(Theoretical investigation of this point is in progress.) But to produce any significant error in our assumption, the effect would need to be significantly different in carbon and oxygen and there is experimental evidence that this is not the case for pions (H. Koch, personal communication quoted in ref. 22). There is also the more important possibility that direct nuclear capture of pions by hydrogen can occur from highly excited molecular states[12,13]. The contribution of transfer of pions from hydrogen to heavier atoms would then be reduced in comparison to transfer of muons.

From previous measurements[23] of muon capture in tissues and tissue equivalent materials we have taken the concept of transfer from hydrogen to the nearest heavier atom but the particular model used, with $\delta = 1$, does not give the best description of our data. Furthermore, there is a factor of three discrepancy between the muon results reported for pig fat[23,24]. A detailed comparion with the pion and muon data, including muon measurements made as part of our experiment, are given elsewhere[16] and indicate that there are sufficient differences to make this detailed study of pion data necessary.

Discussion

The results for tissues and tissue equivalent materials are of considerable practical importance because the ratio of captures in carbon to captures in oxygen in real tissues is very much less than has hitherto been assumed. Our results confirm the suggestion[25] that materials which are tissue equivalent to X rays, electrons and neutrons are not tissue equivalent for pions. This is clearly due to major differences in molecular structure. Hitherto, only atomic and nuclear properties, such as electron density, effective atomic number and neutron cross-section, have been taken into account in defining tissue equivalence.

The Z-law, and its variations, fail to fit the data. The mesomolecular model contains an essential new feature[13]—the redistribution of the contribution of the valence electrons—because in general $n_i + 2\nu_1\omega_1 \neq Z_i$. The probability ω for atomic capture from the molecular orbit is not proportional to Z^2; instead it seems that ω is sensitive to the electronic structure of the molecule in a manner which relates to the localization of the mesomolecular orbital near to atoms of high electronegativity.

Hydrogen transfer is essential for a quantitative description of the data. The choice $\delta = 2\nu - 1$ may be preferred and different transfer parameters for CH and OH bonds may be indicated. Clearly the transfer parameter a is very sensitive to molecular structure but further work will be needed to give complete understanding of the transfer mechanism.

It had been suggested that muonic X-ray analysis can be used for bulk elemental analysis[23]. Our results suggest, in contrast, that pion capture (and probably also muon capture) is a sensitive means of probing molecular structure in complex materials. It should be very sensitive to changes brought about by substitution of one atom by another of a different element or when bonds are broken, for example, by radiation damage.

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How honey bees use landmarks to guide their return to a food source

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Bees trained to forage at a place specified by landmarks do not construct a cartesian map of the arrangement of landmarks and food source. Instead they store something like a two-dimensional snapshot of their surroundings taken from the food source. To return there, bees move so as to reduce discrepancies between the snapshot and their current retinal image. A computational model embodying these principles mimics the bees' behaviour.

HONEY BEES can learn the position of a source of sugar by reference to nearby landmarks (reviewed in ref. 1). We describe here what bees seem to learn about the spatial layout of landmarks and how this information might guide their approach to the source. Our experimental results strongly support earlier proposals[1–4] that to identify a place to which it will return an insect learns no more than the appearance of the landmarks viewed from that spot—just as though it takes and stores a panoramic snapshot of the landmarks from that position. Then, to find its way back, it compares the image on its retina with the stored snapshot and moves until the two match. It is not immediately obvious that this hypothesis can work, and we have therefore developed a computational model to show that it does.

