VISUAL NAVIGATION IN INSECTS: COUPLING OF EGOCENTRIC AND GEOCENTRIC INFORMATION

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Summary

Social hymenopterans such as bees and ants are central-place foragers; they regularly depart from and return to fixed positions in their environment. In returning to the starting point of their foraging excursion or to any other point, they could resort to two fundamentally different ways of navigation by using either egocentric or geocentric systems of reference. In the first case, they would rely on information continuously collected *en route* (path integration, dead reckoning), i.e. integrate all angles steered and all distances covered into a mean home vector. In the second case, they are expected, at least by some authors, to use a map-based system of navigation, i.e. to obtain positional information by virtue of the spatial position they occupy within a larger environmental framework.

In bees and ants, path integration employing a skylight compass is the predominant mechanism of navigation, but geocentred landmark-based information is used as well. This information is obtained while the animal is dead-reckoning and, hence, added to the vector course. For example, the image of the horizon skyline surrounding the nest entrance is retinotopically stored while the animal approaches the goal along its vector course. As shown in desert ants (genus *Cataglyphis*), there is neither interocular nor intraocular transfer of landmark information. Furthermore, this retinotopically fixed, and hence egocentred, neural snapshot is linked to an external (geocentred) system of reference.

In this way, geocentred information might more and more complement and potentially even supersede the egocentred information provided by the path-integration system. In competition experiments, however, *Cataglyphis* never frees itself of its homeward-bound vector – its safety-line, so to speak – by which it is always linked to home. Vector information can also be transferred to a longer-lasting (higher-order) memory. There is no need to invoke the concept of the mental analogue of a topographic map – a metric map – assembled by the insect navigator. The flexible use of vectors, snapshots and landmark-based routes suffices to interpret the insect's behaviour.

The cognitive-map approach in particular, and the representational paradigm in general, are discussed.

Key words: visual navigation in insects, navigation, skylight compass, landmark guidance, spatial memory, cognitive maps.

Introduction

Unlike monarch butterflies (Brower, 1996), bees, ants, wasps and other social hymenopterans do not travel seasonally over distances of thousands of kilometres. Nevertheless, on their day-to-day foraging trips they may leave their nesting site for some hundreds or thousands of metres, i.e. for distances of the order of a million times their body length, and then return to the starting point, the central place of their foraging area, with seemingly unerring precision (for a review, see Wehner, 1981). In covering such substantial distances, they rely most heavily on visual cues provided by both the sky and the terrestrial environment. As they cannot take a bird's-eye view – not even a bee's-eye view – of the entire area over which they travel, they must obtain the necessary navigational information in a stepwise manner as they move through their nest environs.

The question of how they acquire this spatial information has recently raised an upsurge of interest among behavioural scientists and neurobiologists (for a review, see Wehner, 1992). It has culminated in the hypothesis that the insect navigator assembles and uses a large-scale map-like internal representation – possibly in the form of a metric cognitive map – of its environment (Gould, 1986; Gallistel, 1990; for reviews, see Wehner and Menzel, 1990; Dyer, 1991). While increasing numbers of biologists, psychologists and even ecologists (Real, 1993) are attracted to this cognitive approach, others (e.g. Bennett, 1996) argue that it has generated more portentous rhetoric than tangible results. In any event, the one thing upon which everybody agrees is that the cognitive map hypothesis is a powerful stimulator of controversy.

In trying to keep Ockham's razor sharp, we shall take a more cautious approach. In particular, we focus on a detailed experimental analysis of an insect's navigational performance. The insect in question is the Saharan desert ant *Cataglyphis*. This ant is a solitary forager that scavenges for other

arthropods that have succumbed to the physical stress of their desert habitat and, most importantly in the present context, does so by relying upon visual rather than chemical cues. It never lays pheromone trails for either recruitment or homeward orientation. In experimental terms, another advantage of *Cataglyphis* is that it walks rather than flies, so that its navigational courses can be recorded in full detail.

While foraging, *Cataglyphis* follows a circuitous path but, once it has found food, it returns to the starting point not by retracing its outbound path but by setting a straight course back home. The home vector is determined by the integration of the outbound path rather than by reference to landmark information. The path-integration (dead-reckoning) system works even in areas that are entirely devoid of any reliable landmark cues, e.g. in the vast expanses of the Saharan salt pans. Even more convincingly, it continues to work after the ant has been displaced to a new location. Upon release, the animal chooses a course parallel to its predisplacement course and walks for a distance equivalent to its predisplacement distance. Once it has reached the fictive position of the nest, it switches on a systematic search programme (Wehner and Srinivasan, 1981; Müller and Wehner, 1994). The first part of this article deals with this path-integration mechanism.

Any such egocentric system of navigation has two potential pitfalls. First, it must run uninterruptedly as long as the animal moves and, second, it is inherently susceptible to cumulative navigational errors. Hence, if the animal visited a particular foraging area repeatedly, it would be advantageous for the navigator to be able to take, every now and then, a positional fix by acquiring landmark-based geocentred information. Indeed, desert ants as well as honeybees use such information in addition to that provided by their path-integration system, and it is on this type of information that the second part of this article concentrates.

In the third part, we discuss the question of how the two types of information, egocentric and geocentric, are interrelated, in other words, to what extent the landmark-based information is ever freed from the egocentric framework within which it has been acquired.

We shall complement this case study on *Cataglpyhis* by referring to experimental results obtained in bees (*Apis*, *Trigona*) and wasps (*Philanthus*, *Ammophila*, *Bembix*, *Cerceris*, *Vespula*). Armed with this information, we shall finally return to the map hypothesis and, in discussing its validity, try to fill the gap between rhetoric and reality. Are we really forced to attribute to the insect navigator the computational abilities needed to assemble and use a metric map? This is the final question we address.

Path integration: the insect's fundamental system of navigation

When *Cataglyphis* starts its foraging life, path integration is the only mechanism used in long-distance navigation and, as we shall see later, it remains the fundamental mechanism throughout the ant's lifetime. While following its outbound path, *Cataglyphis* continuously measures all angles steered and all distances covered and integrates them into a mean home vector. This vector provides the animal with a continually updated running total of its direction and distance from the nest. As regards the navigational mechanisms involved, three questions arise. How does the animal measure (i) the angular and (ii) the linear components of movement, and how does it (iii) integrate these data in computing its home vector?

(i) Skylight information is used in *measuring angles steered*. It is clear from the outset that using such an external compass cue largely reduces the potential errors that would result, in full magnitude, from the integration of purely idiothetic, e.g. proprioceptive, signals (for a theoretical treatment, see Benhamou *et al.* 1990). In particular, ants and bees can derive compass information from the azimuthal position of the sun as well as from spectral gradients in the sky (for a review, see Wehner, 1994), but the predominant and most precise compass cue is provided by the pattern of polarized light, i.e. the pattern of the electric (E-) vectors of light, in the sky.

