

## STRUCTURE AND FUNCTION OF LEARNING FLIGHTS IN BEES AND WASPS

JOCHEN ZEIL\*, ALMUT KELBER AND RÜDIGER VOSS

*Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany*

### Summary

Bees and wasps perform systematic flight manoeuvres when they leave their nest or a foodplace, during which they acquire or update their visual memory of the goal location. In a typical learning flight, the insect backs away from the goal in a series of arcs that are roughly centred on the goal. The mean rate of turning is rather constant and tends to balance the angular speed at which the arc is described. As a result, the insect views the goal at relatively fixed retinal positions in its left and right visual field, depending on flight direction. The general direction in which the insect backs away from the goal and the transition from one arc segment to the next are influenced by the local scene and by compass cues. Insects returning

to the goal repeat some of the flight manoeuvres of their preceding learning flights. Their orientation in space and the retinal positions at which they view nearby landmarks are similar. One important function of learning flights appears to be the acquisition of visual depth information. We review the consequences of the structure of learning flights for visual information processing and discuss how they may relate to the acquisition of a visual representation and the task of pinpointing the goal.

Key words: Hymenoptera, learning, homing, landmark guidance, vision.

### Introduction

When bees and wasps leave their nest or a newly discovered food place for the first time, they do not do so in a straight line. Instead, they turn around to face the place they are leaving and back away from it in a series of steadily increasing arcs. It was recognised early on that these flight manoeuvres are intimately associated with the homing ability of insects and, more specifically, that they allow the insect to acquire a visual representation of the goal environment (reviewed by Wehner, 1981). Bees and wasps departing from a goal in this particular way have been said to perform ‘locality studies’, ‘orientation flights’ or ‘turn-back-and-look’ behaviour by different authors. In recognition of their function, we will use the term ‘learning flights’ in this review.

There are basically two situations in which bees and wasps perform these systematic learning flights: whenever an insect leaves its nest or a new foodplace for the first time and whenever it had difficulties in finding the goal during its previous return. When young honeybees first leave their hive, they can be seen to spend a few seconds hovering in front of the nest facing the hive entrance. They then back away in a series of zigzags and are last seen circling above the home area at a height of several meters (von Frisch, 1967; Vollbehre, 1975). After the first few returns to and departures from the hive, foraging bees will depart in a straight line and only ‘turn back and look’ for an update of their visual memory when the hive has been displaced. Honeybees and social wasps fly and

learn in a similar way during their first few departures from a newly discovered food source (Lehrer, 1991, 1993; Collett and Lehrer, 1993). After this initial phase, they will leave the goal without turning back. Whenever they have difficulties finding the goal, however, they will perform another learning flight on their subsequent departure. These re-orientation flights after difficulties in locating a goal have also been described for a number of solitary wasps (van Iersel and van den Assem, 1964; Zeil, 1993a). Some wasps and bees which provision nests in the ground perform a learning flight each morning on their first departure (Brünnert *et al.* 1994; Zeil, 1993a).

Attempts to understand the significance of learning flights in detail have been made only recently. The initial part of these flights is distinctly structured, in certain aspects invariant across species and, therefore, must reflect the principal constraints in small-scale navigation. We are looking at a complex behaviour pattern which serves the crucial task of allowing the insect to acquire and store all the information necessary to find its way back to the goal. Our ultimate aim is to understand the reasons for the particular design of learning flights. In this review, we therefore describe first what is known about the geometry and dynamics of learning flights and the consequences of their structure for visual information processing. We then go on to ask how these flights are controlled and how they are influenced by local scene and compass cues. In the last section, we explore the relationship

\*Present address: Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, PO Box 475, Canberra, ACT 2601, Australia.

between learning flights and homing by comparing the insects' behaviour during departure and during their subsequent approaches to the goal. As yet, too little is known about this relationship, but it will be the key to our understanding of two crucial aspects of landmark guidance: when the insects acquire information about the goal location and how they recall and use this information to pinpoint the goal.