Bee tests

Single marked bees were trained to fly through an open window into an experimental room (floor area 4 m × 4 m) to collect sugar

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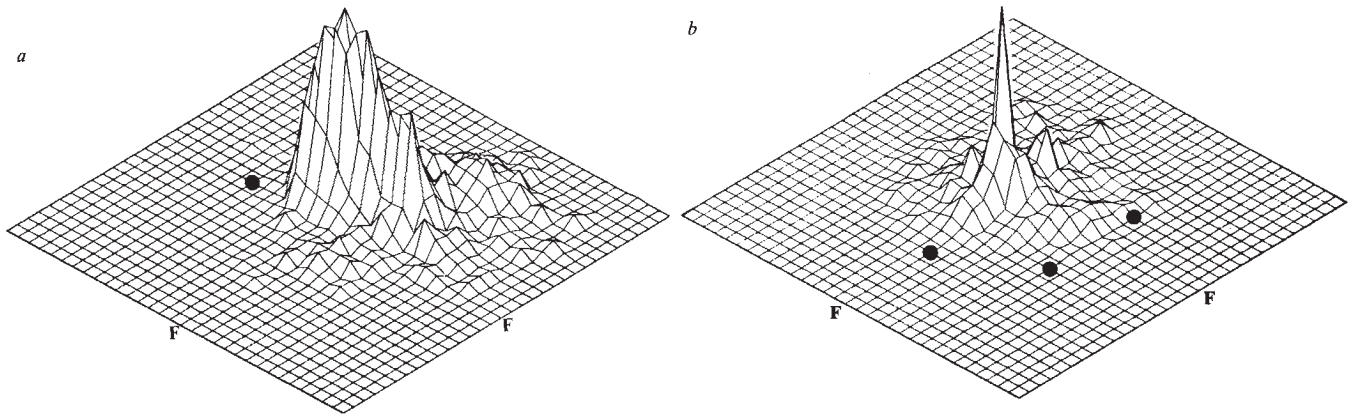

Fig. 1 *a*, Distribution of a single bee's flight time within the area surveyed by the camera when trained to a food source 50 cm from a single cylindrical landmark and tested with the same-sized landmark (4 cm diameter and 40 cm high). The position of the food source during training is marked by 'F' on the *x* and *y* axes. The position of the base of the landmark is indicated by filled circles. Height shows relative times spent in different regions of the testing area. Lines on grid are 8.7 cm apart. *b*, Distribution of bee's flight time when trained and tested with three landmarks in the standard array described in Fig. 2.

solution from a small reservoir (diameter 1.5 cm) on the floor. The room was painted entirely white, except for random green markings on the floor to help the bee stabilize its flight, and the window was covered by white sheeting. The location of the reservoir was indicated by the position of one or three matt black cylindrical landmarks standing upright on the floor. The bee returned to the room every 5 to 10 minutes. To encourage the bee to associate the food source with the landmarks, between visits the whole arrangement of cylinders and reservoir was shifted in register to a new position, without changing its orientation.

After a day of training with a standard array, tests were conducted at ~40-min intervals. The food source was then removed and the flight path of the bee recorded for 2 min by an overhead video camera suspended on runners fixed to the ceiling. The camera surveyed an area of floor 2.7 m × 2.7 m centred on the position of the missing reservoir, and the testing site was varied systematically within the room. Sometimes the size, number or spatial arrangement of landmarks was altered between training and the subsequent test. An individual bee was given several types of test, each replicated 5–10 times. Each type of test was conducted on at least two bees.

The position of a bee was recorded every 100 ms from the video tape and the results from 5–10 tests of the same type are combined to show in Figs 1 and 2 how an individual bee distributed its time in the vicinity of the landmark array. Our aim was to infer from the bee's searching pattern where it thought the reservoir was to be found, and from this to deduce what it knew about the arrangement of landmarks.

When a bee was trained to a food source at a constant distance from a single cylindrical landmark, and then tested with the food source removed, it searched roughly where it had previously foraged with respect to the landmark (Fig. 1*a*). Although a radially symmetrical landmark does not define direction, the bee does not fly in a circle around the landmark, implying that some other cue (possibly the window) must specify in which direction from the landmark the food lay. Tests with single landmarks smaller (or larger) than the training size result in a search area shifted closer to (or further from) the landmark (ref. 5 and B.A.C. and T.S.C., in preparation). This suggests that the bee has not learnt the distance between landmark and food source but rather how large the landmark appears when viewed from the food source, and also that to find the reservoir the bee flies to where the image of the landmark on the retina is of the right size.

