee continues to fly around inside the corner of three landmarks just as in Figure 5C. In general, this behaviour is predicted by the model, if the distance of a landmark is very different from its distance during training, then the mismatch in average distance will completely remove the match in sector occupancy and the landmark will have no effect upon the total matching score. This is an important property of the model, if a landmark is greatly displaced it will be ignored.

The same effect was found when the type of landmark was changed. In Figure 5E, the single landmark to the right was replaced by one having horizontal black and white stripes of width 5 mm. The bee's distribution of visits now returned to that found in Figure 5C, the striped landmark had no effect of "pulling" the bee out of the corner but was ignored. Clearly, it is necessary to add a description of landmark type to the model, this will be mentioned again in the Discussion.

The effect of a small movement of one landmark from the original square training constellation is seen in Figure 5G. The most visited area is slightly displaced from the centre towards the moved landmark. This is predicted by the model as, although the pattern of surroundedness is not affected by this movement of the landmark, the optimal position for matching average distance scores is slightly displaced from the centre.

Training Situation 3. The training constellation contains a long row of landmarks, this arrangement was chosen to see if the bee pays particular attention to unique segments of the pattern of surrounding landmarks. If it does then we would expect the model to fail to make correct predictions when some parts of the constellation are missing (Fig. 6A to H). However, it can be seen that even when the long row of landmarks is presented on its own (Fig. 6G), the bee's behaviour does not deviate greatly from the predictions made by the model.

Training Situation 4. The training constellation is again circular but this time the bee was trained to visit a sugar source half way between the centre and the circumference, here arbitrarily shown in the bottom half of the circle. When the training set of landmarks is presented in a test situation, the model predicts that the best fit occurs in a ring shaped area inside the circle. The bee did visit a ring shaped area but its most frequent visits were directed towards