### The structure of learning flights

At the level of flight paths, no two learning flights are the same. Yet, even across species, we find similarities in certain details, which we introduce in Fig. 1, using the learning flight of a *Cerceris* wasp as an example. Departing insects initiate a learning flight by turning to face the goal. They then back away from it in a series of arcs with increasing radius that are roughly centred on the goal (Fig. 1A). The insects fly sideways along an arc segment, facing slightly inwards and turn at a rate that matches their angular displacement relative to the goal. They thus view the goal with the lateral retina at 30–70° azimuth for most of the time and see it only briefly in their frontal visual field at the beginning of a new arc. The turning rate  $\theta$  and the arc velocity  $\beta$  (that is the rate with which the vector connecting the insect with the goal changes direction) are roughly constant and independent of distance from the goal (Figs 1B, 2A). The insects thus increase their ground speed with distance (Fig. 2C). They also gain height above ground at about the same rate at which they back away from the goal and therefore view the goal approximately 30–60° below the horizon (Fig. 2E,F). Events at the turning points that link two successive arc segments are meticulously timed: the insects first reverse flight direction and continue turning until the goal has crossed the frontal visual field. Turning direction is reversed about 400 ms later to clamp the goal again in a lateral retinal position (Fig. 1B).

It is hard to say, at present, how representative this learning flight structure is. Detailed studies are available only for a few ground-nesting wasps and bees (Zeil and Kelber, 1991; Zeil, 1993a) and for social wasps (Collett and Lehrer, 1993; Collett, 1995). These studies show, however, that the learning flights of different individuals and of different species of bees and wasps are invariant in certain dynamic and geometric features. The insects pivot around the goal at a fairly constant arc velocity, maintain a constant turning rate to view the goal with the lateral retina and seemingly make carefully timed decisions at the ends of arcs. To understand the functional significance of these flights, answers to the following three questions are needed. Why is the goal as the pivoting centre viewed with the lateral retina? What is the significance of the dynamic constancy during these flights? What makes the insect decide to switch flight direction at the end of each of the arc segments?

### Invariant elements and their consequences for information processing

During learning, bees and wasps pivot around the goal as a

centre. In egocentric coordinates, their 'home vector' has a relatively constant orientation at any time during their flight: it points down, 30–60° below the horizon, in a direction between 30 and 70° azimuth in the left or right visual field, depending on flight direction (Fig. 2D,F). The insects are thus anchored to the goal. Fixating the goal with lateral, rather than with frontal, eye regions would seem to have three possible reasons. First, lateral fixation keeps the frontal visual field, which, at least in sphecid wasps, is the region of highest resolution, free to scan the scene to the side of the goal. Second, it produces the same frontal views of the panorama and objects behind the goal at