Experiments using three landmarks, when the search area is rather more sharply defined (Fig. 1*b*), reinforce these conclusions. If a bee is trained to a particular configuration of landmarks and then tested with a different spatial arrangement of those same landmarks, it always searches in an area where the inter-landmark angles (as shown in Fig. 2) are the same as when seen from the food source. The actual distances of the landmarks from each other or from the search area are of minor importance.

Figure 2*a*, *b* shows a bee's search area when it was confronted with an array in which the distances between landmarks differed from those with which it was trained. The bee spent most of its time where the inter-landmark angles matched those experienced during training. Furthermore, if the test configuration was such that a bee could search where either the distances from the landmarks or the inter-landmark angles were correct, it chose to do the latter (Fig. 2*c*).

A bee tested with cylinders that were larger or smaller than the ones used in training also searched where the inter-landmark angle was approximately correct. Figure 2*d* illustrates that this behaviour persists for very dramatic changes of landmark shape and size, when cubes with 30-cm edges were substituted for the training cylinders (4 cm diameter, 40 cm height). We conclude that to a bee the most important feature of the landmark array is the retinal position of the landmarks as seen from the food source.

At first sight, the bees' neglect of landmark size would seem to conflict with their behaviour when they are trained to a single landmark and its size is changed. However, whatever the size of a single test landmark, a bee can always find a position where there is a perfect match between its 'snapshot' and the retinal image of the test landmark. But with three landmarks both their sizes and the distances between them must be changed in a coordinated way for a position to exist where retinal image and snapshot are congruent. If just one of these parameters is varied, then wherever the bee searches there will be some degree of mismatch. Simple geometry suggests that in this case the retinal sizes of landmarks should carry less weight than the angles between them, because the inter-landmark angles are much larger than the angle subtended by the landmark itself. Thus, were the bee to station itself where the angle subtended by one of the landmarks is correct, the positions of the other landmarks on its retina would be very wrong.

It seems, then, that a bee will search within a circumscribed area without requiring a perfect match between its postulated snapshot and its current retinal image. This can be shown in another way by testing bees with landmarks added to or taken away from the training array. Figure 2*e* shows that with two extra landmarks the bee's search area, although slightly larger than normal, is roughly in its usual position. When a bee was tested with any of the three landmarks removed, it still spent most of its time looking where the inter-landmark angle formed by the remaining two landmarks was the same as it was during training (not illustrated). This test also demonstrates that the bee must learn the sizes of the landmarks, for it is only their size that tells the bee whether or not the two remaining landmarks are neighbours and whether the inter-landmark angle should be 60 or 120°.

