

MIDDLE-SCALE NAVIGATION: THE INSECT CASE

RÜDIGER WEHNER

Department of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

What is the large-scale spatial representation that insect foragers such as bees and ants form of their wider nest environs? This is the principal question which the following contributions aim to answer.

Whatever the result of this inquiry, there is one point that should be made at the outset. A high selection pressures must have acted upon the evolutionary design of the navigational strategies employed by insect foragers. Had the insect's brain not proved capable of accomplishing the underlying navigational tasks, the social superstructure of ant and bee societies could not have evolved for the simple reason that, during foraging excursions of individual workers, the spatial coherence of the 'superorganism' becomes somewhat relaxed, or even lost, and is re-established only by means of the insect's navigational skills.

The question of how an insect finds its way between the nest and distant feeding sites has been investigated most intensively in two species of social hymenopterans, the honeybee (*Apis*) and the desert ant (*Cataglyphis*). Additional information is available for a number of ground-dwelling sphecid wasps (e.g. *Ammophila*). In all these cases, the fundamental navigational strategy used by these central-place foragers is path integration or, in more technical terms, dead reckoning. This strategy implies that the insect must be able to measure and integrate the angular and linear components of its movements, i.e. it must possess a compass, an odometer and an integrator.

The compass is a skylight compass based on the azimuthal position of the sun and the pattern of polarized light (E-vector pattern) (Wehner *et al.* 1996). The use of an external compass cue rather than internal (idiothetic, e.g. proprioceptive) signals has the advantage of reducing integration errors. Relying on 'skymark' rather than landmark information further frees the insect from the need to disentangle the components of retinal image motion due to its rotations and translations. As skymarks are virtually at infinity, self-induced image motion results from the rotatory but not from the translatory components of the insect's locomotion and, hence, fulfils the conditions that any compass system must meet. However, as the sun and with it the E-vector pattern move across the sky during the course of the day, celestial cues do not provide the animal with geostable information. Instead, the position of any skymark must be calibrated against an earth-bound system of reference. Most probably it is the landmark skyline at the horizon that provides the necessary information. The calibration problem is the more intriguing as the sigmoidal solar ephemeris function, i.e. the function that relates the azimuthal position of the sun to the

time of day, varies with season and geographical latitude. Dyer (1996) presents clear evidence that bees are genetically programmed with a 180° step ephemeris function, in which the sun stays at a constant azimuthal position in the eastern sky during the morning hours and at noon switches to the opposite position in the western sky, where it remains during the whole afternoon. This finding is in accord with what has been described for desert ants (Wehner and Müller, 1993). The simple step function, which has been reconstructed fully only in bees, can be regarded as the mean of all possible ephemeris functions as they occur at different latitudes and times of year. With experience, this innate approximation of the movement of the sun's azimuth (or the rotation of the E-vector pattern) is later moulded into an ephemeris function that closely resembles but, as shown in *Cataglyphis* (Wehner, 1992), does not fully coincide with the actual one valid at the time and place concerned.

The E-vector compass of bees and ants provides another example of an approximate rather than exact navigational tool (Wehner *et al.* 1996). Although the E-vector pattern changes with the elevation of the sun, the insect's internal representation of these patterns, its E-vector template, stays put. It resembles the pattern actually present in the sky when the sun is at the horizon. Furthermore, in the insect's internal template, the degree (percentage) of polarization does not vary, as it does in the external patterns. However, owing to the insect's temporal foraging characteristics, the use of this approximate skylight template as a compass does not induce systematic errors.

When it comes to gauging distance travelled, it is again the sense of vision that plays a major role. The insect can assess the distances it has covered by integrating self-induced retinal image speed over time (for ants, see Wehner *et al.* 1996; for bees, indirect and direct evidence is provided by Esch and Burns, 1996; Srinivasan *et al.* 1996). Ants and bees exploit optic flow preferentially over the ventral and lateral retina, respectively. Using optic flow as experienced by the ventral retina makes sense in walking insects such as ants, because their eyes move at a constant height above ground. Flying insects, however, must first acquire information about their distance from landmarks. Otherwise, the integration of optic flow yields reliable results only if the insect flies at a constant height and follows a fixed route. It would not work properly during path-integration in novel territory, when successive segments of the insect's flight path might lead the animal through differently structured types of landscape.

The final component of path integration, the integration of angles steered and distances travelled, is again based on an approximate computational rule. As reported by Wehner *et al.* (1996), this conclusion is derived from experiments in which ants were trained to run through a system of channels that offered them a view of the sky, but not of landmarks, and in which they were later tested in an open, landmark-free experimental area. Under particular test situations, systematic path-integration errors occurred. These errors led to the formulation of an algorithm that solved the path-integration problem approximately. Under natural conditions, foraging ants employ a spatial locomotor programme that ensures that systematic errors are cancelled out.