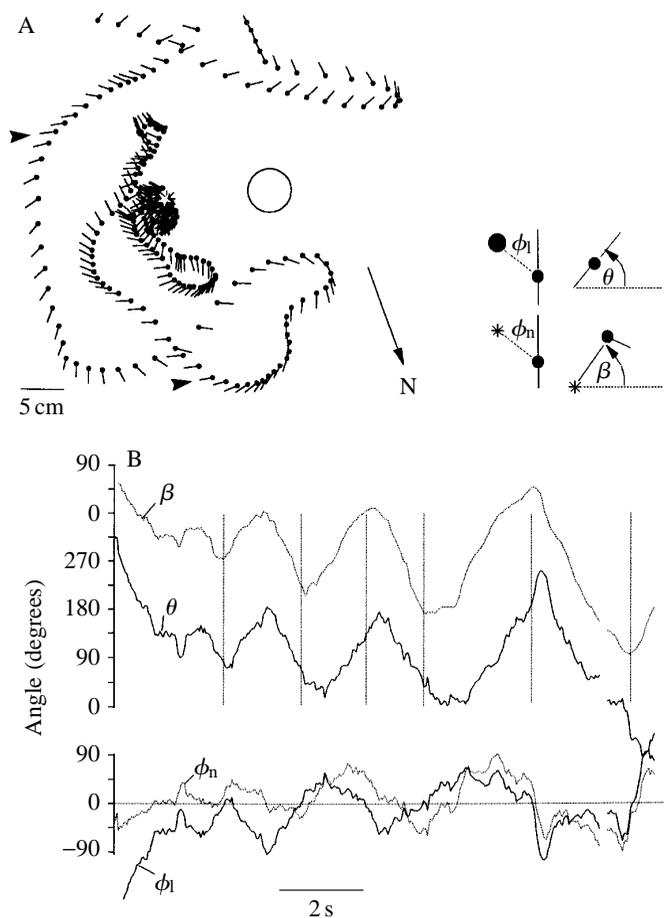
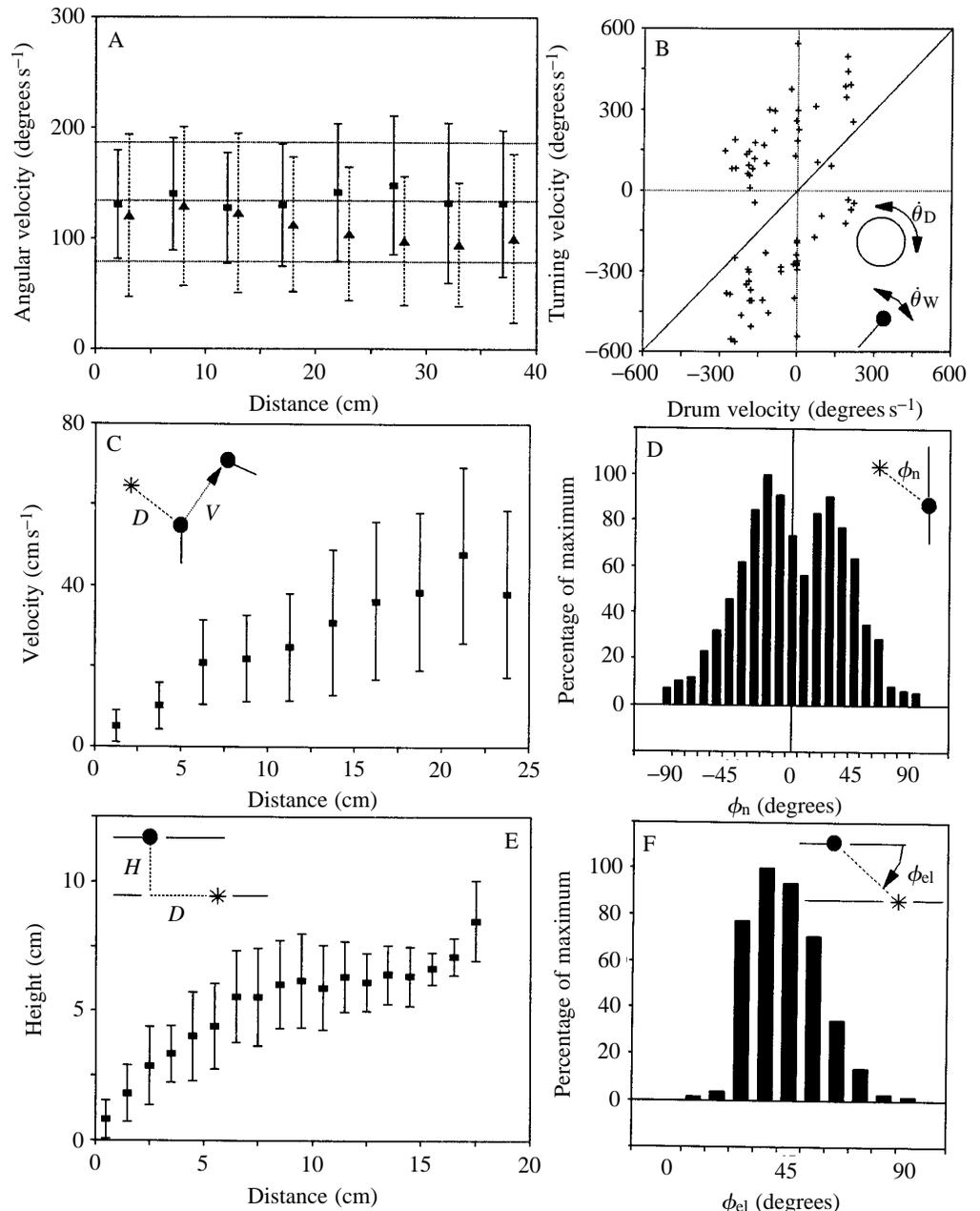


Fig. 1. The structure of learning flights. (A) A typical learning flight of a *Cerceris rybyensis* wasp (Hymenoptera: Sphecidae) as viewed from above. The position of the wasp's head (black dots) and the orientation of her longitudinal body axis (line) are shown every 40 ms. The large circle symbolises a landmark approximately 12 cm west of the nest entrance (marked by a white star). The black arrowheads indicate two positions with different bearings from the nest where the wasp faces in the same direction (see text). (B) The time course of various parameters of the same flight; for definitions, see insets at top right.  $\theta$ , longitudinal body axis orientation;  $\beta$ , angular position relative to the nest entrance (marked as an asterisk in the inset);  $\phi_n$ , retinal azimuth position of nest entrance;  $\phi_l$ , retinal azimuth position of the landmark. The vertical lines in the upper part of B indicate moments during the flight when the wasp views the landmark with the frontal retina.