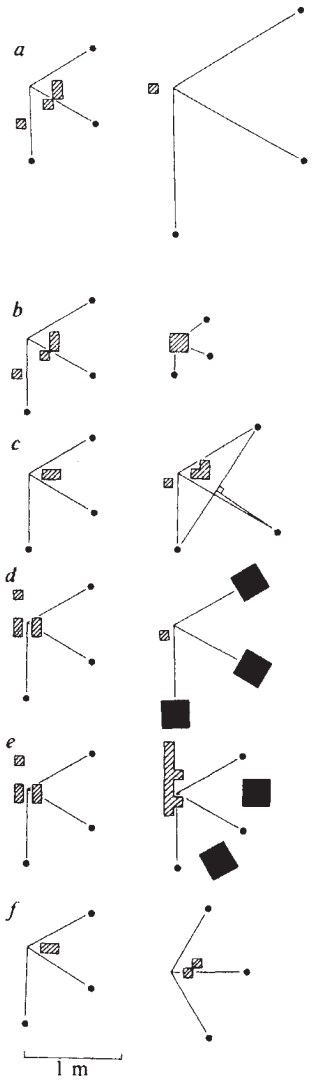

Fig. 2 Tests with three landmarks. The training configuration is shown in plan view in the left-hand column. The food source was placed 76 cm from each landmark at the intersection of the three lines drawn from the landmarks. Inter-landmark angles refer to the angles between these lines. In *a* and *b*, the cylinders were 5 cm in diameter and 50 cm high. In *c* to *f* they were 4 cm × 40 cm. Each row of the figure presents a pair of test arrays. The left half shows where a single bee searched when presented with the training array. On the right is the same bee's search area when presented with a variant of the training array. The hatching represents the search area defined as those squares within the test area (as in Fig. 1) that are at least 80% as high as the peak value. *a*, Distance between landmarks doubled; *b*, distance halved; *c*, landmarks arranged so that bee could search either where the inter-landmark angles or where the distances from the landmarks were the same as during training; *d*, cubes substituted for cylinders; *e*, cubes added to landmark array; *f*, landmark array rotated through 30° from training orientation. The point of intersection of the lines in the right-hand column show where the bee would need to search to see the same inter-landmark angles that it experienced when foraging at the food source. This is generally where the bee spends most of its time.

The snapshot model

All the above findings argue that the representation of landmarks in the bee's memory can be described in terms of a snapshot taken from the food source (see also ref. 1 for somewhat similar experiments on desert ants). The bee does not seem to be equipped with anything akin to a floor plan or cartesian map. We have therefore explored how well a model bee can guide itself using a representation of this kind. The basic idea is that the direction in which the bee moves at any moment is governed by the discrepancy between the snapshot and its current retinal image (Fig. 3).

To construct such a model we must make assumptions about the way images are coded in the visual system and the snapshot. In part these are arbitary. However, we have some evidence that the most important features of the retinal image are the edges between the dark landmarks and the light ground (B.A.C. and T.S.C., in preparation). Accordingly, in the model the retinal image consists of edges lying on a circular retina and the snapshot is represented in a compatible way (Fig. 3). The positions of the edges on both retina and snapshot are defined as compass bearings with respect to Earth-based coordinates. This assumption is supported by several experimental results. First, the tests with single landmarks (Fig. 1*a*) imply that cues external to the landmark specify the direction of the food source from the landmark. Second, when bees were tested with a three-landmark array rotated by 90° from the training orientation, the search area shifted away from the position predicted by the inter-landmark angles experienced during training. Third, bees find it difficult to use landmarks if, during training, the array is rotated between each of the bee's foraging visits. The simplest way to picture how edges in the snapshot can be given Earth-based coordinates is to suppose that the snapshot is fixed in the bee's head and that the bee always maintains the same orientation. This is not in fact so, and one needs to assume that as the bee turns, the snapshot counter-rotates.

Algorithms for calculating flight direction

We have examined two algorithms for generating the bee's direction of flight. These were programmed in Basic and run on a PDP8/a computer. The first, the simplest we could devise, fails to mimic all the bee's behaviour, but the second and more elaborate version performs very much as real bees do.

In the first algorithm (Fig. 4*a*) a unit vector is associated with each edge in the snapshot. The direction of the vector depends on the bearing of the closest edge of the same sign (that is, dark–light or light–dark) on its retina. Imagine each edge in the snapshot putting out an extensible arm to reach the nearest retinal edge. Once the edge is located, a unit vector is generated lying perpendicularly to the bearing of the retinal edge and pointing away from the paired edge in the snapshot, tending thus to align the two edges. These unit vectors are then summed, in the conventional way for adding vectors, to give the bee's flight direction. As the bee moves through the field of landmarks, it will continually update its direction as the edges shift over its retina. Note that it is not necessary for all edges in the retina to be matched to partners in the snapshot. Some may have more than one partner and others none at all. Furthermore, the bee is not required to assess the goodness of fit between its snapshot and the retinal image.

