Chapter 7

Visual Homing in Insects and Robots

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Abstract Insects use memorised visual representations to find their way back to places of interest, like food sources and nests. They acquire these visual memories during systematic learning flights or walks on their first departure and update them whenever approaches to the goal have been difficult. The fact that small insects are so good at localisation tasks with apparent ease has attracted the attention of engineers interested in developing and testing methods for visual navigation on mobile robots. We briefly review here (1) homing in insects; (2) what is known about the content of insect visual memories; (3) recent robotics advances in view-based homing; (4) conditions for view-based homing in natural environments and (5) issues concerning the acquisition of visual representations for homing.

7.1 Homing in Insects

The ability of animals to recognise places of significance and to revisit them is fundamental to life on Earth. Without this navigational skill, for instance, many flowering plants would not be pollinated by insects and animals, in general, would be unable to provide for their offspring. There is ample evidence showing that animals including insects use memorised visual representations to pinpoint a goal location. The goal can be the nest location as in bees, wasps and ants (e.g. [2, 63, 68, 72], reviewed in [15]), the location of food as in bees (e.g. [9]) or hovering stations in flies and bees [16, 38, 39]. Visual spatial memories are crucial for local navigation but can also guide the animal during long-range navigation: routes can be formed from sequences of multiple stored views [14, 36]. Moving between these views, insects make use of compass and odometric information (see Chaps. 2 and 9). We will, in the following, focus on local homing methods that allow animals and robots to pinpoint a goal.

It is clear since Tinbergen's seminal experiments [63] that distinct objects in the vicinity of a goal location can act as landmarks and guide an insect's return path. What constitutes a landmark under natural conditions, however, is still an open question. From a functional point of view, the following properties of objects are likely to make them useful as landmarks (see, e.g. [18, 26]): *salience* – landmarks should be unique and easy to distinguish from other parts in the scene; *permanence or reliability* – landmarks and their position should be constant over time; *relevance* – a landmark should help to recognise important places or decision points.

However, when a homing agent has to acquire a visual representation of a place it wishes to return to it has – with the exception of salience – no obvious access to all these crucial, task-related properties of objects in the environment. How, for instance, is an insect or a robot to decide whether a particularly salient object it sees is permanent, reliable and relevant enough for the subsequent task of pinpointing that particular location? For the purpose of this chapter, we thus identify a number of open questions that should

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be of interest to both biologists and robotics engineers: What are the contents of the visual memories used by homing insects? What are the conditions for homing under natural conditions? What are the rules for acquiring visual representations for homing? And how can a homing agent acquire information on the salience, the permanence, the reliability and the relevance of visual features that identify a goal location?

7.2 Probing the Content of Insect Location Memories

The basic design of homing experiments is to allow insects to become accustomed to see distinct objects close to a place of interest, be it a nest or a feeding site, and then displacing or modifying these objects with the aim of observing where the insect would search for the goal. This kind of approach allows the experimenter to identify the visual cues that are relevant for homing. One such example is the experiment on a homing wasp shown in Fig. 7.1 The wasp had been accustomed to find its nest hole in the ground a few centimetres east of a small cylindrical landmark. It had performed learning and updating flights on several departures from the nest throughout the day (Fig. 7.1, top left panel). The search distributions in Fig. 7.1 show where the returning wasp searched for her hidden nest entrance relative to the landmark that was displaced in different directions and at one period was even removed (centre panel). This experiment clearly indicates that the goal is predominantly defined by an object that acts as a landmark, not by olfactory or other geocentric cues: the returning wasp searches in the right distance and direction from the landmark where the goal would be found, had the landmark not been displaced. Similar results have been found in experiments with bees and ants (reviewed in [18]). Interestingly, when the landmark is removed, the insect still searches in the general area, indicating that more than just the individual landmark is being remembered (Fig. 7.1, search distribution at the centre of the graph).

When the size of a familiar landmark is changed during a test, some insects search for the goal further away from a larger and closer to a smaller landmark (see Fig. 7.2 and [68, 8]). The insects thus appear to judge how far away the goal is from a landmark by the landmark's memorised apparent size. Honeybees, ground-nesting bees and wasps are also able to acquire information on the *absolute* distance to landmarks, independent of their apparent size (see Fig. 7.3