Fig. 2. Aspects of flight control during the learning flights of *Cerceris rybyensis*. (A) The average angular velocity of wasps plotted against their distance from the nest entrance during 22 learning flights. Squares show mean turning velocities ( $\dot{\theta}$ ) and triangles show mean arc velocities ( $\beta$ ) together with their standard deviation. Angular velocities were determined from 400 ms running averages and sorted into 5 cm distance bins. Data from six wasps. (B) Average turning velocity  $\dot{\theta}_W$  is plotted against the average drum velocity  $\dot{\theta}_D$  during learning flights of wasps inside a rotating striped drum. Each data point represents the slope of a regression line fitted to the cumulative orientation of wasps for each arc segment separately. Data from three wasps. (C) Ground velocity  $V$  of one wasp over her horizontal distance  $D$  from the nest entrance during four flights. Means and standard deviation for 2.5 cm distance bins. (D) Frequency histogram of retinal azimuth position  $\phi_n$  of the nest entrance during eight learning flights of two wasps. (E) Height  $H$  above ground over horizontal distance  $D$  from the nest. Means and standard deviation for 1 cm distance bins. Data from four flights of one wasp. (F) Frequency histogram of retinal position of the nest entrance relative to the horizon  $\phi_{el}$ . Data from four flights of one wasp (see also Zeil, 1993a). In the insets, an asterisk marks the nest entrance.



different bearings on both sides of the goal (see arrowheads in Fig. 1A). If the insects were to face the goal during their pivoting flight, the same views would occur at the same bearings. Third, lateral fixation means that the home vector points in only two directions throughout the learning flight: approximately  $45^\circ$  to the right or to the left of the insect's longitudinal body axis. This last aspect may be important if the insect records images or 'snapshots' of the panorama and the local scene during its learning flights together with the home vector (see Cartwright and Collett, 1983, 1987; Krakauer, 1995). The implication of this vector pointing to the side is that returning insects, provided that they are guided by an image-matching process, would be prevented from overshooting the goal by passing it at the side. A constant retinotopic orientation of the home vector may also facilitate the linking of multiple snapshots.

The dynamic constancy of learning flights, specifically the distance-independent matching between the rate of turning and the arc velocity, generates a pivoting parallax field that is centred on the goal (Zeil, 1993a). The pivoting centre lies in an area of minimal image motion that is surrounded by a vortex of motion vectors. Viewed across the pivoting centre, motion vectors are horizontally aligned in the visual field and increase in size with the distance of contours. The apparent speed of distant contours is equal and opposite to the insect's rate of turning. Pivoting parallax could provide learning insects with information on the proximity of contours to the goal. At the same time, pivoting might be a way of continuously scanning for magnetic, panoramic or celestial compass cues and also brings the insect from one position in space to another in a regular and reproducible manner. In the

remaining paragraphs, we summarize the currently still somewhat patchy observations and experimental results that throw some light on the significance of these invariant features of learning flights.

### The control of flight behaviour

It would obviously help us in our attempt to understand the spatial pattern of learning flights if it were in any way influenced by local scene or compass cues. If such an influence could be found, it would suggest a reference frame for landmark memories and might allow us to identify the moments of acquisition during learning flights (Collett and Baron, 1994). The picture is somewhat confusing at present. Honeybees departing from a recently discovered feeder tend to face south during learning and during their search for the goal. In an initial phase, this preferred orientation can be influenced by magnets (Collett and Baron, 1994). Later on, bees prefer to use the panorama as a directional cue. A recent study of the learning flights of social wasps at a feeder reveals that these insects tend to adopt consistent compass directions whenever they view the goal in their frontal visual field at the ends of arcs (Collett, 1995, and personal communication). The ends of arcs are thus aligned along lines radiating from the feeder (Collett and Lehrer, 1993). Aligned inspections, however, are not a universal feature of learning flights. The flights that ground-nesting bees and wasps perform when leaving their nest do not show this clear pattern. Mean viewing directions during learning are, however, influenced either by panorama cues, as in *Dasyglossa* and *Lasioglossum* bees (A. Kelber, unpublished observations), or, in some cases, as in *Cerceris* wasps, by the goal-landmark bearing (Fig. 1; see also Zeil and Kelber, 1991; Zeil, 1993a). The end points of the arcs in *Cerceris* wasps often seem to be contour-triggered: they tend to occur after the passage of a close landmark through the frontal visual field (Fig. 1A,B).