Figure 4*b* shows the computed vector directions for different points within the field of landmarks for a bee which is trained and tested with the same array of three landmarks. If the algorithm is to be successful, then from any starting point the vectors must lead the bee to the food source. The extent to which this is the case is shown in Fig. 4*c*. For most starting points the

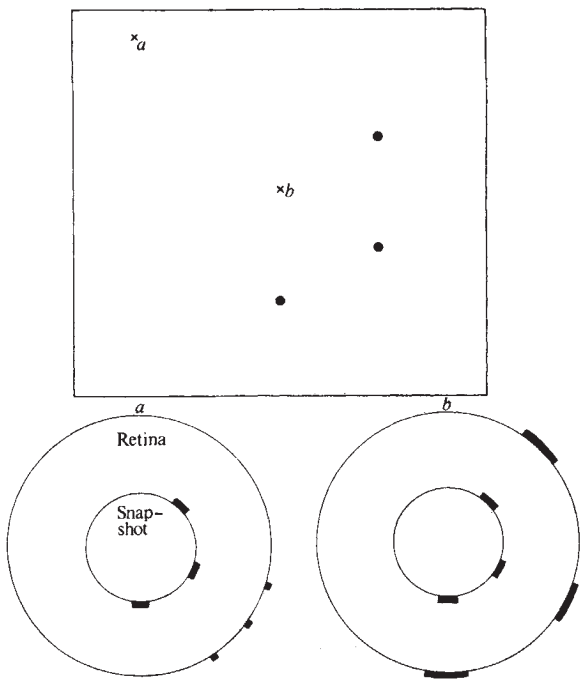

Fig. 3 The snapshot model. Positions of images of landmarks on circular retina (outer circle) and in snapshot (inner circle) viewed from two points within the landmark array as shown by crosses. *a*, Distance from food source; *b*, at food source, where snapshot and retinal image match. The aim of the model is to move the insect from *a* to *b* using the discrepancy between retinal image and snapshot as a guiding cue. Note that positions of edges on the circular snapshot and retina are compass bearings with respect to external coordinates. Frame round landmark array shows area viewed by video camera.