Fig. 7.1 Landmark orientation in ground-nesting wasps (*Cerceris*; see *bottom centre photograph*). A wasp has learnt to associate her nest location (at the intersection of *white lines*) with a 5 cm diameter cylindrical landmark (*white circle*) during learning flights on departure (*top left panel*). On her return, the nest was hidden and the landmark was displaced in different directions away from the nest. The diagrams show 30 s search density distributions of the wasp for different landmark displacements. Photograph shows a wasp carrying prey to her nest (courtesy of Waltraud Pix)
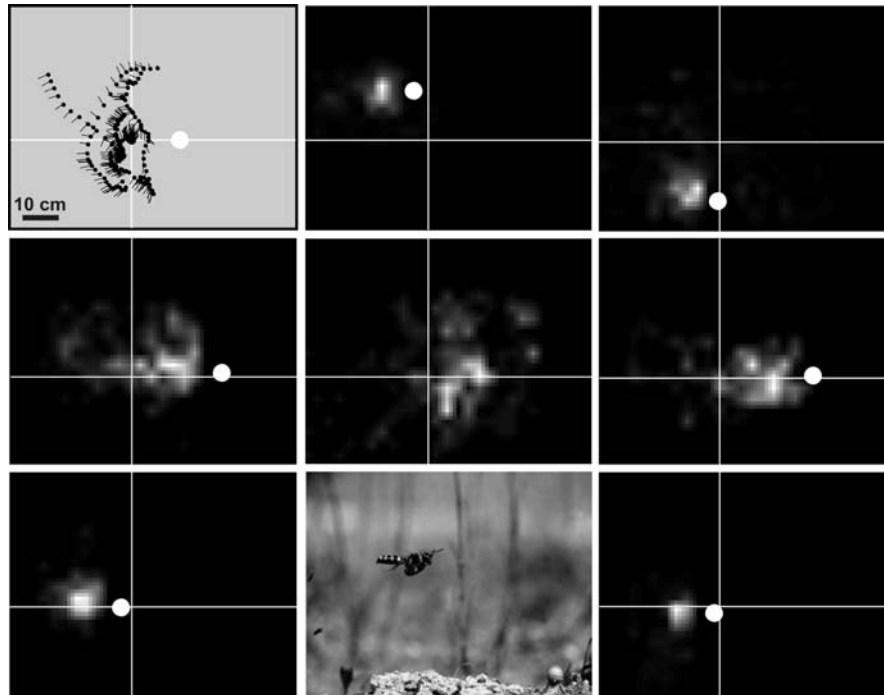
Fig. 7.2 Ants remember the apparent size of landmarks. Desert ants searching for their nest halfway between two cylindrical landmarks. Search paths on the *left*, search density histograms on the *right* (from [48]; data replotted from [68]). *Top row*: original landmarks at training distance from the nest. *Middle row*: original landmarks placed at double the original distance apart. *Bottom row*: landmarks of double the original size placed at double the original distance apart. Modified after [48]
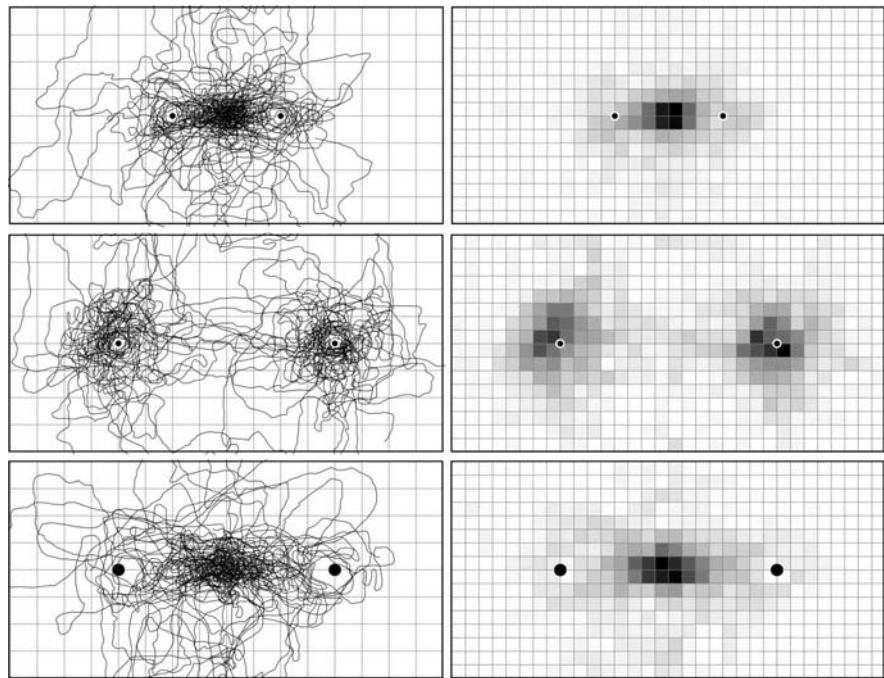
and [73, 45, 4]). This suggests that these insects are guided by motion parallax as a cue to distance [67, 57] (see also Chap. 4). The selection of cues appears to depend on learning history: after their first learning flights in the morning, the search of ground-nesting wasps is predominantly driven by distance rather than angular size cues [73]. Lehrer and Collett [45], who analysed the development of search and return flights over time in honeybees, found that absolute distance dominated the bees' behaviour in the initial phase of learning while apparent size did so later on.

Homing insects thus memorise both pictorial, purely image-based information about the goal environment and derived aspects, like image motion cues that provide information on the distance of landmarks. Honeybees at least have been shown to remember several visual attributes of a scene for identifying targets: they can detect food sources that are identified visually by contour orientation (e.g. [30]), by colour (e.g. [37]), by shape (e.g. [33]), by complex image properties (e.g. [22]) and by relative image motion (e.g. [58]).

How does insect visual pattern memory relate to their ability to pinpoint a goal location, which itself may be very inconspicuous? We will return to the