For more than a decade, this E-vector compass has been investigated in quite some detail, both behaviourally and neurophysiologically, but in the present context only one aspect of the compass mechanism is important. As shown by extended series of parametric behavioural tests, bees and ants are programmed with a strikingly simple internal representation, or template, of the E-vector patterns in the sky (Fig. 1, for a review, see Wehner, 1994). While the actual patterns change with the elevation of the sun, the insect invariably applies its hard-wired internal template. It might do so in a template-matching mode. At any one time, the best match between the internal template and the external pattern is achieved when the insect is aligned with the solar (or antisolar) meridian. At this point, maximal overall responses summed over all detectors of the neural template occur. The match decreases as the animal deviates from this reference meridian (0° or 180°, respectively, in Fig. 1). If this line of argument is correct, the animal must exhibit navigational errors when it is trained under the full E-vector pattern but later tested with, say, an individual E-vector. As there is no exact point-to-point correspondence between the internal template and the external pattern, the individual E-vector is matched with the corresponding detector of the template only when the animal deviates, by a certain angular amount, from the solar meridian. Consequently, navigational errors arise; it was these navigational errors that, in the first place, enabled us to reconstruct the ant's and bee's E-vector template. Of course, navigational errors do not occur when the animal is trained *and* tested under the same stimulus conditions, i.e. presented with either a full E-vector pattern or the same patch of skylight. Under these conditions, which the insect usually experiences during its short foraging excursions, it always uses the same reference direction of its compass, be this the actual solar meridian or another point of the compass characterized by the best possible match between the internal template and the outside world.

In more general terms, the insect's E-vector compass

A

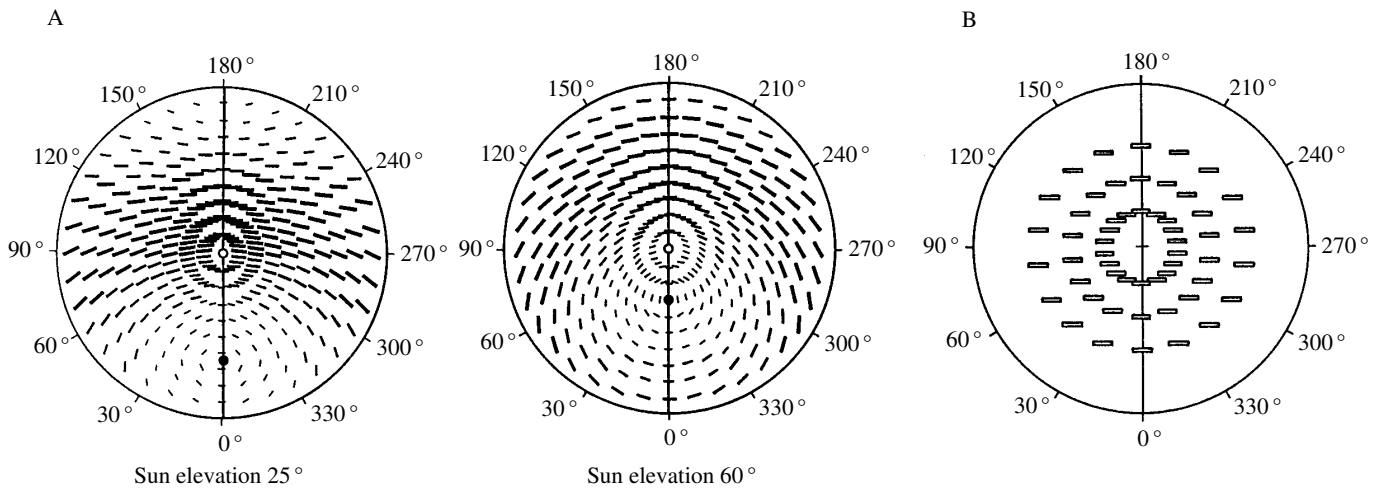Sun elevation 25°

B

Sun elevation 60°

Fig. 1. External E-vector patterns in the sky (A) and the ant's and bee's stereotyped internal representation of these patterns (E-vector template; B). In A, the distributions of E-vectors (black bars) are shown for two elevations of the sun (25° and 60°). For the experimental paradigm that led to the reconstruction of the E-vector template, see Rossel and Wehner (1982, 1984), Wehner and Rossel (1985) and Fent (1986).

provides a striking example of how evolution has designed a particular neural mechanism to accomplish a particular task rather than arrived at an all-purpose mental representation of the outside world. This conclusion is further corroborated by what we now know about the neural hardware of the compass mechanism, and particularly by the fact that the E-vector compass is confined to a separate neural pathway within the ant's and bee's visual system. This neural pathway, which receives its input from a distinct part of the retina at the uppermost dorsal rim of the eye, is specialized exclusively to process E-vector information from the sky.

(ii) To *estimate distance travelled*, desert ants use self-induced retinal image flow (Ronacher *et al.* 1994; Ronacher and Wehner, 1995). This result was obtained by training and testing *Cataglyphis* within Perspex channels in which patterns were presented underneath a transparent walking platform. In the training situation the patterns were stationary, but under test conditions they were moved in the same direction or in the opposite direction relative to the ant's direction of movement. In the latter cases, homing distances were overestimated or underestimated, respectively. We also showed that the estimation of distance depends on the speed ($m s^{-1}$) of image motion rather than on the contrast frequency (s^{-1}). As deduced from experiments in which the ants walked on a featureless floor or in which they were provided with ventral eye covers, *Cataglyphis* might also use kinesthetic (most probably some kind of pedometer) information to gauge its travel distance. For a given walking speed, step length is constant (Zollikofer, 1994), and during a particular foraging trip, *Cataglyphis* maintains a constant walking speed (Wehner and Srinivasan, 1981). Hence, the number of steps is proportional to the distance travelled.

Energy expenditure, which has long been regarded as a means for distance estimation in bees (Heran, 1956; von Frisch, 1967), could be excluded as a relevant cue. Loading *Cataglyphis* with artificial weights of up to four times its body weight did not affect its measurement of walking distance (Schäfer and Wehner, 1993). More recently, it has also been shown for bees that distance travelled is assessed by measuring self-induced visual image flow (Esch and Burns, 1995, 1996; Srinivasan *et al.* 1996).