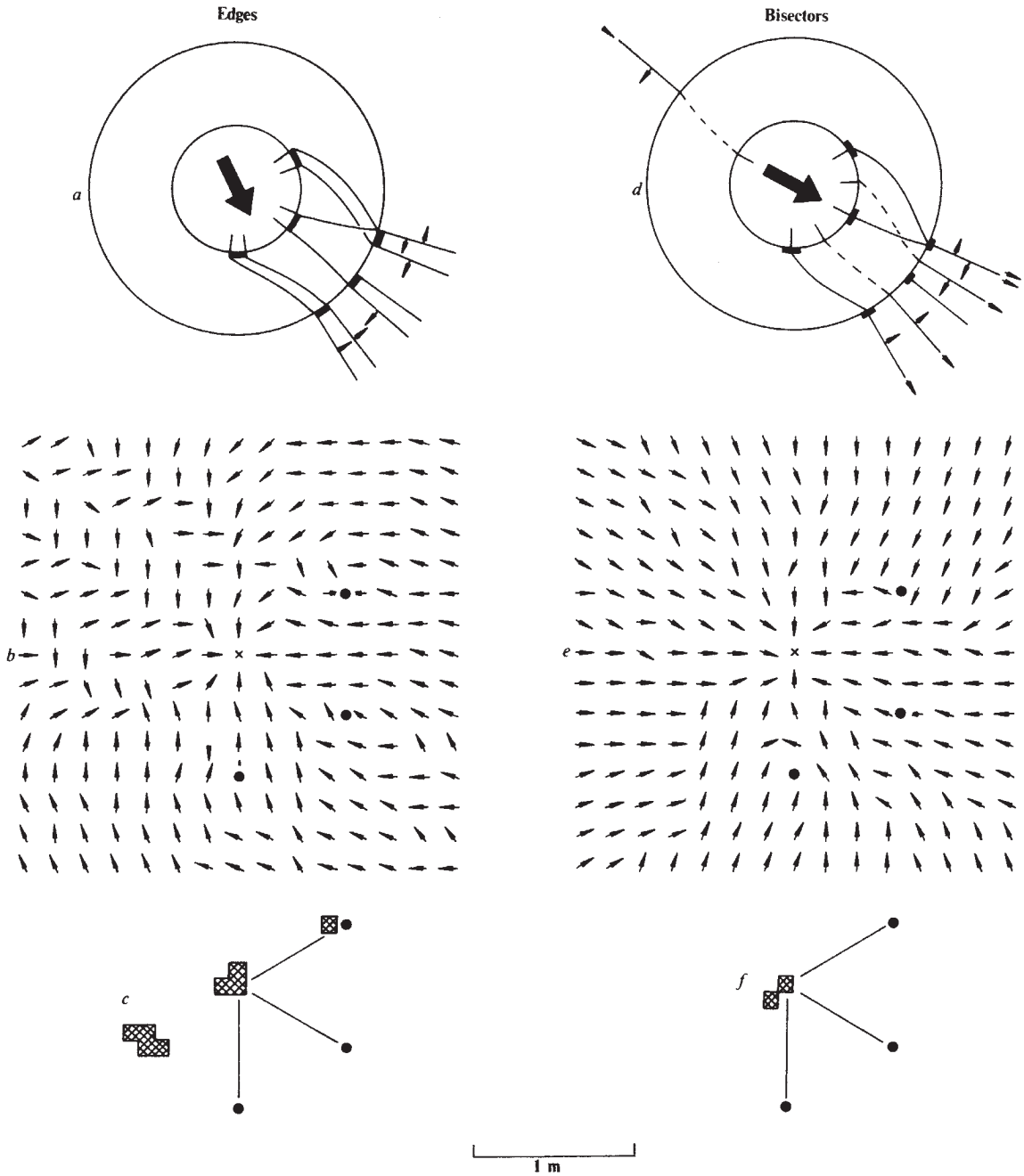

Fig. 4 Two algorithms for transforming retinal image to snapshot. *a*, Edge algorithm. Each edge in snapshot paired with closest edge on retina. Unit vector, shown by arrows around outer circle, is associated with each pair and lies perpendicularly to edge on retina, pointing away from edge in snapshot. Larger arrow in centre of circle shows flight direction of bee obtained by summing the unit vectors. *b*, The flight direction for different positions of the bee within landmark field, computed as outlined in *a*. Model bee trained and tested with landmark configuration of Fig. 3. *c*, Positions of end points are shown by cross-hatching. The bee is started at different positions within the landmark field and it follows the vectors as shown in *b* until it stops. *d*, Bisector algorithm. Unit vectors of positional component shown by arrows lying tangentially to outer circle, those of angular component by radially aligned arrows (details in text). *e*, Vector field for bisector algorithm. *f*, Position of end points for bisector algorithm.

bee does indeed end up at the food source. However, there are mishaps which arise because partial matches exist. There is one position within the field, for instance, where the two outer landmarks form an inter-landmark angle of 60°. The bee is trapped there because within a region on either side the vectors have opposite directions, pointing towards the partial match. Real bees do not make this mistake. The algorithm's performance can be improved if it takes into account the amplitude of the summed vectors. However, it still does not work in all the situations we have tested. In particular it fails if the array of landmarks is rotated by 30° from the orientation to which the bee was trained—a situation with which the bee can cope (Fig. 2*f*). Because the algorithm depends on the positions of edges defined with respect to external coordinates, a changed orientation of the landmark array will generate several points in the field where the edges of two landmarks can be roughly matched with edges in the snapshot, but none where all edges can be correctly matched.

To overcome these problems the second algorithm requires the bee to assess not only the position of each edge, but also the angular distance between them (Fig. 4*d*). Its first step is to decide on the basis of the signs of neighbouring edges whether the angles between them are dark or light. It then measures the size of each dark and light angle in the snapshot and on the retina, and locates the positions of their bisectors. Next, each bisector in the snapshot searches out the closest bisector on the retina with

the same sign (dark or light), so pairing angles in the snapshot with angles on the retina. As in the first algorithm, a unit vector (the positional component) is associated with each pair, tending to move the bee perpendicularly to the bearing of the bisector on the retina, pointing away from the bisector in the snapshot (or toward it if the retinal angle is greater than 180°). The additional feature of this algorithm is a second unit vector (an angular component) which depends on the differences between the sizes of the paired angles. This vector faces centripetally along the bisector on the retina if the angle in the snapshot is the smaller, and centrifugally if it is the larger. It thus takes the bee away from retinal angles that are too big and towards those that are too small. All the component vectors are then summed to determine the bee's flight direction, which is shown by the arrow in the centre of Fig. 4*d*.