question what identifies a location in the natural world later, but would like to make the point here that for homing insects the salience, reliability and the relevance of landmarks is determined by the patterns of visual stimulation they experience both during learning and during their return to the goal, and by the efficiency with which they can relocate the goal. For instance, in some situations, given the choice between flat patterns on the ground and three-dimensional objects, insects appear to pay less attention to flat patterns on the ground [64]. However, when these patterns are large (*salient*), compared to the apparent size of a three-dimensional object, they can dominate search (see Fig. 7.4). Equally, many experiments have shown that homing insects pay particular attention to landmarks that are close to the goal (e.g. [11, 73]) and that are therefore particularly *relevant* for the purpose of pinpointing its location. And finally, the *reliability* of visual features associated with the task of locating a goal will both depend on their *salience* (e.g. size, contrast, colour) – which may change depending on the direction of illumination, and the intensity and the spectral composition of both illumination and background – and their constancy in location, in their reflectance properties and their shape. Honeybees, for instance, learn the colour of landmarks [12], a property
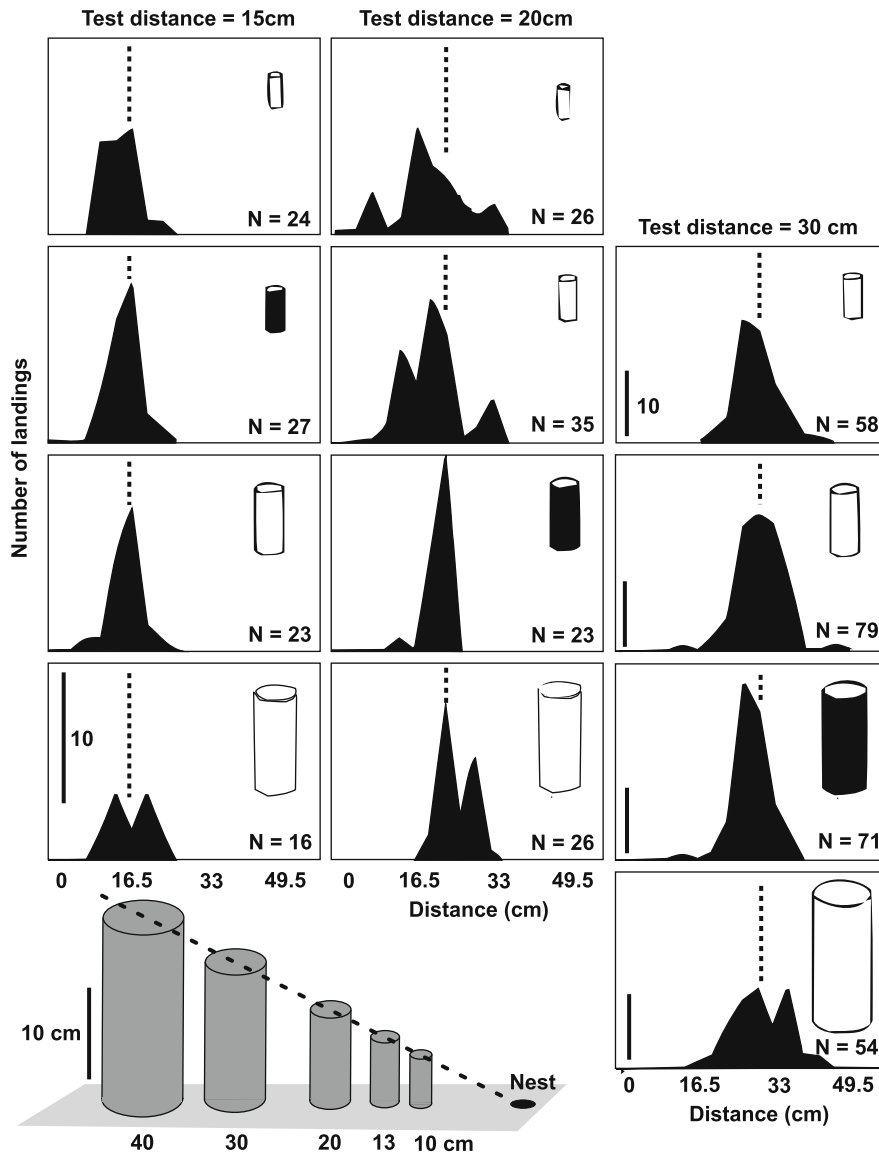
Fig. 7.3 Ground-nesting bees search for their nest at the absolute distance from a landmark, independent of the landmark's apparent size. Bees learnt to see one of a number of differently sized cylindrical landmarks placed in such a way that they all had the same angular size as seen from the nest entrance (*bottom left*) and were tested with landmarks of different sizes on their return to the nest. The three columns show search histograms of bees searching for their nest entrance in the presence of differently sized landmarks. Training landmark size is shown in *black* and training distance is marked by a *dotted line*. Modified after [4]

that allows them to remain recognisable even under changing light conditions, because bees possess colour constancy [70]. Homing insects also monitor the reliability of what they have learnt: depending on the level of difficulty they have in relocating a goal, they update their visual representation by repeating their learning flights (e.g. [35, 72, 69]). Even while performing their learning flights, which we will discuss in detail later,

the insects have the opportunity to test the reliability of their visual representation [76, 74].