(iii) In discussing the *path-integration scheme*, let us first emphasize that the insect does not store in its memory the spatial details of its outbound path (and hence does not compute its homeward course only upon finding food), but solves the problem in an incremental way. Consult, for example, Fig. 2. At point P_n the ant is informed about the home vector (ν_n, $\mathbf{r_n}$), but not about the path leading from N to P_n. Mathematically, trigonometric computations are necessary to obtain such vector information, i.e. to compute (ν_{n+1}, $\mathbf{r_{n+1}}$) from (ν_n, $\mathbf{r_n}$).

In order to understand how this incremental operation works, we constrained the ants to follow a particular path by training them to run through a system of narrow channels. Within these channels, the ants had a view of the sky but not of surrounding landmarks. When they were trained, for example, to run a two-leg outward path and then transferred to an open test area, they did not choose the true homeward course, but deviated systematically by an error angular ε from that course (Fig. 3). By studying how ε varied with the training angle α and the ratio s_1/s_2 of the lengths of the two legs, we arrived at an approximate non-trigonometric algorithm that described the ants' behaviour surprisingly well (Müller and Wehner, 1988). It also describes, at least approximately, the results of some similar experiments performed in bees, spiders and mammals, including man (for references, see Wehner, 1992; in addition, see Séguinot *et al.* 1993; Fujita *et al.* 1993). In the ant's real foraging life, however, the angular errors ε usually do not show up, because *Cataglyphis* employs a particular locomotor programme which ensures that all such systematic errors cancel each other out (Wehner and Wehner, 1990). If the foraging ant does not obey this locomotor regime

$$\Delta \mathbf{s} \ll \mathbf{r}$$
$$\delta = \lambda - \nu$$
$$\Delta \mathbf{r} = \Delta \mathbf{s} \cos \delta$$
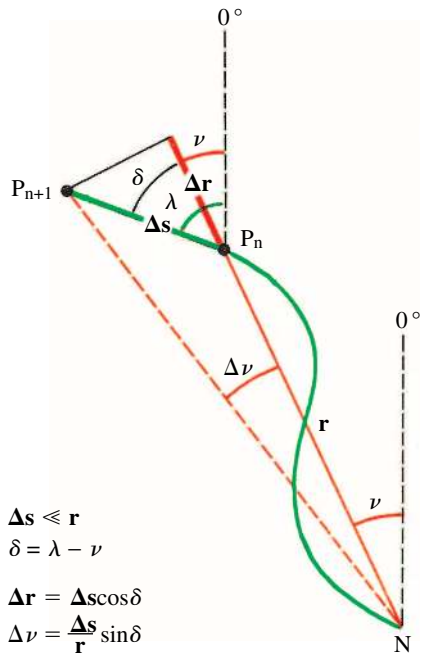$$\Delta \nu = \frac{\Delta \mathbf{s}}{\mathbf{r}} \sin \delta$$

Fig. 2. Path-integration scheme. The position P_n of the animal in relation to the starting point of its foraging excursion (nest) is described by the vector $(\nu, \mathbf{r})$. If the animal proceeds in the direction λ by a path increment $\Delta \mathbf{s}$, the new position P_{n+1} $(\nu + \Delta \nu, \mathbf{r} + \Delta \mathbf{r})$ is reached. Adapted from Hartmann and Wehner (1995).

strictly, as is sometimes the case, systematic errors occur that are of the sign and magnitude predicted by the model.

Does the approximate solution mean that the ant's brain is not able to solve the problem properly, i.e. to perform trigonometric computations? First, there is no *a priori* reason to assume that trigonometric computations are more difficult to solve by any kind of neural hardware than is a non-linear arithmetic computation. Second and foremost, however, one must not take an algorithm that is able to describe the performance of a neural mechanism for the mechanism itself. Hartmann and Wehner (1995) have outlined a simple way in which a path-integration system could be implemented neurophysiologically. Although the structure of the proposed neural architecture does not matter in the present context, we mention this architecture to stress an important point. The neural system is able to produce the ant's (approximate) solution as well as the exact solution by only slight changes in some of its parameters. This result supports our assumption that the ant's solution of the path-integration problem is adaptive rather than an outcome of inherent neural imperfections. The adaptive significance becomes immediately apparent if one recalls that all path-integration systems are open integrators and, thus, prone to cumulative errors. One back-up system employed by *Cataglyphis* to reduce such homing errors is the additional use of landmark information, especially of landmark-based route information. Notice that the ant's path-integration system brings the animal closer to the first and mostly straight leg of its foraging excursion (see Fig. 3) and hence increases the probability that the animal, while reeling off its home vector, will hit its familiar landmark route. We have now set the stage for the following section.

Use of landmark information

As will have become apparent from the Introduction, in discussing the use of landmark information, we enter mined territory. Let us therefore proceed along a carefully designed route of experimental paradigms.

In one paradigm, the ant's working memory is cleared from any homebound vector information. This is accomplished by testing individuals that, after having completed a successful foraging excursion, have arrived at the nest entrance and hence reset their path-integration system to zero ('zero-vector ants'). If such ants are displaced to a landmark-free landscape (test area), they immediately start a non-random systematic search for the nest (Wehner and Srinivasan, 1981; Müller and Wehner, 1994). The search paths are perfectly centred about the fictive position of the nest, i.e. the point of release, and do not show any azimuthal bias in the direction of the previous home vector. The result, however, is completely different if the nest entrance has previously been surrounded by landmarks, e.g. an array of black cylinders. Then, the zero-vector ants, when displaced to a test area in which the same array of landmarks has been installed, move towards that array and
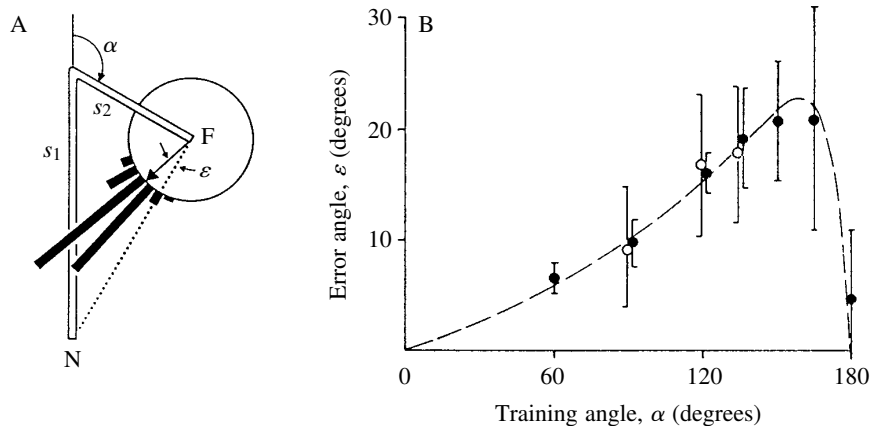