It is not clear at present to what extent there are species differences in the way in which learning flight paths are influenced by the direction of the magnetic field or the panorama (Collett and Baron, 1994), by celestial compass cues (Vollbehr, 1975) or by directional cues derived from the layout of local landmarks (Zeil, 1993a,b). Different questions have been asked in different species and visual environments, and the context in which learning flights were observed and analysed was not the same. Social wasps and bees, for instance, were studied at feeders that were new to them and the location of which they had to learn for the first time. We, in turn, have worked with ground-nesting bees and wasps at their home. These insects operate from the same location for weeks at a time and, experienced as they are, they may indeed be influenced more by local scene or panorama cues than are bees and wasps at a novel feeder. Nearby landmarks are preferentially used by returning insects to locate their goal, as we will see later. If, as has been suggested, the carefully timed behaviour during learning flights does have a function in scanning the scene for appropriate landmarks, then the

outcome of this scanning process would be expected to have some influence on the flight behaviour during learning.

The control problems during pivoting flight are not trivial. The insects manage to fixate an often inconspicuous goal, circle around it at a surprisingly constant rate and do this independently of their distance from the pivoting centre. When the insects fly along an arc, they do not turn smoothly but in a series of body saccades (Zeil, 1993a). In *Cerceris* wasps, the variations in angular speed during these saccadic turns are correlated with changes in the retinal position of the nest entrance with a delay of 40 ms. Retinal position, in turn, depends on variations in the wasp's arc velocity 80 ms previously. The control system thus appears to function as follows: the wasp generates thrust in a direction perpendicular to the line of sight to the nest, an action that leads to an accumulating position error of the nest image in the lateral visual field, which is subsequently corrected by a turn in the appropriate direction (J. Zeil, in preparation). Generally, however, the insects move through equal angles in equal time along their arcs, irrespective of their distance to the goal. They could achieve this constancy by increasing sideways thrust as they gain distance, always producing a given retinal position error, before correcting it by counter-turning. However, both turning rate and arc velocity (which is a consequence of sideways thrust) are also influenced by panoramic image motion, and it is an open question how the insects can control both the retinal position of the nest entrance and the background image speed. Wasps that perform their learning flights inside rotating striped drums turn and fly faster than the drum when they fly an arc into the direction of drum rotation. When they move in the opposite direction, their turning rate and arc velocity are low (see Fig. 2B for turning rate). They adjust their slip speed to approximate the image speed that they would normally experience when performing their learning flight with an unobstructed view of the panorama (J. Zeil, in preparation). It is possible that monitoring the speed of background image motion helps the insects to scale the pivoting parallax field which could then provide them with cues to the distance of contours (Zeil 1993a,b).

### The relationship between learning flights and landmark guidance

In the previous sections, we have attempted to understand the functional significance of learning flights by studying their geometry, dynamics and control. We turn now to the question of what information insects use during homing and how the structure of learning flights may help them to acquire the cues that will guide them back to the goal.

The design of learning flights suggests that they serve to record the scene around the goal from defined vantage points and to acquire distance information through motion parallax. A number of recent experiments have focused on this last aspect and were designed to determine whether insects do make use of absolute distance information during homing. Insects pinpoint the goal with the aid of local landmarks