In many homing experiments, insects have been shown to associate individual landmark objects with the goal and their return paths or search paths are clearly determined by the location of such individual landmarks. The fact that homing insects search for the goal not only in the right distance from a landmark
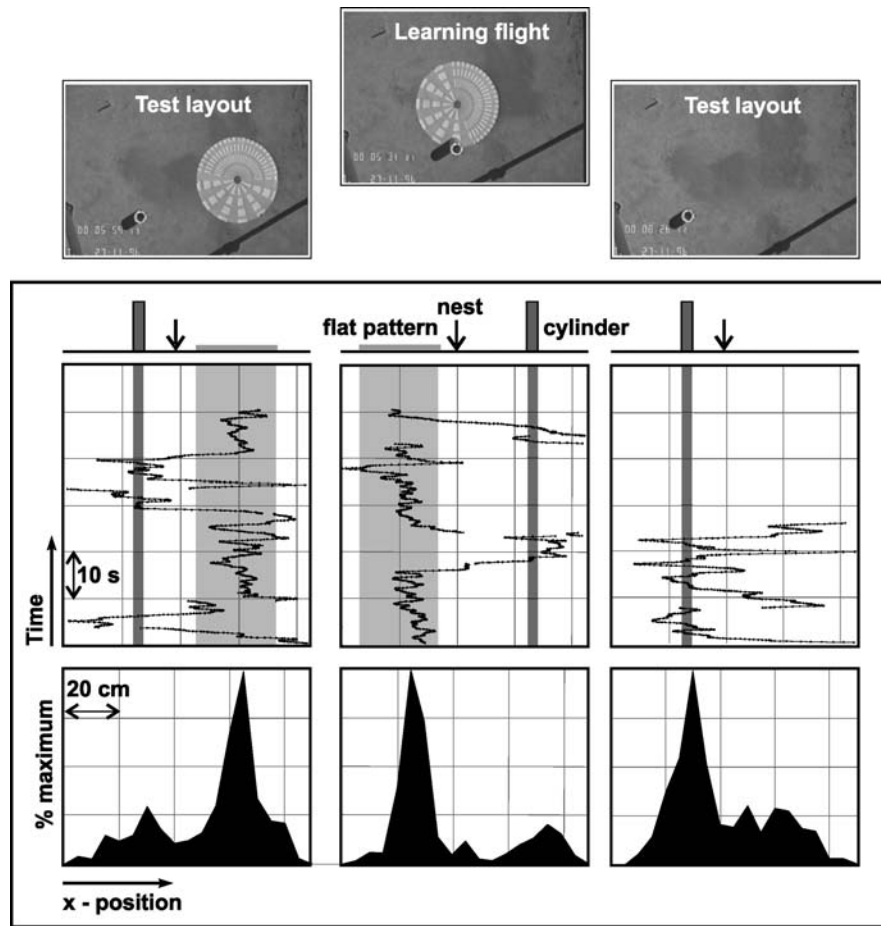
Fig. 7.4 How ground-nesting wasps (*Cerceris*) search for their nest entrance in the presence of dissociated visual features. On departure, the wasp was used to see a large flat pattern around her nest entrance and a cylindrical landmark to the south of the nest entrance (image on *top centre*). The returning wasp was confronted with the pattern and the landmark displaced to the east and to the west of the hidden nest entrance (e.g. *top left* image), or with the displaced landmark on its own (image on *top right*). Diagrams: *Left column*: Search distributions of the wasp with landmark east of the nest and pattern west of the nest. *Middle column*: pattern east of the nest and landmark west of the nest. *Right column*: Landmark east of the nest and pattern removed

but also in the right compass bearing, however, indicates that they remember more than just the appearance of that object: visual representations contain, or are associated with, compass information. Honeybees, for instance, become unable to locate a goal when the landmark constellation that helps them identifying the goal is rotated by more than 30° [9]. There are many compass cues that may be involved, including celestial cues (e.g. [31]), magnetic cues (e.g. [25]) and the full visual panorama (e.g. [75, 62]).

Evidence that landmarks are being remembered in the wider visual context comes from experiments in which goal- or route-defining landmarks were removed during a test phase. Ground-nesting wasps then continue to search in the general area for their nest (see Fig. 7.1) and ants that used to walk on a curved path past a landmark towards a feeder in a room continue to walk along the original curved path that had led them past the landmark in its original location when the landmark is removed or displaced (see Fig. 7.5 and [28]). In their natural habitat, the wasps thus had information on the nest location, independent of the dominant landmark, and the ants must have remembered the view transformations along their usual path and were now guided by landmark-independent cues in the room.
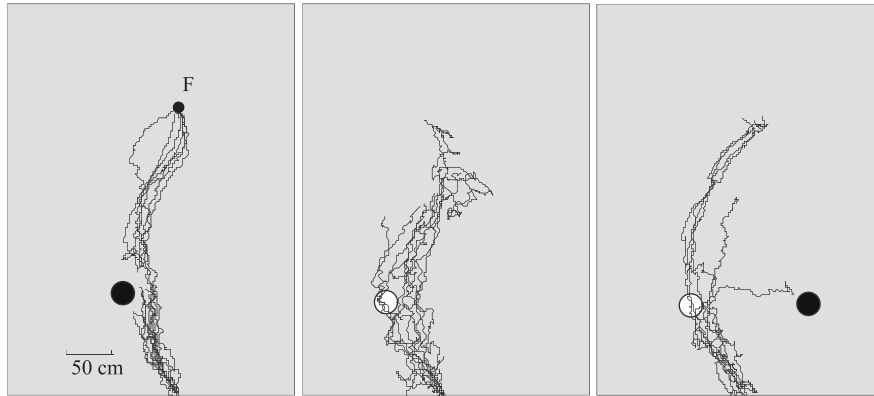
Fig. 7.5 Landmark guidance and visual context. Graham et al. [28] trained ants to a feeder (F) past a landmark (*black circle*) in an indoor arena. The ants tended to walk first towards that landmark and then towards the feeder. When the landmark is removed (*open circle in centre panel*) or displaced (panel on *right*), the ants still walk along the original curved path that had led them past the landmark in its original location. This indicates that the ants had learned the view transformations along the path with the aid of distant cues in the room. Modified after [28]

7.3 Modelling Homing: Computer Simulations and Robotics Experiments

Computer simulations and in particular mobile robots that can move in real environments allow testing models of animal navigation strategies in closed loop. Interestingly, most visual homing algorithms implemented on mobile robots make use of a panoramic imaging system mimicking the large field of view of insect eyes.

Homing algorithms can be classified into methods that establish correspondences between image features and global methods that use the similarity between images. Correspondence-based algorithms extract features from the raw images and compute motion commands directly from paired features.[1] They differ in the type and number of features extracted from the images, in the way in which correspondences between features are established (e.g. nearest neighbour or feature similarity measures) and whether both translations and rotations are determined. Examples of correspondence-based algorithms are the "snapshot model" (see Fig. 7.6 and [9]) and the optical flow-based homing methods by Vardy and Möller [65]. Goedeme et al. [27] use a feature-based visual homing algorithm for topological navigation.