Fig. 3. Path integration in ants *Cataglyphis fortis*. (A) Experimental arrangement and result (example given for $\alpha=120°$). Ants trained along the angular route s_1, s_2 from the nest (N) to a feeder (F) are captured at F and released in an open test field. (B) Error angles (ε) exhibited by the ants for different training angles (α). Mean values and standard deviations; $N=1412$. The dashed line represents the prediction of a non-trigonometric integration model. Data from Müller and Wehner (1988).
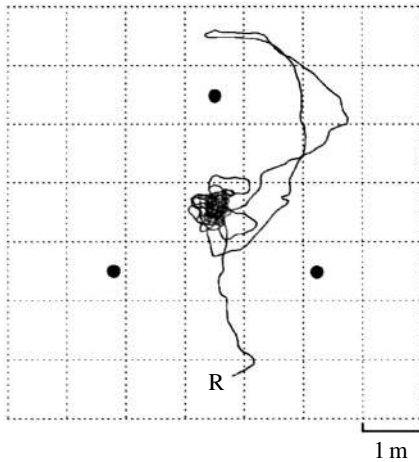
Fig. 4. Search pattern of an ant *Cataglyphis fortis*, trained to the centre of a triangular array of cylindrical landmarks (11.5° high, 6.4° wide). R, point of release. The search path was recorded for 5 min (path length 41.3 m).

search, with amazing precision and persistence, at the proper location of the non-existent nest (Figs 4, 5A).

What kind of information does the animal acquire and store in its visual spatial memory and how does it later retrieve and use this information? A simple experiment shows that the ant's memory contains a rather unprocessed two-dimensional snapshot of the visual scene around the goal. It does not resort to a more generalized strategy such as 'search in the centre of a set of identical landmarks' (Fig. 5B). From these and other experiments in which ants as well as bees were presented with landmark arrays that were distorted versions of the training array, one can conclude that, in most cases, the insect moves so as to decrease the discrepancy between the stored snapshot and the current retinal image (Wehner, 1972; Cartwright and Collett, 1983; for reviews see Collett, 1992; Wehner, 1992; but see also Brünnert *et al.* 1994). Furthermore, motion parallax cues can be used to distinguish between closer and more distant landmarks and to enable the insect to rely more heavily on the former (Cheng *et al.* 1987; Zeil, 1993). This makes sense because the precision with which a goal is localized is higher the closer the visual objects used in localization are positioned to the goal. Compare, for example, Fig. 5A and Fig. 5C. In the experiments described there, the landmarks appear under the same angular subtense but at different distances. The search density profile is much flatter when the more distant landmarks are used in pinpointing the goal.

Snapshot matching is quite a powerful strategy capable of guiding the animal over substantial distances. As illustrated in Fig. 6B, zero-vector ants can effectively return home when released at arbitrary sites even 30 m away from the nest. Their homing performance certainly looks like map-guided behaviour, but can be fully explained by an image-matching mechanism. It is immediately apparent from the particular nest environment selected for this experiment (Fig. 6A, upper part) that, if the ants moved so as to transform their current retinal image into one resembling the nest-site snapshot, they should all move towards the centre of the small salt pan in which the nest is located; and this is what they actually do. However, the
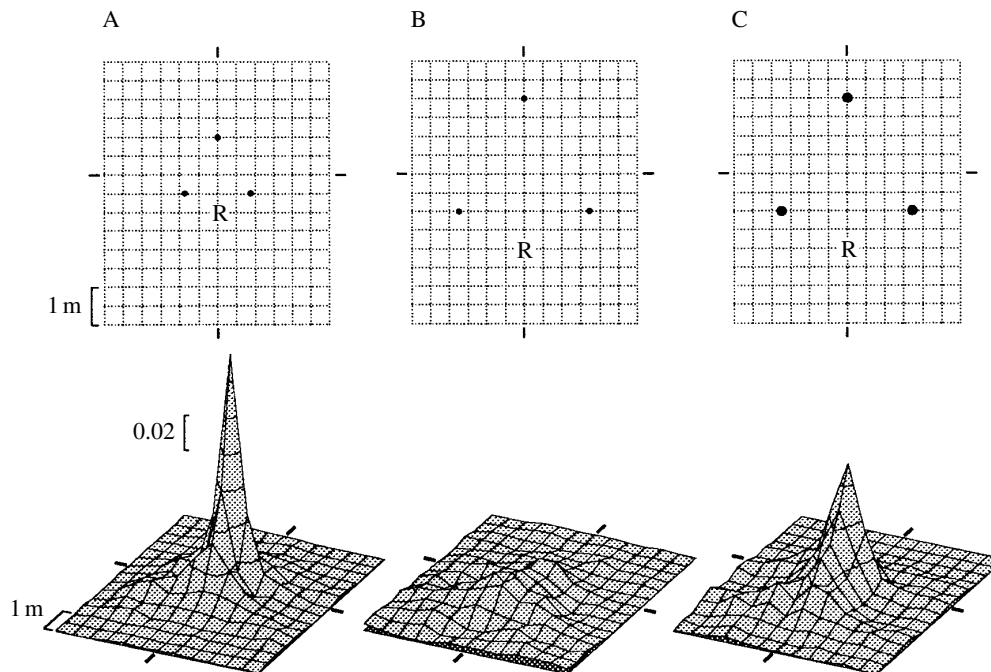
Fig. 5. Search density profiles of *Cataglpyhis fortis* trained, as in Fig. 4, to an array of three cylindrical landmarks. (A) Landmarks in the training situation. In the training area, the nest is in the centre of the equidistant triangle formed by the three cylinders. (B) Landmarks separated by twice the training distance. (C) Landmarks twice the training size and separated by twice the training distance. 8–12 ants were tested for 5 min each. R, point of release.
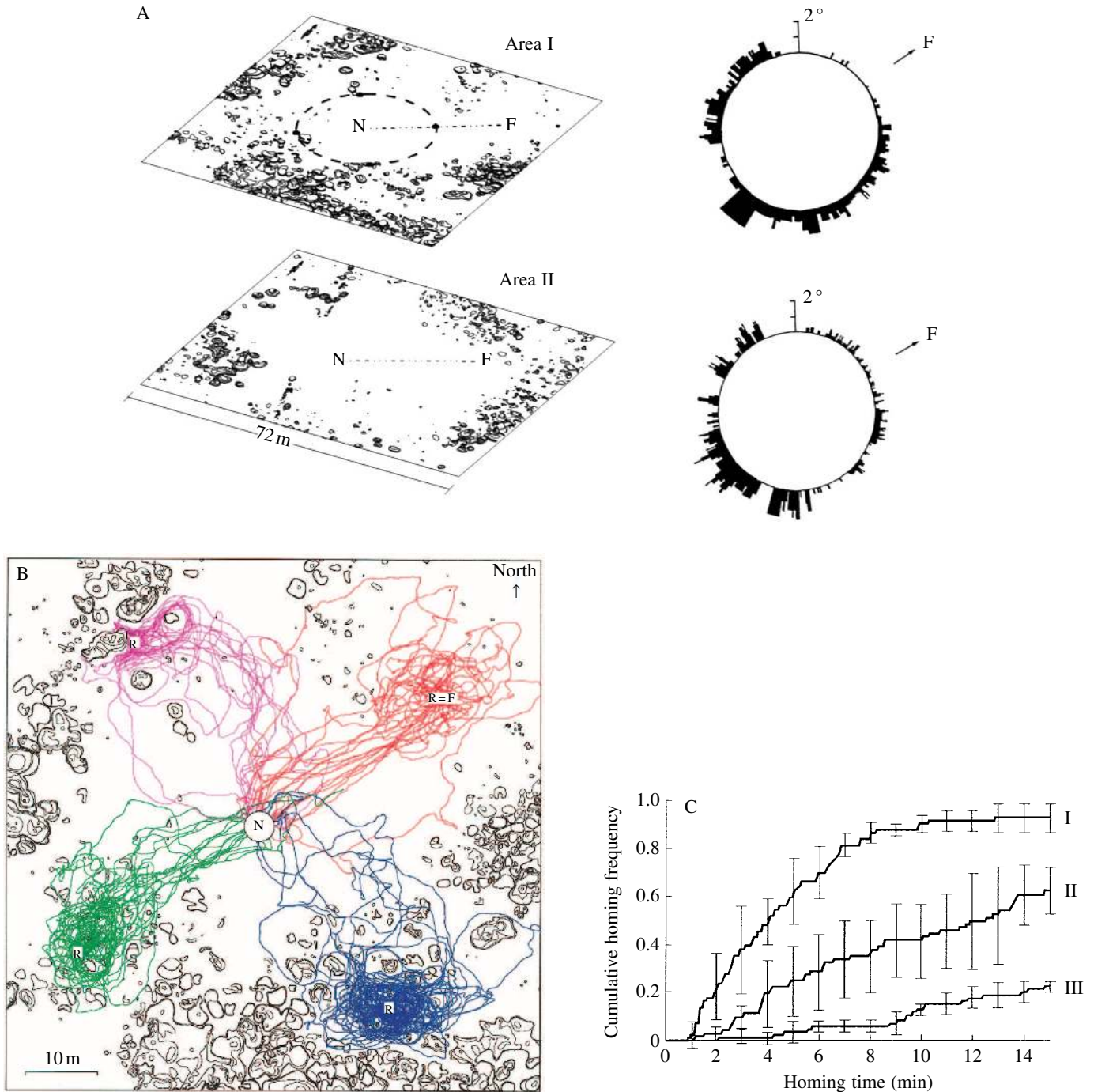
Fig. 6. Navigation by image matching in *Cataglyphis fortis*. (A, left-hand side) Location of nest (N) and feeding site (F) within a low-shrub desert. Ants from areas I and II are tested in area I. Black dots mark the points of release, which in B are indicated by R. (A, right-hand side) Horizontograms (angular distributions of landmarks) as seen from N. (B) Area I. Shrubs are indicated by contour lines in 15 cm height intervals. 17–20 ants, which had returned from F to N, were displaced from N and released at sites R. Homing paths were recorded until the ants had approached N for 2 m or, if this was not the case, for 15 min. The nest entrance N is an inconspicuous hole in the desert floor. (C) Cumulative homing frequencies of ants released in area I at the four sites marked by the black dots in A. I, II, ants taken from the nests in area I and II, respectively. III, ants searching in a test area devoid of any landmarks. The latter data serve as a control to indicate the homing times needed by ants in a landmark-free environment. Values are means ± S.D. *N*=79 (I), 72 (II) and 84 (III). The distances R–N were 30 m and 15 m in B and C, respectively.