(reviewed by Collett, 1992) and, if they are trained to find the goal at a certain distance from a single landmark, they have two ways of knowing where the goal is. They could simply record the apparent size of the landmark as seen from the goal and, on returning, move to a position where the actual size corresponds to the memorized one. Alternatively, they could obtain a size-independent measure of the absolute distance of a landmark from the goal. The experimental design that allows one to distinguish whether insects during their learning flights acquire one or the other cue to distance involves presenting them with a single landmark at a certain distance from the goal during departure on their learning flight and then testing them when they return to the goal area with landmarks of different size. If the insects' search for the hidden or removed goal was driven by cues informing them about the absolute distance of the landmark, their search distance should be independent of the real size of the test landmark: they should search for the goal at the learnt distance regardless of whether an object is larger or smaller than the training landmark. These kind of tests produce quite clear results: bees and wasps do acquire absolute distance information (Fig. 3; Zeil, 1993b; Brännert *et al.* 1994; Lehrer and Collett, 1994; see also Cartwright and Collett, 1979; Cheng *et al.* 1987). Learning flights play a crucial role in this acquisition. By carefully monitoring what approaching and departing honeybees see, Lehrer and Collett (1994) demonstrated that true distance information is acquired specifically during learning flights. Honeybees only perform these flights during their first few departures from a novel feeding place, and it is only in this initial phase that their search for the goal is driven by the true distance of a landmark.

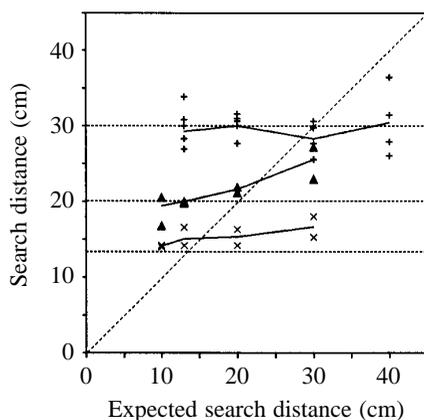


Fig. 3. The use of absolute distance cues by homing bees. Ground-nesting bees *LasioGLOSSUM malachurum* (Hymenoptera: Halictidae) were tested with landmarks of widely differing sizes compared with the one they had seen close to the nest on departure. The graph compares the distance at which they should have landed at a row of dummy nest entrances (x-axis) if their search had been driven by the apparent size of the landmark with their actual choice distance (y-axis). Training distances are marked by horizontal lines and training landmark heights were 6.7 cm (crosses), 10 cm (triangles) and 15 cm (plus signs). If the bees' search were driven by the apparent size of the test landmarks, data points would lie on the line of equality (diagonal dashed line). Modified from Brännert *et al.* (1994).

Learning flights thus help insects to identify suitable nearby landmarks which, at a later stage, can be memorized by their apparent size. While *Cerceris* wasps and honeybees use absolute distance information only transiently, ground-nesting bees seem to make long-term use of absolute depth cues (Brännert *et al.* 1994).

Small as they are, bees and wasps cannot use binocular stereopsis in a range that is useful in landmark guidance, and their fixed-focus compound eyes also exclude accommodation as a means of distance measurement (e.g. Srinivasan, 1993; Wehner, 1994). The most likely way in which the insects learn about the distances of landmarks therefore seems to be by exploiting cues derived from image motion (see Brännert *et al.* 1994). As we have seen, they do produce appropriate image motion during learning flights. Evidence that the insects in fact exploit the image motion field they experience during these flights is, however, still indirect. One hint comes from a comparison of learning and return flight paths. Since the insects use the memorized distance information upon returning to the goal, we must assume that they repeat some of the flight manoeuvres that they performed during their learning flights. When *Cerceris* wasps search for their hidden nest, they indeed fly through arc segments similar to those of their learning flights and at a similar speed (Zeil, 1993b). To demonstrate the use of image motion directly, we would ideally need either to eliminate all other possible cues to depth or to manipulate the image motion that insects experience during their learning flights. Neither experimental condition is easy to realize.

So far, we have argued that the insects could learn about the distances of landmarks by exploiting cues derived from image motion. The geometry of learning flights, however, suggests another possible strategy for acquiring depth information. Lateral fixation of the goal during learning flights has the specific consequence that, during the second part of each arc, the insects take up viewing directions that are similar to the views of the scene that they had during the last section of the previous arc. Each view is thus encountered twice at different positions in space during each zigzag but at similar distances from the goal. Recording paired and aligned snapshots at these positions and comparing them could yield depth information, since objects close to the nest would show large disparities in the two images. In practice, there is no obvious test to distinguish the motion parallax and the successive stereopsis procedure. All we can say at present is that the latter would explain lateral fixation and the former the dynamic constancy of learning flights. Both are part of the 'information content' of learning flights.