The average landmark vector (ALV) model [42, 47] uses a very parsimonious spatial representation, a single vector computed from viewing directions to surrounding landmarks. It is different and special insofar as it extracts features (vertical edges) from the visual input without establishing correspondences between features. These features belong to all landmarks that identify the goal. Each step on the way home is calculated from the difference of two ALVs: the ALV at the current and the ALV at the goal position. The ALV algorithm, however, is extremely sensitive to slight differences in orientation, because the reference frames of both ALVs have to have the same orientation.

The second class of algorithms does not solve the correspondence problem explicitly. These approaches usually estimate the movement parameters by minimising the difference between (possibly processed) images,[2]

$$d(P[\mathrm{I}^{\mathrm{h}}], P[\mathrm{I}^{t}]),$$

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[1] If the coordinates of at least three corresponding features in two images are known, the rotation and direction of translation between the two camera positions can be estimated (see [29, 32]). Without knowing the distance to or between features, only the direction of translation and not its absolute size can be determined [5].

[2] We avoid the term "image distance" because it can be easily confused with metric three-dimensional distance, and use "image difference" instead.
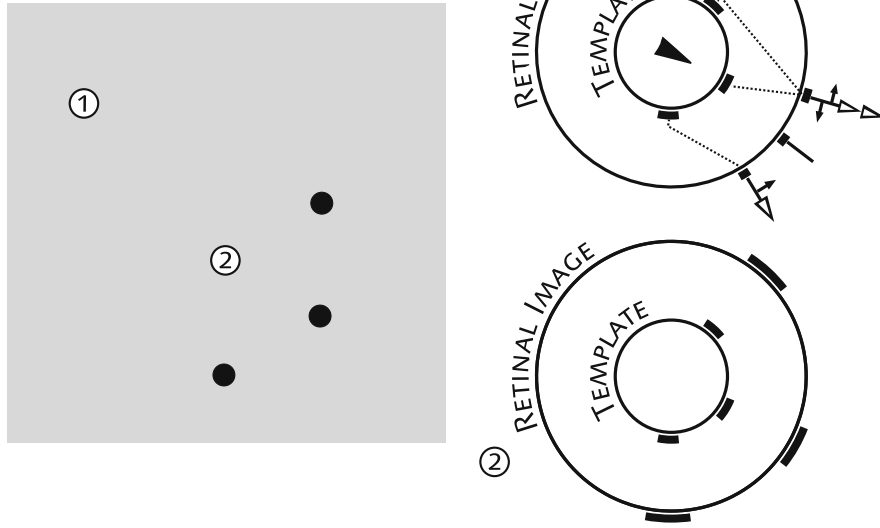
Fig. 7.6 The snapshot model of homing [9]. At the goal location (2) a snapshot template is recorded. The mismatch between remembered snapshot and the current retinal image at a location some distance away from the goal (1) can be used to generate goal-seeking movement instructions by finding the closest matching contours and generating for each a rotation that would align them. Averaging over the rotations needed to align contours and over the translation needed to minimise the mismatch in apparent size of landmarks generates a command in which direction to move next. This procedure brings the agent back to the goal location. Modified after [10]

where $d(\,\cdot\,)$ is the metric (e.g. the sum of squared differences, SSD), $P[\,\cdot\,]$ the image processing operations (e.g. low-pass filtering, corner detection or Fourier transformation), I^h the memorised image at the goal position[3] and I^t the current image (at time t). The basic idea is that the physical distance to the goal is reduced by moving in the direction that increases the similarity of images. While Zeil et al. [75] use actual movements in space to estimate the gradient of image differences, Möller and Vardy [51] employ – similar to Labrosse [41] – matched filters derived from two translational optic flow fields to approximate the gradient,[4] thus avoiding the need for test steps. The image warping method of Franz et al. [24] computes image changes for several hypothetical translations and rotations based on assumptions on the distance distribution of objects in the scene in order to find the direction that reduces image differences. Although this approach uses only one-dimensional pixel arrays along the horizon, its homing performance is quite remarkable [65]. Stürzl and Mallot [61] describe a fast and memory-efficient implementation of this warping method by means of Fourier transformation of panoramic images. Recently, Möller [50] extended the warping algorithm to two-dimensional images, improving its homing performance further. All approaches based on image differences described so far operate on raw, on low-pass filtered images or on their Fourier-transformed equivalent. These homing methods are thus susceptible to changes in illumination which is of special significance in natural environments (see below and [60, 75, 62]). Image differences that develop due to changes in illumination can be minimised by lateral inhibition and local contrast normalisation [62]. One possibility to reduce the effect of changes in illumination may be to, in addition, use information on the depth structure of a scene that could be estimated by motion parallax or stereo computation. For correspondence-based approaches the use of features with high-illumination

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[3] Instead of the raw image I^h, the processed image $P[I^h]$ can be stored.

[4] Assuming equal distances to surrounding objects and movements that are small compared to object distances, the first-order approximations of pixel shifts can be estimated when moving in x or y direction.

tolerance may offer a solution to homing in time-varying scenes. Möller [49] suggested that a colour-opponent representation can make visual representations immune against changes in illumination, by emphasising the contrast between terrestrial objects and the sky. The problem here is that such a procedure is likely to emphasise large distant objects that do not allow precise localisation.