same behaviour is shown by ants that have never seen this area but are transferred to it from another nest located in a similar environment (Fig. 6A, lower part). Owing to the slight differences between the snapshots acquired by either group of ants, the homing efficiency of the 'foreign' ants is reduced relative to that of the autochthonous ants (Fig. 6C).
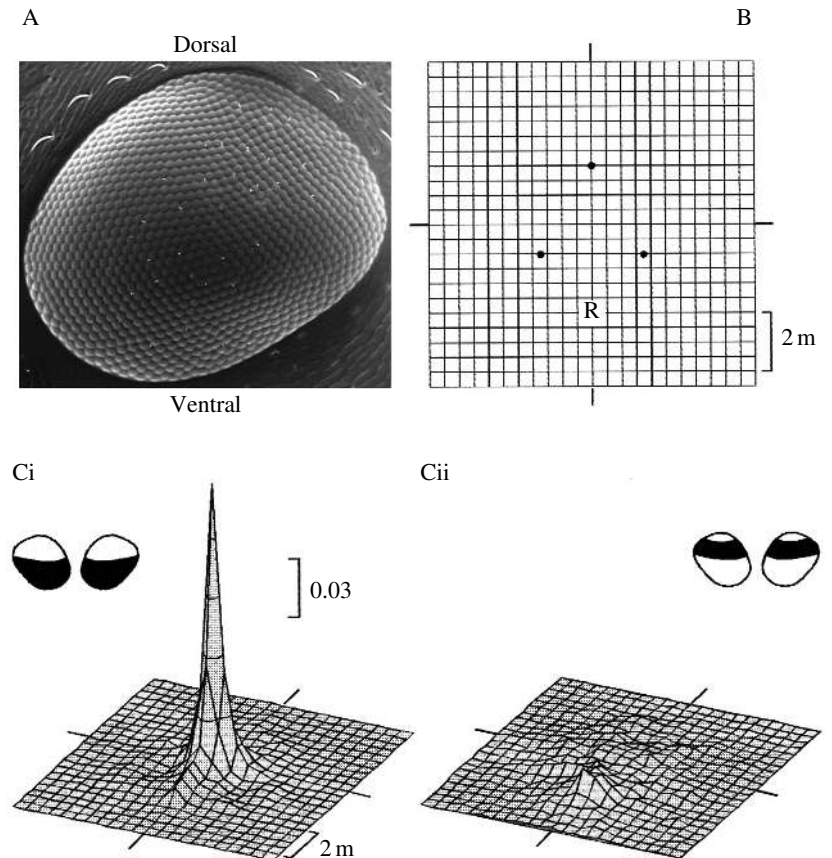
Fig. 7. (A) Left compound eye of *Cataglyphis fortis*. (B) Array of landmarks to which ants had been trained; see Figs 4 and 5. (C) Search density profiles of ants in which either the ventral (Ci) or dorsal (Cii) halves of the eyes had been covered. In the latter case, the dorsal rim area specialized for detecting the E-vector patterns in the sky had to be left uncovered. Otherwise, the ants would have stopped foraging. 46 runs of 18 ants (Ci) and 44 runs of 16 ants (Cii) tested for 5 min each. Adapted from Antonsen and Wehner (1995).