The use of absolute distance information by bees and wasps implies that acquisition requires either integration of image motion over some time and path length or that snapshots are recorded at different positions in space. We would expect, in any case, that there should be a correlation between the learning flight paths and those flown by the insects on their return to the goal area. At present, there are only a few studies that have attempted to find this correlation.

*Cerceris* wasps, when searching for their hidden nest in the ground, adopt viewing directions that closely match those during their learning flights. As a consequence, they view landmarks near the nest at similar retinal positions (Zeil, 1993b). While the preferred directions in which ground-nesting wasps view the local scene around the goal are influenced by the bearings of nearby landmarks during learning and return flights, honeybees and social wasps align themselves with consistent compass directions (Collett and Baron, 1994; Collett, 1995).

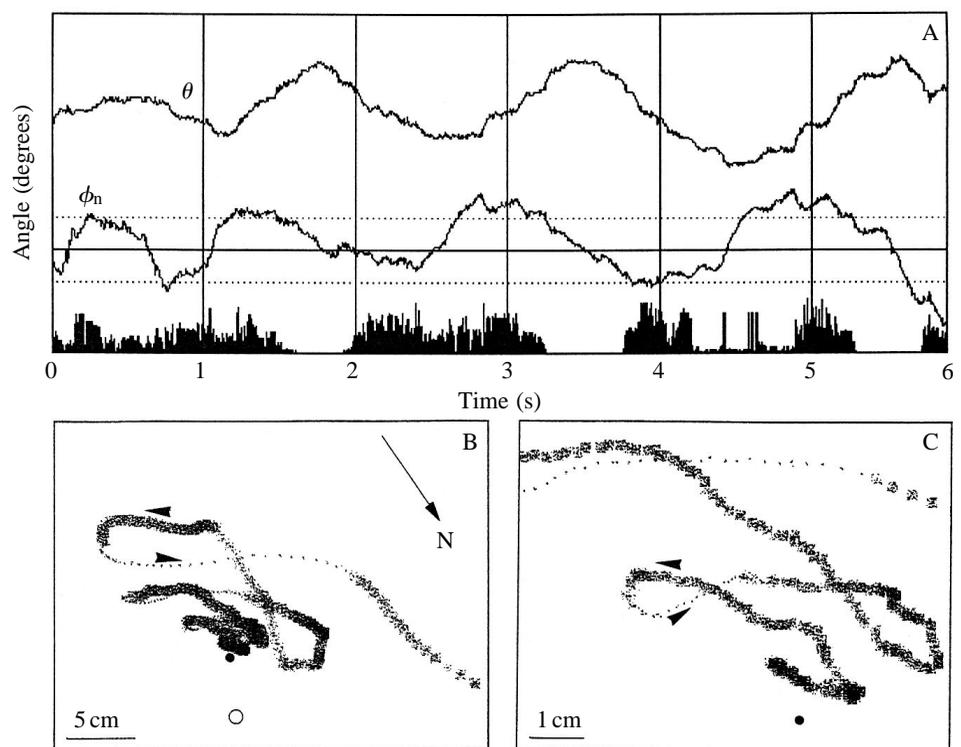
These global similarities between the flight behaviour of learning and homing insects do not tell us during which part of their learning flights the insects learn. The situation is complicated by the fact that the flight paths of returning insects can be rather straightforward and often bear little obvious resemblance to the preceding learning flights (e.g. Zeil, 1993b; Collett and Lehrer, 1993). We have recently started to compare learning and homing flights in a detailed similarity analysis. By asking at which positions in space flight parameters and viewpoints during learning and return flights show maximal correlations, we hope to determine during which segments of their learning flights the insects acquire information on the goal location. Each position and orientation of an insect during its learning flight is compared with all the positions and the orientations it maintains during its return to the goal area. As a crude measure of similarity ( $M$ ), we calculate the sum of squares of the differences in position ( $dx$ ,  $dy$ ,  $dz$ ), multiply them by the angular deviation