Some recent vision-based techniques aim at integrating local visual representations and homing methods into a large-scale navigation scheme. For instance, the purely vision-based scheme by Franz et al. [23] connects local visual representations (panoramic one-dimensional snapshots) in a graph model of the environment without metric information. The agent is able to move between locations at which individual snapshots were acquired (snapshot positions) by means of a local visual homing method. Similar vision-based topological maps are used in several robotics experiments and implementations (e.g. [27, 3]). Metric information about distances and angles between snapshot positions are obtained, for instance, by path integration and can easily be integrated in a graph-like representation (e.g. [34]). Davison et al. [20, 21] use an extended Kalman filter (EKF) for real-time estimation of camera position, orientation and velocity as well as three-dimensional positions of features in a Cartesian reference frame from the video stream of a single moving camera. Sparse vision-based three-dimensional maps of this type are now used in a number of robotics applications (e.g. [55, 56, 5]), but also as a new approach to understanding the "knowledge base" of homing insects. Recently, Baddeley and Philippides [1] applied the EKF approach to simulated learning flights of bees. They showed that learning flights (see below) actually improve the simulated agent's ability to localise itself with the help of a landmark.

7.4 Homing in Natural Environments

As we have seen, insects use salient objects during homing. In most cases in which this has been documented, landmarks were artificial, high-contrast objects. In the natural habitat of an insect, however, it is often not clear which objects in the environment should be selected as guideposts for homing. It is interesting

therefore to ask how well locations in the natural world are identified by the panoramic views taken from them, without segmenting the scene into distinct landmark objects. The question can be answered by analysing how the mean pixel difference between images develops with distance from a reference location. Surprisingly, the resulting "image difference functions" (IDF) are cusp shaped and smooth, without pronounced local minima [75, 62]. In outdoor scenes, panoramic snapshots thus have useful catchments for a homing agent sensitive to image differences. Once the edge of such a catchment is reached, simple gradient descent methods can be employed to reach the minimum in image differences that coincides with the location at which the reference image was taken (e.g. [75]). The range over which a given snapshot can be used, or, which is equivalent, the width of the IDF at any one location depends on the way in which objects are distributed in depth: in the presence of near-by objects, IDFs are narrow and steep, while in open habitats, they are wide and shallow. Importantly, since pure rotational IDFs are usually narrow and steep, they can be used to recover the orientation of the reference image, even without additional compass information [75]. This continues to be true at some distance from the reference location, where the minimum of the rotational IDF takes on the value of the translational IDF at that location [75]. The implication is that a homing agent should at any point along its return path minimise first the rotational IDF and then the translational IDF, as has been suggested by Cartwright and Collett [10].

As we have pointed out before, the visual appearance of natural scenes can be very dynamic. Over time, the image difference of a reference view at the same location (the temporal IDF) becomes slowly larger due to changes in the direction and the spectral composition of illumination as the Sun moves across the sky (Fig. 7.7, see also [75]). Superimposed on this slow increase of the temporal IDF are rapid deflections that are due to the movement of clouds, which change the intensity and the spectral composition of illumination. The variability in the presence and the location of shadow contours associated with these illumination changes in natural environments is likely to cause serious problems for view-based homing under real-life conditions. However, as discussed above, visual representations can be made quite robust against these changes in illumination, in the simplest way by pre-processing images (see [62]). A second
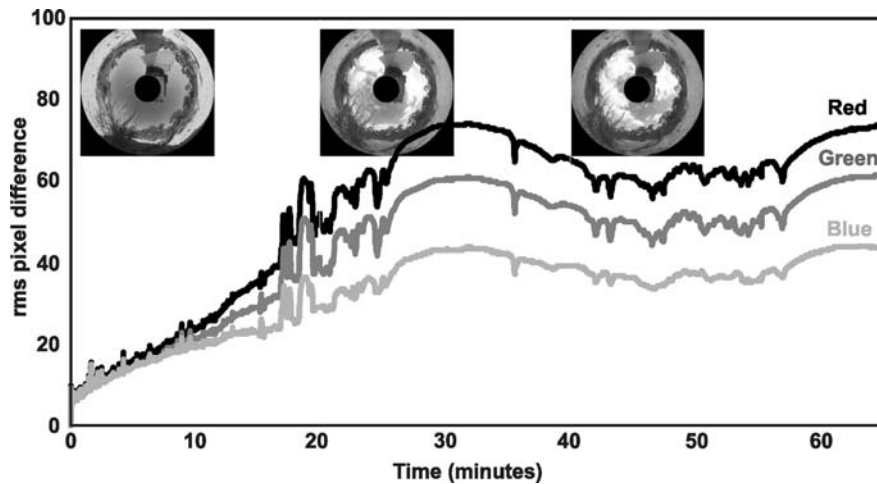
Fig. 7.7 Under natural conditions, the view of a scene changes due to the movement of the Sun and the movement of clouds. Panoramic images were recorded for 1 h close to the ground in a ground-nesting wasp colony by pointing a video camera down onto a reflective cone (see inset example pictures and [75] for details of recording technique). Root mean-squared pixel differences over the whole image were calculated every 10 s relative to a reference image at the beginning of the sequence for the red (*black line*), green (*dask grey line*) and blue channels (*light grey line*) separately for 65 min from 1200 to 1305 hours

source of noise in visual scene representations still awaits a detailed quantitative analysis in the context of homing: the effect of environmental motion – the wind-driven movements of plants – that changes the appearance of scenes on shorter timescales than those due to changes of illumination (e.g. [71, 54]).