Recent research carried out in our laboratory throws some light on how the insect's visual system might accomplish the matching-to-memory task. First, the dorsal halves of the ant's eyes (and visual systems) are necessary and sufficient to acquire and use the relevant information. If they are occluded by light-tight eye caps, the ants behave as though lost, but if the ventral halves of the eyes are covered instead, the animals are as precisely oriented as the untreated controls are (Fig. 7). Second, the snapshot is fixed relative to retinal coordinates and does not rotate within the ant's head to compensate for changes in the orientation of the animal's longitudinal body axis. If the snapshot is acquired by one eye (or by a particular part of one eye), it cannot be retrieved by the other eye (or by another part of the same eye). These results were obtained by exchanging eye caps between the left and right eyes (Wehner and Müller, 1985) or between different parts of the same eye (Fig. 8). They all show that neither interocular nor intraocular transfer occurs. This has important implications. If the snapshot is retinotopically fixed, and if it should later be matched to a current retinal image, this match can be accomplished only if the animal assumes the same orientation of its body as it did while acquiring the snapshot.

Before we tackle this question in the next section, let us consider the case in which central-place foragers store landmark information not only about their central place, but also over larger spatial scales. Fidelity to particular routes radiating from the nesting site has been inferred from various observations in honeybees (von Frisch, 1967), bumblebees (Heinrich, 1976), orchid bees (Janzen, 1974) and sphecid wasps (Baerends, 1941), but the use of vector-based and landmark-based route information has not been disentangled experimentally and the routes have not been manipulated artificially. Fig. 9 provides two examples of *Cataglyphis* ants which consistently follow their idiosyncratic routes through a cluttered environment. As the same routes are taken when the animal is either provided with or deprived of its home vector, it must have learned the visual features characterizing its route, be it the route through a natural (Fig. 9) or an artificial (Fig. 10) landmark environment. Once released at the former feeding site, the vector-bound ants immediately enter the route, while the very same animals when deprived of their vector information first become engaged in rather extensive search behaviour until they accidentally find the route. After retraining to another feeding site, *Cataglyphis* can learn (at least) two separate route (*A* and *B*). Having been displaced from the nest to one or the other food source, it follows either route irrespective of the one previously travelled. For example, it is able to follow route *B* after having returned to the nest along route *A* (for similar experiments in bees, see Wehner *et al.* 1990; Dyer, 1991).

We do not know yet what visual features of the familiar route are learned and how they are later used in following the route. In any event, the memories of landmarks are not necessarily tied to the home vector in the sense that a particular
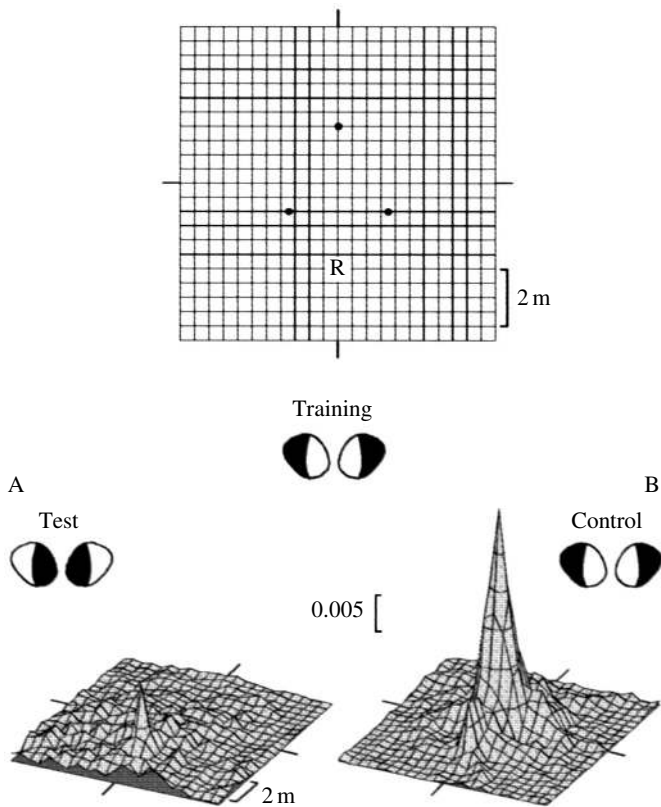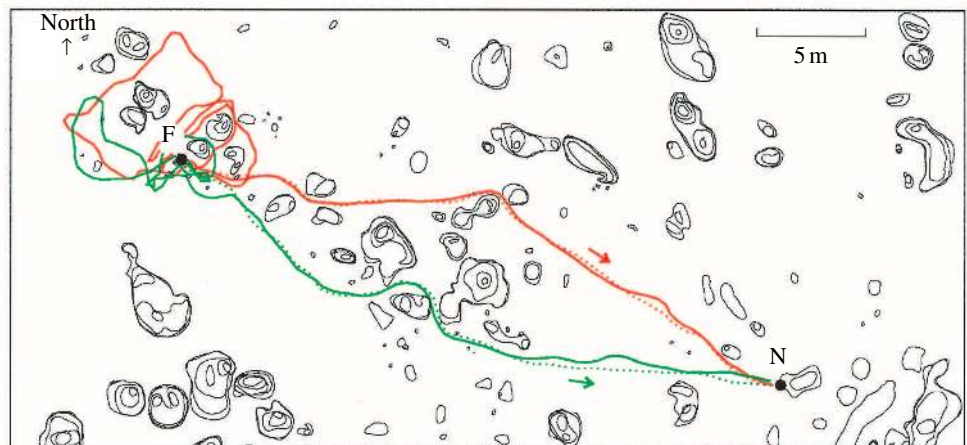
Fig. 8. Test for intraocular transfer. Search densities of ants *Cataglyphis fortis*, trained to the centre of an array of three cylindrical landmarks; see Figs 4 and 5. During training, the posterior parts of the eyes were covered with light-tight caps. (A) Test with eye caps mounted on the anterior halves of the eyes. (B) Post-experimental control: eye caps again mounted on the posterior halves of the eyes. Equivalent results were obtained in ants in which during training the anterior halves of the eyes had been covered. 43 runs of 15 ants (A) and 41 runs of the same 15 individuals (B).