( $d\theta$ ) and scale the resulting factor with the distance from the goal during the learning flight ( $d_{nest}$ ):

$$M = [(dx^2 + dy^2 + dz^2) \times d\theta^2 / d_{nest}]^{1/2}.$$

For each recorded instance throughout a learning flight, the value of  $M$ , averaged over all return flight positions, indicates how closely the flight path and the viewing directions of the returning and searching wasp correspond to that particular position and orientation during learning.  $M$  will be small if the correspondence is high. Our first results show that correspondence is maximal during those sections of learning flights where the insects turn and view the goal with the lateral retina (Fig. 4A). The similarity analysis does not identify distinct positions, such as the end points of arcs or the instances where the goal appears in the frontal visual field during learning. Instead, it clearly divides each arc into a significant and a non-significant section: correspondence tends to be low during the first part and high during the second part of arcs (Fig. 4B,C). The insects thus learn on the move and seemingly record the scene while viewing the goal with the lateral retina. This last observation may force us to reconsider the role of visual memory in landmark guidance. For the sake of argument, let us assume that the insects record snapshots during the second part of arcs while viewing the goal with the lateral retina. Let us further assume that homing insects are guided by an image-matching procedure. The catchment areas of these snapshots would then line the edges of the flight corridor. Whenever a returning insect finds a good match

Fig. 4. The relationship between learning flights and homing. (A) The time course of body axis orientation ( $\theta$ ) and retinal azimuth position of the nest entrance ( $\phi_n$ ) during the learning flight of a *Cerceris rybyensis* wasp. Dotted lines correspond to viewing directions  $45^\circ$  on either side of the wasp's midline (continuous horizontal line). The same scale applies to the  $\theta$  trace. The histogram at the bottom of the graph indicates which sections of the learning flight correspond most closely to the positions and orientations of the wasp during her subsequent return to the goal area. The histogram shows  $\sum(3-M)$  for all values of  $M$  less than 3 (see text for further details of the similarity analysis). (B) The flight path of the same learning flight. The density of the cloud of dots around each position indicates how well the orientation and the position of the wasp correspond to all her orientations and positions during her subsequent return to the goal area. A large number of dots indicates high correspondence. The flight path was recorded and reconstructed at  $200 \text{ frames s}^{-1}$ ; the open circle marks the position of a small cylindrical landmark; the location of the nest entrance is indicated by a small black circle; arrowheads point in the flight direction. (C) The early part of the same learning flight at greater magnification.



between a stored snapshot and the current scene, it would be informed that it is off course and consequently needs to move away from the catchment area into the direction of the home vector. Homing insects may not ride down a guiding beam towards the goal, but rather bounce off the sides of a tapering flight corridor.

### Outlook

Our present state of knowledge suggests that learning flights serve at least two specific purposes. First, they allow insects to inspect and to record the local scene around a goal from distinct positions and along directions that are determined by celestial or earth-based compass cues or by the bearing of close landmarks relative to the goal. Second, they allow insects to acquire information about the true distance of nearby landmarks.

However, we are unlikely to have fathomed the full significance of learning flights. Although learning flights must have been shaped by them, we know little about the ecological and neural constraints of acquiring, storing and using a visual representation in home navigation. Natural scenes, for instance, contain strong shadows that change unpredictably during the insect's absence, irregular objects that are hard to identify from different viewpoints and vegetation that offers an equal share of gaps and contours. Since close landmarks are essential to pinpoint the goal accurately (see Cartwright and Collett, 1983, 1987; Cheng *et al.* 1987; Zeil, 1993a,b; Krakauer, 1995), they must be identified and tagged in a representation that probably also contains the distant panorama (van Iersel, 1975; Collett and Baron, 1994). Identification and foreground-background segregation of contours may well be the real problem for insects acquiring and using a visual representation under natural operating conditions. For a realistic assessment, however, we do not know enough about the limits of accuracy of distance filtering with biological motion detectors, about the problems of noise for image matching in natural scenes or about the storage capacity of insect brains. These constraints are rarely addressed in models of landmark guidance. Krakauer (1995), for instance, who studied neural network models of landmark guidance, left some possibly crucial questions open: how do insects identify landmarks during acquisition and how do they gain information on their distance from the goal?

To gain insight into what is difficult and what is easy in landmark-guided homing, we have started to reconstruct what wasps see during their learning flights by recording their orientation and their flight paths in three dimensions. We then film the natural panorama with a video camera and synthesize the movements and transformations that the natural scene undergoes in the visual field of freely flying insects. These simulations are realistic in the sense that they are based on the natural intensity distribution, the reconstructed orientations and the three-dimensional flight paths of the insects (Voss and Zeil, 1995). In combination with modelling visual spatial memory (e.g. Krakauer, 1995), reconstruction of the visual

world will allow us to explore the constraints of visually guided homing under natural conditions.

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