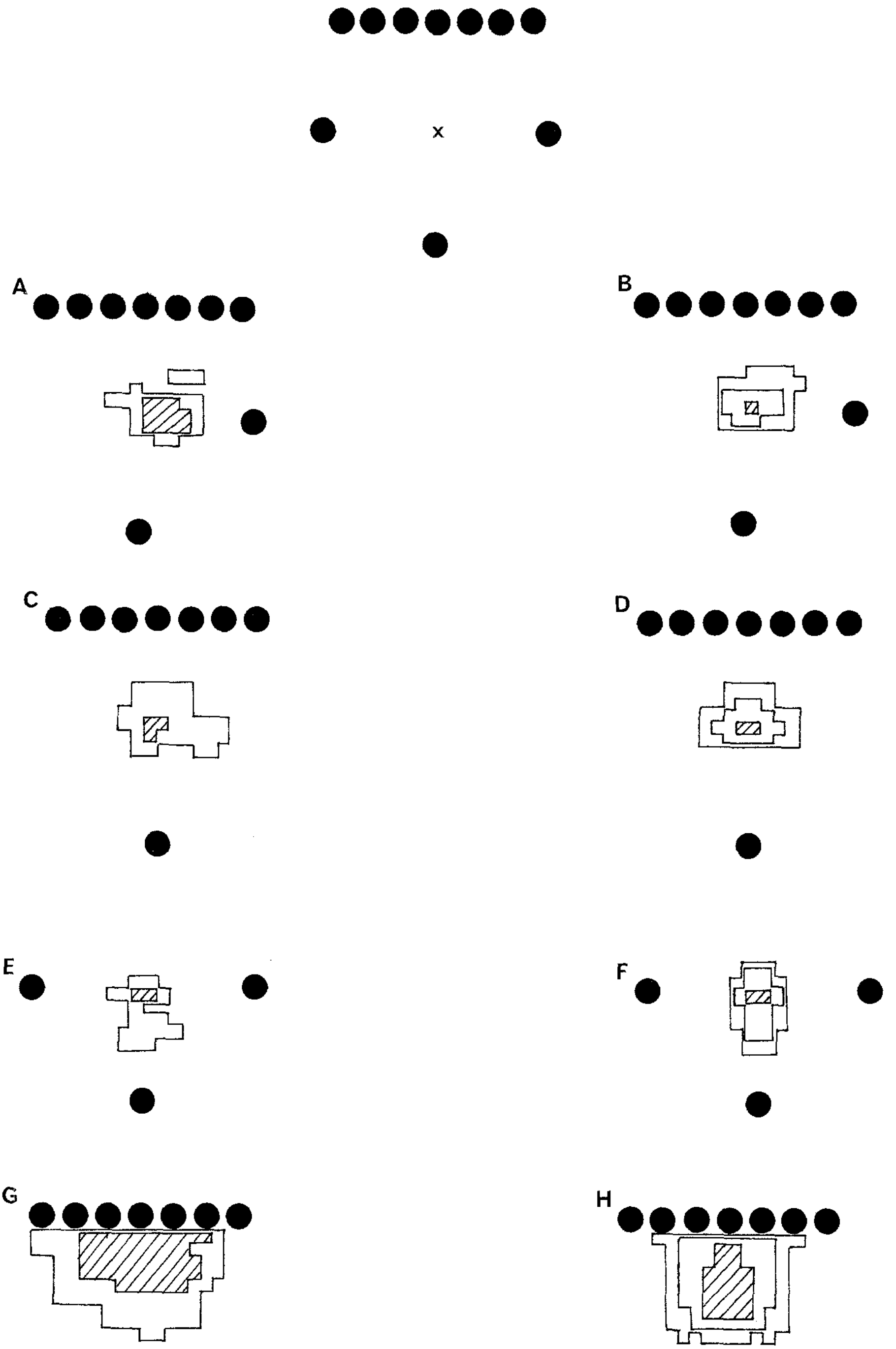

Fig. 6. The training situation is shown at the top of the figure with the sugar source marked by a cross. The line of landmarks is of length 360 mm. The left hand column shows the summed results from a set of 4 tests (**A**), 4 tests (**C**), 3 tests (**E**) and 2 tests (**G**). Computer predictions for each test are shown in the right hand column. All contours are drawn as in Figure 5

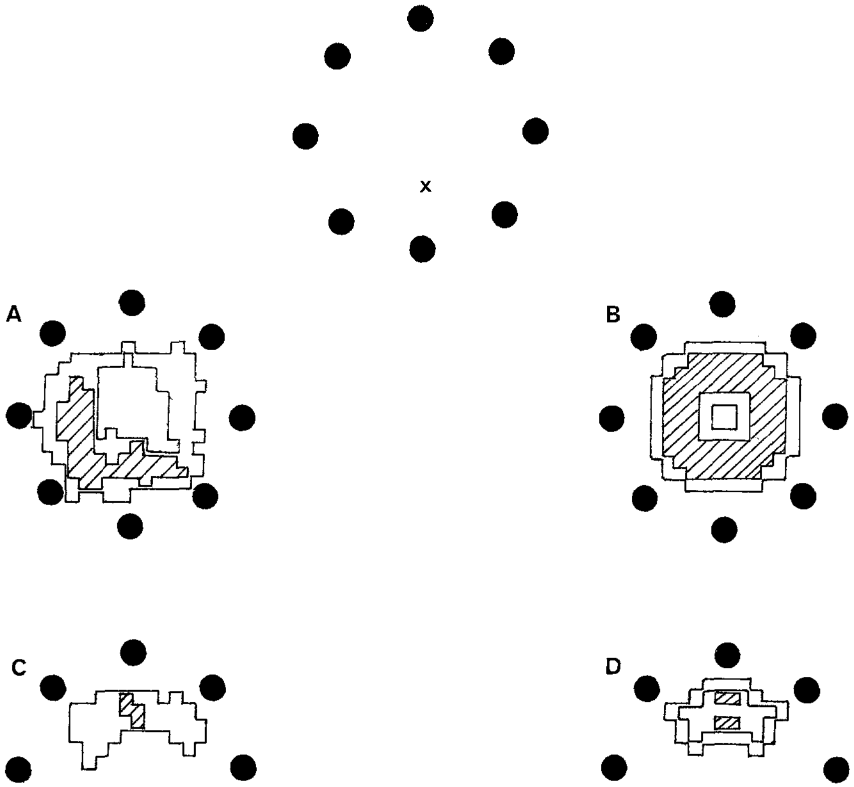

Fig. 7. The training situation is shown at the top of the figure with the sugar source marked by a cross. The diameter of the circle is 360 mm. The left hand column shows the summed results from a set of 3 tests (**A**) and 4 tests (**C**). Computer predictions for each test are shown in the right hand column. All contours are drawn as in Figure 5

the "bottom" of the ring (Fig. 7A). This polarity in visits must be explained by the bee using a landmark outside the circle, a circle of landmarks is not able to uniquely define its own "top" or "bottom". Probably the bees were also responding to the direction of the light coming in through the window as the sugar source had always been in the part of the circle nearest the window.

When three of the landmarks are removed, the bee moves into the resulting semi-circle (Fig. 7C). Its visits, however, are distributed quite differently from when it had been tested on a semi-circle after training to the centre of a circle (compare Figs. 7C and 1D). This difference in pattern is predicted by the model (Fig. 7D).