landmark is expected to occur after a particular amount of the vector course has been covered. As described above, the ants follow a familiar route even if their vector store has previously been emptied. (The possibility that the vector could have been recalled from some higher-order memory store can be excluded

as well; see below.) This leaves us with some kind of sequential matching-to-memory process. The ant might store a series of snapshots and later retrace its route by trying to match the current retinal images to sequentially retrieved visual images. It might not be necessary to number the individual snapshots, because the ant travels through a stable visual world in which visual images occur in a fixed sequence. Hence, the ant could rely only on its current visual input to trigger the snapshot that is appropriate at any one time. Again, however, this strategy has snags. The ant's natural habitat, a low-shrub desert, consists of arrays of rather similar objects, which are not easily distinguishable by specific visual characteristics. Does the ant, then, store a sequence of changing visual flow fields and later use this sequence to adjust its path? In experiments in which the route was labelled just by a few artificial landmarks, the ant's behaviour could be simulated by a far simpler strategy. According to this model, the ant does not learn the fine details of the trajectory, but merely to keep any particular landmark on the correct side of its body (Collett *et al.* 1992).

Interrelations between egocentric and geocentric information

If landmark-based and vector-based information compete with each other, the former succeeds only in situations in which the ant's home vector is zero (Fig. 11; for bees, see Wehner and Menzel, 1990; Wehner *et al.* 1990). This is somewhat surprising, because if the animal possesses the correct landmark information (as shown by the ants in the zero-vector mode; Fig. 11, red paths), it would be advantageous always to use it, because this information invariably leads the animal back home. The observation that, in contrast, landmark information competes unsuccessfully with vector information demonstrates the predominant role played by vector information in insect navigation. This is also borne out by the result illustrated in Fig. 12: an array of landmarks that characterizes the nest induces searching for the nest only if the home vector is close to zero. Otherwise, the familiar landmarks are ignored.

This immediately leads to the question posed above of how

Fig. 9. Route guidance in desert ants *Cataglyphis fortis*. The natural environment consists of low shrubs (see black contour lines in 15 cm height intervals). N, nesting site; F, feeding site. Homing paths of two ants (red and green paths), which had arrived at F (dotted trajectories) and were subsequently, after returning to N, displaced back to F (solid trajectories). Vector information was available to the ants for the dotted paths but not for the solid paths (zero-vector mode of behaviour).
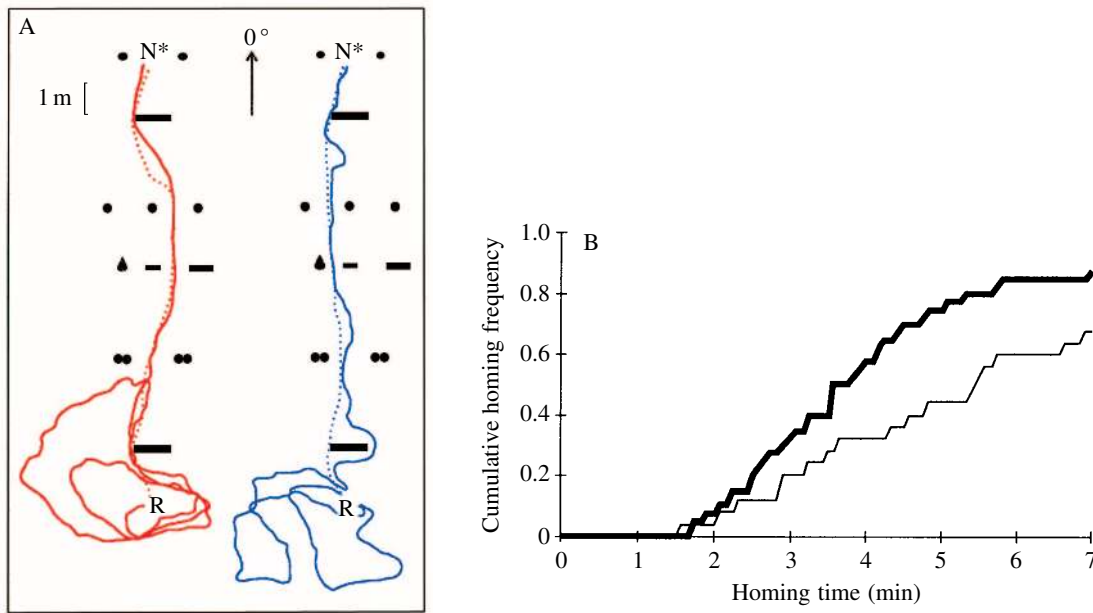
Fig. 10. Route guidance in desert ants *Cataglyphis fortis*. Artificial landmark environment. (A) Homing paths of two ants (red and blue traces). For experimental design and explanation see Fig. 9. N*, fictive position of nest. (B) Cumulative homing times of zero-vector ants (see solid trajectories in A). Heavy line, landmark array oriented as during training (0° direction); thin line, landmark array rotated by 90°.

the retinotopic snapshot is coupled to an earth-based reference (compass) system. One way to investigate this problem is to train *Cataglyphis* to a particular spatial position within an artificial landmark array (e.g. the two-cylinder array shown in Fig. 13A) and later to let it approach this array from either the

Fig. 11. Competition between vector-based and landmark-based modes of navigation. N, nest; F, feeding site (30 m distant from N); R, point of release. Blue and red paths refer to the same ants that had been displaced to R either from F or after they had returned to N, respectively. Inset: circular distribution of the ants' bearings at distances of 2, 4, 6 and 8 m from R. *N*=17.

original (training) or the opposite direction, presenting the array in either its original orientation or rotated by 180°. As indicated schematically in Fig. 13B, the search density profiles exhibit well-pronounced peaks only at locations at which snapshot, current landmark image and compass coordinates are in register (Fig. 13Bi,iii). This is independent of the position at which the ants have been released. Nevertheless, shallow peaks also occur when the landmark image is matched to the snapshot when the ant views the array while heading in a different direction from the one in which the snapshot had been acquired (Fig. 13Bii,iv). Notice that the compass reference linked to the landmark information does not depend on the state of the current home vector because it is also used by ants that have returned to the nest and, hence, have reset their path-integration system to zero. In summary, landmark patterns are learned with reference to compass cues (for bees, see Dickinson, 1994; Collett and Baron, 1994), but can be decoupled, to a certain extent, from such cues.