Although the "information content of panoramic images" with respect to the homing task is now fairly well understood, both in natural and in experimental spaces (e.g. [59]), it is still unclear whether homing insects actually do memorise and make use of the full visual panorama. In Sect. 7.2 we provided two examples of experimental evidence that seem to indicate that the wider visual scene is being remembered by homing insects, but experiments specifically addressing this question are still lacking. Recent evidence at least demonstrates that insects are able to recognise and discriminate between visual patterns that resemble natural scenes in all spatial aspects, except the distribution of objects in depth [22]. It is also not clear at present to what extent homing insects are affected by limited storage and processing capacity for visual patterns. In the fruitfly *Drosophila*, at least two pattern properties, elevation and contour orientation, are stored in two distinct brain regions, when pattern memory is required [46]. However, we do not know whether such storage areas are modified both qualitatively and quantitatively in homing insects.

7.5 Acquisition and Use of Visual Representations

Few theoretical studies (e.g. [19, 1]) and robotics experiments (e.g. [44]) have considered systematic ways in which an agent could actively acquire and test robust visual representations of a goal environment. Yet many homing insects do appear to do exactly that: upon leaving a significant location (like a food source or a nest) for the first time, they move in highly stereotyped ways that have become to be called orientation or learning flights and walks ([35, 66, 43, 72, 73, 17, 45, 13, 52], reviewed in [76]). These learning routines are crucial for subsequent successful homing as every beekeeper knows. When bee hives are shifted, various precautions have to be taken to force experienced foragers to perform an orientation flight at the new site (e.g. [2, 7]), otherwise the bees would be lost or would return to the old hive location if the new location is within their familiar foraging range. Equally, ground-nesting wasps need to be allowed to perform a learning flight on departure in order to learn changes in their nest environment (e.g. [63]).

The behaviour of insects during these learning routines is surprisingly similar across different species: the insects turn to face the goal and then back away from it in ever-increasing arcs (Fig. 7.8, [72, 17, 45, 13],
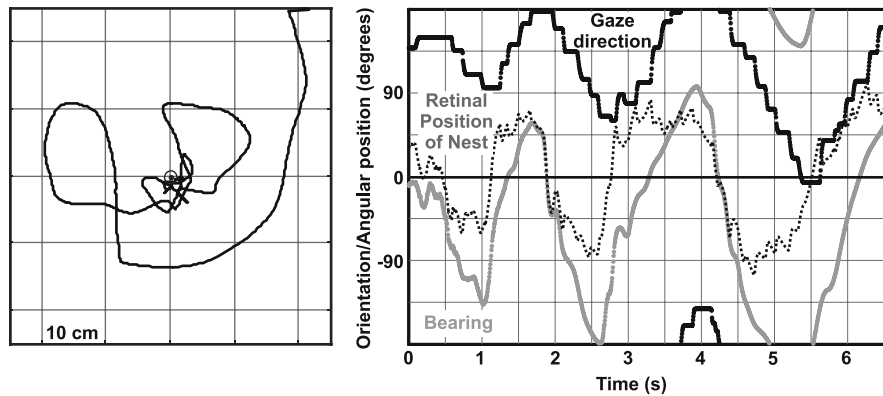
Fig. 7.8 The organisation of learning flights. *Left*: Learning flight path of a ground-nesting wasp (*Cerceris*) as seen from above. Nest entrance is marked by a *circle*. *Right*: Time course of gaze direction (*fat black*), retinal position of the nest entrance (*dotted*) and angular bearing relative to the nest entrance (*grey*) for the same flight. Data were recorded at 250 fps with a Redlake high-speed digital camera

reviewed in [76]). After this initial sequence, honeybees at least circle the area at some height and then fly off for an initial orientation flight, lasting a few minutes (e.g. [2, 6, 7]).

The fact that the insects fixate the goal visually can be used to show that they specifically acquire visual information on the location of the goal during these flights (see also [53]). In ground-nesting wasps, a high-contrast collar can be placed around the nest entrance with a hole in the centre through which the insects can emerge. Once a wasp has started to perform her learning flight, the collar can be carefully shifted some small distance to the side of the nest entrance, while the insect continues to fly along arcs centred on the collar. The search distributions of returning wasps that have been shifted to the left or to the right of the nest entrance during their learning flights are shifted accordingly with respect to the true nest location and surrounding landmarks (Fig. 7.9 and [72]).

The relationship between the organisation of learning flights and the control of flight when insects return to the goal is thus of great interest if we are to understand the type of visual representations and of algorithms insects employ during homing. The first point to note is that the insects actually have to move during learning, although – as we have seen in Sect. 4 – a single panoramic snapshot of the goal environment is in principle sufficient to uniquely identify the location of the goal. The specific mode and pattern of movement suggests at least five reasons for the need to move:

(1) Insects like wasps and bees, with their close-set eyes, have to move in order to generate the only distance information available to them, namely motion
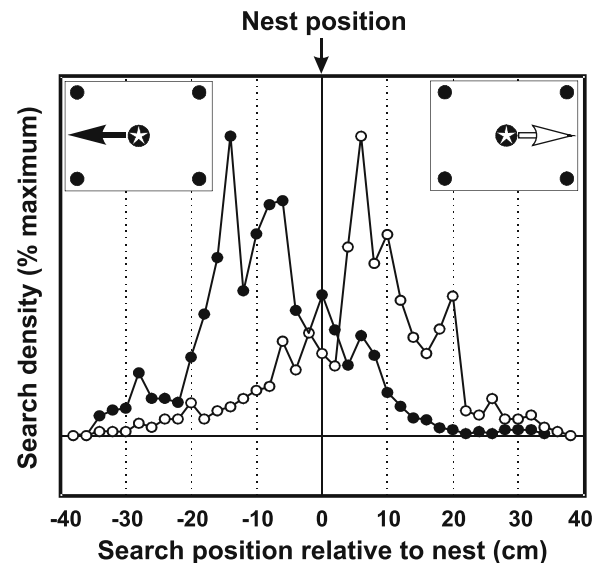