Results of van Beusekom. Although many of van Beusekom's (1948) experiments are of rather a different kind from those reported here, several of them are sufficiently similar for their results to be used to test the model. In his experiments, van Beusekom trained the wasp to a circle of 16 pine cones, the entrance to the nest being in the centre of the circle. He then recorded the choices

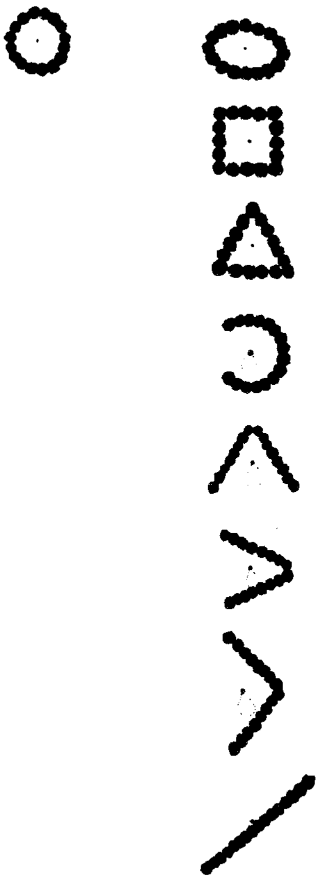

Fig. 8. Results redrawn from van Beusekom (1948). The digger wasp was trained to the circle of pine cones on the left and then given a series of choice tests between the training figure and each of the figures on the right. The test figures are shown in their order of preference

the wasp made between the training circle and each of a set of test shapes. The test shapes are shown in their order of preference in Figure 8; note that here we are concerned not with a preferred position relative to one set of landmarks but with the overall preference for one landmark constellation or another.

The model was used to calculate the preference for a landmark constellation by totalling the average matching scores from randomly distributed points around the constellation. Twenty viewpoints were considered for each set of landmarks, randomly distributed within the area in which the fit was greater than zero. The preference order calculated on this basis agrees with that found by van Beusekom. Looking at the landmark arrangements it is easy to see why this is so. The least preferred figures produce low matching scores whatever point they are viewed from. In the more preferred figures some of the random viewpoints fall inside the figures and produce high matching scores, the highest scores of all coming from figures which are most like the training circle in their landmark distribution.

Arbitrary Features of the Model

The model may be varied in several ways without fundamentally affecting the results it produces here, although these alterations could be tested in other experiments. Variations are possible in the following:

1. The number of sectors; four was chosen only because it was the minimum necessary to give a reasonable fit between the predictions and the results. In some cases the fit could be improved by increasing the number of sectors.
2. The fixed boundaries of the sectors; an object was considered to be in either one sector or the other. It would be possible to have overlapping sectors without absolute boundaries in which the probability of an object being included fell as its distance from the centre of the sector increased.
3. The sectors relation to the bee; it was assumed that the sectors had a relation to the body of the bee but this is not essential. A study of the effect of the bee's orientation upon its choice of position would show whether this assumption was needed.

Discussion

The success of the model in explaining the results described here suggests that any explanation of the bees use of landmarks will have to incorporate its essential properties. However, the specific way in which the concept of "surroundedness" has been implemented may not be correct, it may merely mimic the result of some quite different mechanism which the bee uses to measure landmark distribution. The advantage of the proposed model is that it is strictly defined, particularly when contrasted with concepts such as "Gestalt", and can produce testable predictions for any experimental landmark arrangement. Its important properties will now be described and then we shall see how it might behave when faced with "real world" problems.

The problem encountered with the bee and the digger wasp is that both appear to learn the distribution of landmarks in space rather than the precise bearing of individual landmarks. Dividing up the visual space surrounding the bee into a circular array of sectors enables us to deal with the pattern of sector occupancy rather than individual landmark bearings. Note that this implies more than saying that a landmark may be anywhere within a particular sector. This model does not just add a degree of "tolerance" to the precise position of a landmark, but being circular describes a particular pattern of the surroundings. In the case of the four sector model there are only five unique patterns of surroundedness; these are:

1	0	0	0
1	1	0	0
1	0	1	0
1	1	1	0
1	1	1	1

Each pattern of landmark distribution is then qualified by its average distance characteristics.