The frame of reference used in path integration is an egocentric one. Metaphorically, the home vector resembles a rigidly tightened thread of Ariadne that invariably ties the animal to home. It is fixed to the animal rather than to the terrain over which the animal moves. Hence, owing to the cumulative errors that necessarily result from such an egocentric integration system, the tip of the home vector is blurred, so to speak, rather than sharply pointed. To reduce the time needed to locate the goal, desert ants employ a systematic (non-random) search strategy and, in addition, use landmark information whenever the latter is available.

In principle, landmarks can provide the animal with geostable information. The navigator could take positional fixes at various points within its foraging area and learn the spatial relationships among these locations by mapping them within a common system of reference. As a result, it would have at its disposal the analogue of a topographic map (a cognitive map). However, are insects – and particularly the most highly advanced navigators such as the social hymenopterans – really capable of acquiring and using such maps?

Let us look at the experimental data available. First, bees and ants are able to store in memory visual snapshots of the landmark scenes around nesting and feeding sites. As shown for desert ants (Wehner *et al.* 1996) and inferred from experiments with honeybees (Collett, 1996), these snapshots are retinotopically fixed and coupled to a common (compass) system of reference. The latter condition is a necessary consequence of the fact that the snapshot does not counterrotate in the insect's head to compensate for changes in the insect's orientation. A match between the snapshot and the current retinal image is possible only if the animal assumes a constant compass orientation.

Second, bees and ants acquire landmark-based route information, which might consist of a sequence of local snapshots. Individual ants can learn at least two such routes independently. Are these memorized routes oriented, and hence mapped, in a common frame of reference? If this were the case, i.e. if the positions of landmarks were specified in geocentric coordinates, the insect would be able to travel novel routes within the area defined by the landmark routes. In a stimulating paper, Gould (1986) has claimed that bees are able to compute such novel routes, but several authors have found

it difficult or impossible to replicate his results. In one particular test situation, Dyer (1996) succeeded, but concluded from the specific arrangement of landmarks prevailing in this test situation that bees 'do not organize their experience on different routes into an integrated map of the landscape'. In desert ants, Wehner *et al.* (1996) showed that an array of (artificial) landmarks used by the insect as a familiar route could be rotated by 90° relative to earth-based coordinates and was still followed by the ants. Hence, whatever the sequence of landmark images might have been that the animals used in following their route, this sequence was not oriented within a geocentric system of reference.

Finally, the insect forager might construct a large-scale map by associating, say, home vectors with various feeding sites and storing these location-based vectors within some higher-order memory. This vector map would provide the animal with the necessary information to compute novel routes by vector summation and subtraction. In their contributions to this volume, Collett (1996) and Menzel *et al.* (1996) claim that this is what bees are able to accomplish, but their observations are open to other interpretations as well.

Taken together, the present evidence does not support the hypothesis that bees and ants chart the positions of different sites within their foraging area in a common geocentric frame of reference. Path integration and the flexible use of landmark memories acquired at particular sites and along particular routes, and potentially taken from various vantage points, suffice to describe the data. In conclusion, I would like to credit the insect navigator with a gazeteer-like memory for sites and routes rather than with the capacity to compute geometrical relationships among familiar sites.

The map hypothesis has stirred up both enthusiasm and controversy. Data obtained from insects have often been interpreted as being compatible with the concept of a cognitive map but, as shown in this brief outline, the experimental data can be explained by assuming that the insect employs and combines a number of simpler navigational strategies. We should aim not merely to nominalize the navigational problem but to inquire about the underlying mechanisms. Hence, operational definitions are needed that lead to novel experimental designs and, hence, to an understanding of the computations that the insect's – and not the human investigator's – brain must perform.

References

- COLLETT, T. S. (1996). Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *J. exp. Biol.* **199**, 225–226.
- DYER, F. C. (1996). Spatial memory and navigation by honeybees on the scale of the foraging range. *J. exp. Biol.* **199**, 147–154.
- ESCH, H. E. AND BURNS, J. E. (1996). Distance estimation by foraging honeybees. *J. exp. Biol.* **199**, 155–162.
- GOULD, J. L. (1986). The locale map of honey bees: do insects have cognitive maps? *Science* **232**, 861–863.
- MENZEL, R., GEIGER, K., CHITTKA, L., JOERGES, J., KUNZE, J. AND MÜLLER, U. (1996). The knowledge base of bee navigation. *J. exp. Biol.* **199**, 141–146.

- SRINIVASAN, M. V., ZHANG, S. W., LEHRER, M. AND COLLETT, T. S. (1996). Honeybee navigation *en route* to the goal: visual flight control and odometry. *J. exp. Biol.* **199**, 237–244.
- WEHNER, R. (1992). Arthropods. In *Animal Homing* (ed. F. Papi), pp. 45–144. London: Chapman & Hall.
- WEHNER, R. AND MÜLLER, M. (1993). How do ants acquire their celestial ephemeris function? *Naturwissenschaften* **80**, 331–333.
- WEHNER, R., MICHEL, B. AND ANTONSEN, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *J. exp. Biol.* **199**, 129–140.