Figure 4*e* illustrates the directions of the summed vectors within the standard three-landmark array. The improvement over the first algorithm is obvious: there are paths from all points to the food source, and when the bee is flown from different starting points it now always finishes there (Fig. 4*f*). It is easy to see that neither the positional nor the angular component of the summed vector would by itself be sufficient to locate a food source specified by a single landmark, although either can do so when there are three landmarks. With one landmark the positional component defines direction but not distance, so that the bee would search along a line originating at the landmark and passing through the food source. The angular component, on the other hand, only specifies distances and would leave the bee flying in an annulus centred on the landmark. The two acting together are needed to identify the intersecting point.

This algorithm copes with all the one- and three-landmark tests we have tried, including those with landmarks added or deleted. The 30° rotation of the three-landmark configuration on which the first algorithm founders is taken care of by the angular component. However, to prevent aberrant solutions, the angular component must be given a greater weighting than the positional one (3:1), a weighting which works in all situations. When the landmark array was rotated through 90° from the training orientation, the search area was displaced for the model, as it was for real bees.

The algorithm will not only move bees to the right position within an array of landmarks, but it will also bring a bee successfully to a foraging position in the centre of a ring of eight landmarks from points well outside the circle, as in tests with real bees[6].

The model does not specify how directional information is abstracted. The information is assumed to be provided by an independent system. We have attempted, but failed, to generate a simple alternative model in which direction can be automatically obtained from an array of close and distant landmarks.

Despite the success of the model in our artificial environment, it is rash to conclude that this is how bees operate in the real world. For a start, sensory processing is undoubtedly more complicated than we have allowed it to be here. However, what does seem to be certain is that bees do not need a three-dimensional representation of their immediate surroundings in order to use nearby landmarks to locate a food source. A much simpler model will work: one in which the bee is not required to identify landmarks as such, or even to separate figures from the background. There is, of course, a price to be paid for simplifying one's visual world in the way the experiments suggest that the bee has done. It is that the bee can only use the information provided by its snapshot of the landmarks to return to the food source. The snapshot provides it with no means of navigating to anywhere else within the array of landmarks.

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Rate of turnover of structural variants in the rDNA gene family of *Drosophila melanogaster*

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A high degree of polymorphism for the length and copy number of rDNA spacers, in both the X and Y chromosome clusters, has been found in a wild population of Drosophila melanogaster. *The genetic behaviour of rDNA structural variants in separate and mixed populations derived from isofemale lines suggests that they are not subject to strong selection and are stable for over 1,000 generations. The high structural variability suggests an evolutionary rapid process of turnover in the family which could partly explain widespread sequence homogeneity (concerted evolution) of rDNA within a species.*

SEVERAL studies on the evolution of tandem and interspersed repeated DNA families have revealed an unexpected greater family homogeneity within than between species. This phenomenon is known as concerted evolution and has been observed in a wide variety of genic and non-genic families.

The degree and extent of homogeneity in each species cannot easily be understood solely in terms of natural selection and drift, and is more probably the result of molecular mechanisms of homogenization (see refs 1–3 for reviews). Smith[4] and Ohta[5] have described the possible dynamics of homogenization in tandem arrays based on the mechanism of unequal exchange; and others[6–8] have discussed the potential of gene conversion for homogenizing tandem and interspersed families. Mechanisms of homogenization probably have a significant role in shaping the evolutionary progress of a family of genes and it is important to understand the extent and rates of these mechanisms.

Unequal chromatid exchange has been shown to be taking place in the arrays of sequences coding for ribosomal RNA (rDNA) of yeast[9,10] and *Drosophila*[11–13] (for reviews see refs 1, 14–16). In the rDNA of *Xenopus*[15] and *Drosophila*[12], unequal exchange in and between the spacers generates variation in length and copy number of these regions. Using such structural

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