Conclusion: the map-paradigm and beyond

How is the large-scale spatial memory that the insect uses in navigation organized? Path integration operating within an egocentric system of coordinates and including an external (celestial) compass reference is the most significant mechanism. While continuously applying this self-centred system of navigation, the insect encodes spatial features of the (terrestrial) environment as neural snapshots of the landmark scenes around particular locations (nesting and feeding sites) or along frequently travelled routes. The landmark memories are linked to the state of the home vector (e.g. Fig. 12), but the linkage can be broken (perhaps as foraging time proceeds).
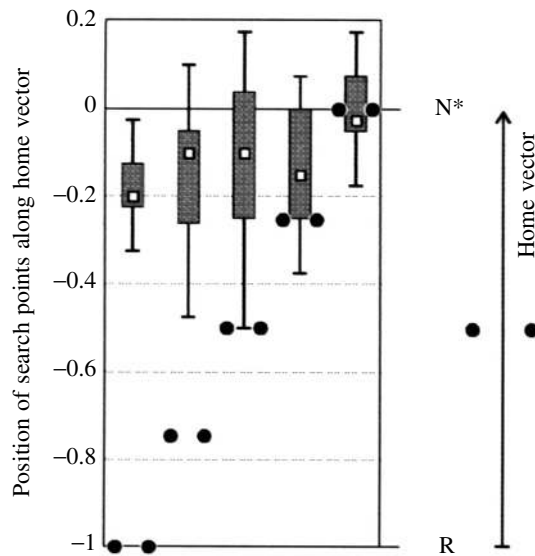
Fig. 12. Search points of ants *Cataglyphis fortis*, which experienced the landmark panorama of their nesting site (two-cylinder landmark array) at different stages of their home vector. R and N* indicate the release point and the fictive position of the nest, respectively. The landmarks are positioned at 100, 75, 50, 25 and 0 % of the length of the home vector. Box plot representations (quartiles); *N*=78. Adapted from Michel and Wehner (1995).

Familiar landmark routes are travelled even if the working memory is cleared from any compass information (e.g. Figs 9, 10) or if any kind of higher-order memory store provides the wrong vector information (e.g. Fig. 13Bii,iv). This conclusion is corroborated by the fact that the snapshots of landmark arrays characterizing particular locations are usually coupled to an external compass reference, but can be decoupled from this reference as well (Fig. 10B). Furthermore, ants (Wehner, 1990) and bees (Dyer, 1991; Dyer *et al.* 1993) can enter a route or approach a familiar site (Dyer *et al.* 1993) from various vantage points. Hence, landmark memories seem to be retrieved and used in quite flexible ways.

In spite of this flexibility, all the available evidence supports the hypothesis that, even in the most highly advanced insect navigators, landmarks are used for route guidance and site recognition but are not incorporated into an extensive map. The problems of maps, however, begin with the term itself. In an earlier paper (Wehner *et al.* 1983) we outlined a number of representations that an animal might acquire and use about spatial relationships in its environment. In the broadest sense of the word, they all might be called maps. (i) A 'route map',

for example, might consist of sequences of memory images experienced along different paths through the environment. Even if such routes are not linked by some external system of reference, they might guide the animal home from considerable distances. Such route maps are sufficient navigational aids particularly as bees and ants remain, usually for many days, within particular parts of their nest environment and hence will repeatedly use the same routes, even if they enter them from different vantage points. (ii) A 'vector map' could be formed by associating vectors with particular locations. In this case, vector summation and subtraction could lead to novel routes. It has sometimes been claimed that bees can recall a goal vector from a long-term memory store and associate it with the appropriate landmark scene around a particular site (Collett, 1996; Menzel *et al.* 1996), but in all these cases the experimental situation could not be controlled sufficiently to rule out the exclusive use of landmark-based information. In the only case in which this was achieved, *Cataglyphis* did not activate any vector store. (iii) The mental analogue of a topographic map – a 'metric map' *sensu* Gallistel (1990) or a 'map' *sensu strictu* – encodes the spatial relationships among familiar sites and routes. This could be achieved, for example, by orienting such sites and routes within a geocentric system of reference. There is no evidence available, either in bees or in ants, that insects could form vector or metric maps. Instead, map-like behaviour can be accounted for by the simpler means of one or the other form of snapshot matching. This strategy might be quite sophisticated in so far as landmarks positioned at different distances can be disentangled by motion parallax, and snapshots from the same scene might be taken from different vantage points.

Let us end with some more general remarks. Of course, the cognitive approach – the representational paradigm – is a level of interpretation in its own right. At best, it is like Ptolemy's system of epicycles, which could describe the movements of the planets in sufficient detail; but, as we now know, the heliocentric view of the world provides a simpler way of understanding this movement and one that comes closer to what is actually the case. By analogy, the cognitive-map approach might obscure some of the most important computational strategies used by the brain. In general, the brain has evolved not to reconstruct a full representation of the three-dimensional world, but to find particular solutions to particular problems within that world (Aloimonos *et al.* 1988; Ballard, 1991; Churchland *et al.* 1994). These particular solutions are usually based on neural modules that have already been established by other means. For example,

Fig. 13. Coupling of the retinotopic snapshot to an external compass reference. (A) Training situation: the position of the nest (N) is defined by two cylindrical landmarks. F, feeding site 30 m distant from N. (B) Test situations: ants that had returned to the nest (N) were captured and released at R. The peaks of the search density profiles are marked by red stars (B. Michel, U. Lingg and R. Wehner, in preparation).
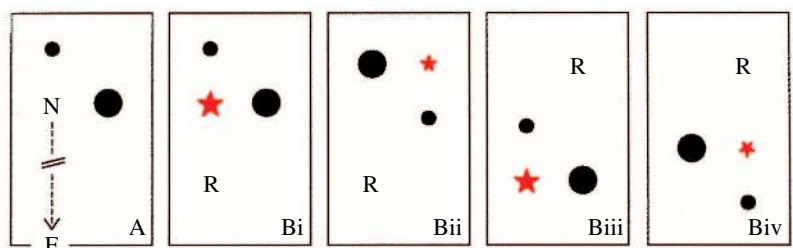
the neural circuitry employed in the insect's E-vector compass – the navigational gadget which we know best in terms of its underlying neural machinery – contains neural tools that, most probably, have been taken over from pre-existing systems (Wehner, 1994). Furthermore, the template mechanism used by the E-vector compass might have some fundamental neural traits in common with the snapshot-matching mechanism used in landmark guidance. The obvious difference between the two is that the external E-vector patterns are predictable, but the landmark panoramas are not. Hence, the skylight template can be hard-wired, as it acutally is, but the landmark snapshots must be acquired during the insect's foraging life. Finally, the capacity to form retinotopically organized neural snapshots might have derived from the fixation response, in which the image of an object is held in a fixed position on the retina (see Wehner, 1981; Dill *et al.* 1993). By entertaining this kind of bottom-up approach to understanding the organization of behaviour, we might finally follow the routes originally taken by evolution in orchestrating the different guiding mechanisms and knitting them into what Fabre (1882) called 'the insect's awe-inspiring system of navigation'.

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