Fig. 7.9 Learning flights serve to acquire information about location. A ground-nesting wasp during her learning flight was pulled to the east (inset *top left*) or to the west (inset *top right*) of the nest entrance by shifting a small moveable collar around the nest entrance. Depending on the direction of shift during learning, the wasp subsequently searched slightly to the east (histogram with *filled circles*) or to the west (histogram with *open circles*) of the hidden nest entrance on returning to the nest area. Black circles in insets mark the positions of four landmark cylinders. Modified after [72]

parallax information. One reason for learning flights thus may be the need for foreground–background separation to identify close landmarks and for landmark distance information that is independent of apparent size. Close landmarks are particularly relevant for precise localisation (e.g. [75, 62]) and recording the distance of landmarks through motion parallax may help making visual representations more robust against changes in illumination and the presence of shadows (e.g. [73]). The insects move along arcs at a constant pivoting velocity (e.g. [76, 13]), but do so in a saccadic manner flying along straight segments of flight during which gaze direction is kept constant. At the end of such flight segments, the insects change gaze direction by rapid head saccades that are followed by changes in flight direction for the next segment of purely translational movement [74]. Wasps and bees during their learning flights thus produce a sequence of translational optic flow fields while moving along these arcs, perpendicular to the line of sight to the goal. The visual consequences are equivalent to those of the peering movements of some insects, which have been shown to provide them with distance information (reviewed in [40]).

(2) The insects may have to move in order to perform a "quality check" on what they have already learnt. It would seem that in the process of leaving a place of significance – especially when a lot of resources have been invested in it, like in the case of a nest – it is crucial for an animal to be certain that it has all the navigational information necessary for a speedy and safe return. Some aspects of learning flights indicate that this need for checking the robustness of the visual representation of the goal environment may be an important aspect of their organisation: learning flights have a repetitive structure, with insects moving along a series of arcs during which certain orientations and vantage points are systematically re-visited, a prerequisite for checking the validity of what has been seen and learnt before. This regularity may also provide a clue as to how insects control these flights: the directions in which the insects face just before they decide to begin a new arc are in some species perfectly aligned [17] and in others are clearly related to the direction in which the insect faced at the end of the previous arc on the same side (Fig. 7.8). It is possible, therefore, that the choreography of learning flights reflects a continuous process of image comparison with new arcs being initiated whenever a previously memorised view is encountered again.

(3) Yet another reason why insects have to move during learning and may have a need to continuously compare what they see with what they have seen before is to organise acquisition depending on how fast the scene changes. For instance, a sensible way of learning a visual representation for homing may be to store a view and then move away from that location while continuously monitoring the increasing image differences that develop with distance from that reference location. The next image would be stored when these differences have reached a certain threshold value (e.g. [10]). Such a procedure would assure that the catchments of successive snapshots are contiguous and that a successful gradient descent on one would trigger the descent on the next one.

(4) The spatio-temporal regularities in learning flights may also reflect the need to acquire an ordered sequence of representations at different distances from the goal (or at different spatial scales). The catchment areas of panoramic snapshots, for instance, depend on the depth structure of scenes (e.g. [62]). When objects are very close, these catchment areas are very narrow and may consequently be easily missed on return to the goal. There are a number of ways in which catchment areas can be broadened, including by low-pass filtering the memorised images (e.g. [61]) or by filtering out close contours (e.g. [10]). Yet another way of increasing the catchment or the active space of a visual representation – while at the same time preserving the accuracy with which it allows the insect to pinpoint the goal – would be to acquire a sequence of representations at systematically increasing spatial scales or at increasing distances from the goal (e.g. [17]). In this case, the sequence in which these representations are acquired during departure and used during homing might be of utmost importance.

(5) The oscillating nature of learning flight, the aligned bearings of the end of arcs and the fact that the average orientation of returning insects closely matches the average orientation they had during learning (e.g. [72, 13]) also suggest that the insects may learn the borders of a v-shaped flight corridor with its apex at the goal. The return flight may then not be guided primarily by attraction to the goal, but by repulsion from the borders of the flight corridor [76].

7.6 Outlook

Homing insects are clearly guided by the appearance of individual objects in the goal environment, provided they are visually salient. They use these objects as beacons, but also memorise their appearance as seen from the goal and as features along the route [15]. What decides whether an object is being memorised as a beacon, a goal or a route landmark? Much evidence indicates that insects constantly monitor the view transformations they experience on departure and on return to a goal and that they remember the visual signatures of objects along a number of dimensions, including their colour, their shape and the image motion signals they generate. These visual memories are associated with compass information, with motor commands and with information from the path integration system. For the task of homing, visual representations of the goal environment are acquired in a systematic fashion during learning flights and walks, the organisation and functional significance of which we still do not fully understand. Equally, little attention has been paid to the flexibility of view-based homing behaviour in insects: in experiments in which a nest entrance, for instance, has been hidden and the landmark array has been altered, returning insects approach the location and after a short period of local search fly off and approach again repeatedly from some distance away. What is it that makes an insect decide to abort an approach or a search and what determines the distance and the direction from which it tries to home again? In ants, the transition from a directed homing run to search behaviour is controlled by the state of the path integrator. Path integration does not seem to offer ants the option to abort search at some stage for an alternative strategy. Insects that employ a visual homing mechanism, however, are able to repeat an approach by flying back along the route to where the scene has not been disturbed and try again.

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