

SHORT-RANGE NAVIGATION: DOES IT CONTRIBUTE TO UNDERSTANDING NAVIGATION OVER LONGER DISTANCES?

T. S. COLLETT

Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

A major reason for analysing short-range navigation is that it is relatively easy to record on video tape the details of an animal's behaviour over an area of about a square metre. Frequently, the orientation of the animal's body is revealed in addition to its trajectory through space. This is particularly useful in the study of insect navigation, the subject of the four contributions to this section. An insect's eyes are fixed in its head, and there are often no significant head movements during flight. Consequently, reasonable assumptions can be made about where the insect looks while it navigates and how the image of its surroundings moves over its retina. All four contributions depend to a large degree upon being able to freeze behaviour on video tape and to infer what the animal sees. To what extent do the conclusions using the abundant information that can be collected in this way extrapolate to navigation on a larger scale? Clearly, the coded information that instructs the monarch butterfly on its migrations from wide areas of North America to northern Michoacan in Mexico contains elements unique to long-distance travel. But there may be many similarities in the mechanisms available to an orchid bee as it travels over its 20 km foraging route from orchid to orchid and a wasp negotiating the last few metres through a complex environment to reach its nest.

This commonality over navigational scales is easiest to appreciate in the paper by Srinivasan *et al.* (1996). Smooth flight towards a learnt goal is helped by several reflexes that exploit the retinal image motion that is generated as an animal travels through its surroundings. Srinivasan *et al.* (1996) have shown that this translational optic flow is used by honeybees to avoid collision, to control speed and distance, and to execute gentle landings. Bees can extract the speed at which the image moves over the retina irrespective of spatial detail. This visual speedometer is blind to distance, so that flying fast at a large distance from a surface generates a similar response to flying more slowly at a shorter distance. This has some benefits: flight speed can be gradually lowered during landing or increased during long journeys by holding image speed constant and by adjusting height above the ground; similarly, by flying low, the bee's odometer can measure short distances accurately and when flying high over long distances the integrator is kept from saturation. It also has limitations: integrating image speed will not give an absolute measure of distance, unless the bee flies at a constant height above the terrain. The bee is thus equipped with a route-specific ruler that allows it to mark out places along a familiar path. These control systems analysed by

observing bees flying through short tunnels are likely to operate in larger-scale environments as well (Esch and Burns, 1995).

Lehrer (1996) discusses the use of optic flow in range finding. Bees will collect sucrose from targets that are raised a specific distance above a surface and they will come to ignore targets at inappropriate distances. Bees tend to land when they fly over discontinuities that generate a sudden increase in translational flow. However, through reinforcement, landings come to be preferentially triggered by specific patterns of flow.

Bees are not simply passive recipients of optic flow. They structure their flight so as to improve the information available to them. With edges oriented randomly on a horizontal surface, optic flow will be generated in whatever direction the bee flies over the surface. But if the surface is covered with parallel black and white stripes, translational flow is only generated if the flight path is perpendicular or oblique to the stripes. Bees flying over such a surface learn to adjust their flight pattern so that they fly obliquely to the stripes and so obtain the parallax that they need.

The theme of active vision is continued by Zeil *et al.* (1996), who describe the intriguingly organised learning flights that wasps and bees perform when they first leave a goal to which they intend to return. During this brief flight, they must acquire sufficient information to relocate the goal on their return. And the flight is elaborately patterned to obtain the requisite information. One spatial attribute that wasps learn then is the bearing of a nearby object relative to the goal. The direction of a small cylinder relative to the nest determines the general direction in which the wasp flies from the nest. The wasp backs away, keeping the nest between it and the cylinder, with both nest and cylinder imaged by the fronto-lateral region of its retina. If an experimenter then displaces the cylinder, the returning wasp searches for the nest facing the cylinder in the same general compass direction as it did on its learning flight, thereby demonstrating that it has stored the compass bearing of the cylinder from the goal. A second important attribute recorded during the learning flight is the distance of the cylinder from the goal, as Lehrer (1996) describes in her contribution.

The geometry of the flight is interestingly scale-invariant. The insect pivots through arcs centred on the goal. It gradually increases the radius of the arcs, adjusting its translational speed so that the arc always covers equal angles in equal times. This provides the insect with parallax information that allows it to

measure the distance of objects from the goal with a flexible ruler whose markings grow apart as the insect moves away from the goal.

Full understanding of the details of learning flights is helped by knowing what navigational strategies guide an insect's return to a familiar goal. My contribution (Collett, 1996) examines some of the different ways in which bees and ants use landmarks. It emerges that a landmark may support different navigational strategies even when a bee or a wasp is within a metre of its goal. An approaching insect often first treats a prominent object close to the goal as a beacon to be approached and only then uses the landmark to specify the goal's location. Aiming at beacons is another instance of a mechanism that operates in both long- and short-range navigation (von Frisch, 1967; Chittka *et al.* 1995).

What then allows a navigational mechanism to function at different distance scales? Height above the ground is one important factor. At ground level, the world is crowded: a pine cone may be as prominent as a more distant pine tree. Some metres above the ground, the world empties: small objects become inconsequential and, visually, distances shrink. The learning flights of bees and wasps demonstrate that they appreciate this piece of visual ecology. The flight starts with a low-flying scrutiny of the area close to the goal, with the insect picking up details for micronavigation. It ends with wide

circling many metres above so that the insect can gain a less cluttered view for macronavigation. This encourages us to suppose that when we focus our video cameras on insects cavorting through wooden and acrylic constructions we are learning something about the way that they guide themselves through the world at large.

References

- CHITTKA, L., KUNZE, J., SHIPMAN, C. AND BUCHMANN, S. L. (1995). The significance of landmarks for path integration of homing honey bee foragers. *Naturwissenschaften* **83**, 341–343.
- COLLETT, T. S. (1996). Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *J. exp. Biol.* **199**, 227–235.
- ESCH, H. E. AND BURNS, J. E. (1995). Honeybees use optic flow to measure the distance of a food source. *Naturwissenschaften* **82**, 38–40.
- LEHRER, M. (1996). Small-scale navigation in the honeybee: active acquisition of visual information about the goal. *J. exp. Biol.* **199**, 253–261.
- 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.
- VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.
- ZEIL, J., KELBER, A. AND VOSS, R. (1996). Structure and function of learning flights in bees and wasps. *J. exp. Biol.* **199**, 245–252.