The differences between a "distribution" model and a "retinal" model can most easily be seen when landmarks are added to or removed from those present during training. The model proposed here predicts that additional markers which are far away from the landmark constellation will be completely neglected as they mismatch in their distances so greatly that they contribute nothing to the matching score. Landmarks added close to the existing array will cause the bee to select a viewpoint in which the new landmarks are incorporated into the same general pattern as present during training. Similarly, when landmarks are removed the bee will choose a new viewpoint in which the remaining landmarks match the overall distribution present during training. If the overall pattern of landmarks is kept the same it should be possible to add and remove landmarks without disturbing the bee. Van Beusekom (1948) showed that after the wasp had learnt to visit the centre of a ring of 8 fir cones it would search in the centre when presented with a ring of 4, 6 or 16 objects.

A "retinal" model, relying on specification of precise positions of individual landmarks (whether these be specified as a set of landmark bearings or as a series of interlandmark bearings) would be expected to react differently to landmark addition or removal. It would either match to those sections of the landmark array which remain undisturbed or, if many markers had been changed, be completely disrupted. A matching in which the overall distribution remains the same but individual landmark bearings are different would not occur.

Although the "retinal" model of Collet and Land (1975) does not fit the experiments described here, it was designed to explain a very different type of situation. The hoverfly makes only short excursions from its "home" and probably does not go out of sight of the major landmarks marking the home's position. It may thus never lose track of the movement of the landmarks across its retina, a very different situation from the bee which flies long distances to its goal and may have to remember the locations of many food sources.

Interestingly, if a bee used a "retinal" model it would be better able to deal with certain changes in the environment than by using a "distribution" model. If we return to the original experiment in which three landmarks were removed from a circle leaving a semi-circle, we can see that if the sugar source had been left in the same position the bee would have entered the semi-circle and searched in the wrong place. A retinal fit, however, matching the size and bearings of the remaining five landmarks, would have directed the bee to the sugar source. The use of a distribution model is thus a positive disadvantage when major changes in the environment occur, although the position chosen would be relatively unaffected by small changes in all the landmarks around it. The changes in the behaviour of the bee we have seen with removal of landmarks are thus not adapted to this situation but rather demonstrate the simplicity of the model used by the bee. However, such major changes are unlikely to be experienced in the natural world; areas of landmark will not suddenly vanish in the course of the short working life of the bee. Changes due to seasonal growth of plants occur so slowly that a constant updating of the model is possible, particularly when we consider that a bee or a digger wasp visits its food source or nest many times a day. A distribution model is well adapted to minor changes in all the landmarks around it, for example changes due to the momentary action of the wind.

Under natural conditions we might expect that most locations will be completely surrounded by landmarks so that a position will be characterised by its average distance scores. It is obviously essential, as we have noted with reference to the one experiment on change of landmark, that landmark type is also characterised. We saw how a change in landmark type can cause the landmark to be ignored in just the same way as a landmark which is at completely the wrong distance is ignored. Landmark type may be treated in the same way as distance by using a measure of landmark type and specifying a value for each sector. When two constellations containing different landmarks are matched, differences in landmark type may be subtracted from similarities in sector occupancy in exactly the same way as differences in distance are deducted from the overall fit.

Important categories of landmark type might be deduced from the experiments of Tinbergen (1938). He showed that the digger wasp exhibits distinct selectiveness in the landmarks it remembers. He demonstrated their preference for:

Patterned over uniformly coloured flat objects;

Large over small objects;

Objects close to the burrow over equally large distant objects;

Objects further away from the burrow over those nearby if both subtend the same angle;

Objects contrasting with the background over those matching its colour;

Objects present at the first departure over those added later;

Three-dimensional over flat objects; the most important characteristic being height above the ground rather than three dimensionality as such.

Studies by Hoefer and Lindauer (1975) with honey-bees confirm this last point. When the position of a food source was marked by a tower they were able to show that the height of the tower affected the rapidity with which the bee learnt the location of the sugar.

The preference for patterned objects is in agreement with many studies of insect shape perception which demonstrate a preference for shapes with a high density of contour (see review in Wehner, 1975) and it has been postulated that a measure of contour density is a critical one for the insects perception of shape (Hertz, 1929a, b, 1935; Anderson, 1977a, b, c). If a measure of contour density is used by the bee to measure landmark type then, when the bee is surrounded by many different objects, it may measure and try to match the sector distribution of the contour density pattern around it, so that it may remember a particular position as being defined by "high density of contour close by in one sector, low density of contour far away in the next sector, etc." In natural conditions then, where there is a great wealth of objects with different properties surrounding the bee, the occupants of different sectors will acquire labels. The "distribution" model then becomes more like the "retinal" model, but it simplifies the description of its surroundings by dealing with categories of visual space rather than the positions of individual landmarks. This is the important feature of the model.

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