DO INSECTS HAVE COGNITIVE MAPS?

Rüdiger Wehner
Department of Zoology, University of Zürich, 8057 Zürich, Switzerland

Randolf Menzel
Department of Animal Physiology and Zoology, University of Berlin, 1000 Berlin 41, Germany

As cognitive maps have come into fashion for behavioral neurobiologists and experimental psychologists (for mammals see O'Keefe & Nadel 1978, Olton 1978, Boesch & Boesch 1983, Sherry 1985, Cheng 1986, Gallistel 1989; for birds see Balda & Turek 1984, Sherry 1985, Stevens & Krebs 1986, Krebs et al 1989) it is not astounding that recently even insects have been claimed to possess cognitive maps (Gould 1986). However, unwarranted this claim might be—see e.g. the critical remarks on Gould's paper (1986) in Cartwright & Collett (1987) and Dyer & Seeley (1989)—we have taken it as a starting point for the present investigation. Of course, any such claim depends crucially on how a "cognitive map" is defined in operational terms, and finally on information about how the map is assembled and how it is used. Even though the term cognitive map is often defined rather vaguely and applied to various kinds of animal orientation, we hope to be in line with most workers in the field—and especially with Tolman (1948), who coined the term—when we use it in the way a human navigator does. Seen in this light, a cognitive map is the mental analogue of a topographic map, i.e. an internal representation of the geometric relations among noticeable points in the animal's environment. In operational terms, this means that an animal using such a map must be able to compute the shortest distance between two charted points without ever having traveled along that route. More generally, it must be able to determine its position, say, relative to home, or to any other charted point,
even when it has been displaced unexpectedly to an arbitrary place within its environment. Do insects have cognitive maps?

Our aim in this chapter is to tackle, and we hope, to answer, this question in those insects that exhibit the most impressive navigational capabilities, namely the social insects, particularly bees and ants. These insects are central place foragers (Orians & Pearson 1976, Houston & McNamara 1985). After each particular foraging trip, which might lead them up to 10,000 meters (Visscher & Seeley 1982) away from their "central place", they invariably return to the center, i.e. the nesting site of their colony. Do they actually use cognitive maps in meeting the navigational requirements necessarily involved in that task, or can their potentially map-based behavior be explained by simpler computational abilities that ants and bees are already known to possess?

Two navigational systems have been found to be of prime importance in foraging bees and ants: path integration (or dead reckoning, to borrow the human navigator's term), and goal localization by using some kind of stored snapshot of the landmark panorama around the goal. First and foremost, while searching for food, bees and ants always know their position relative to their starting point (home) through path integration. During their circuitous outward journeys, they continuously monitor the angles steered and the distances traveled and integrate these data, so that they are always informed about the vector pointing from their current position toward home. Consequently, the foraging insect possesses a continually updated representation of its spatial position relative to its starting point. In the process of path integration, bees and ants use skylight compasses for measuring directions (Wehner 1982, 1989). The final problem of how they continuously compute the mean home vector has recently been tackled and solved in desert ants, *Cataglyphis fortis* (Wehner & Wehner 1986, Müller & Wehner 1988). As all computations involved in path integration are done within a self-center system of coordinates, the mechanism of path integration is inherently subject to cumulative errors. Here, the second navigational system (goal localization) comes to the fore. Ants (Wehner & Rauber 1979, Wehner 1983) and bees (Wehner 1981) finally pinpoint the position of their goal, the nest entrance, by using nearby landmarks surrounding the goal. Before setting out for a foraging trip, they store something akin to a two-dimensional snapshot of the landmarks taken from that point. Upon return, they continuously compare this remembered snapshot with their current retinal images and move so as to reduce the discrepancy between the two (Cartwright & Collett 1983). If even this system fails in localizing the nest site, the insect resorts to a third mode of navigation by engaging in systematic searching behavior (Wehner & Srinivasan 1981).

With these navigational capabilities in mind, let us now inquire about the insect's putative mental map. Here we focus especially on experiments with honey bees, *Apis mellifera*, because it was in this hymenopteran species that Gould (1986) invoked his concept of the insect's map.

There are three possible ways of testing for map-based behavior (Figure 1). In all three cases, bees that have been trained to a food source *F* are
displaced to an arbitrary release site R within the colony's foraging range, 100 to 300 meters away from the hive. Note that this distance between release site and hive is less than 10% of the flight range the bees exhibit in the area in which the experiments described below are performed. The individually marked bees are displaced to site R either from the food source F (experiment A, Figure 1a) or from the hive H — and in the latter case either before departure (experiment B, Figure 1b) or after arrival from a successful foraging trip (experiment C, Figure 1c).

In experiments A and B there are two different predictions about how the displaced bees could behave. If, after release, the bees relied exclusively on their path integration system, they should select the compass courses $c_H$ and $c_F$ leading to the hive and the feeding station, respectively. On the other hand, if they realized the geometric relations among sites R, H, and F, i.e., used map information, they should fly along the map courses $m_H$ and $m_F$ (in experiments A and B, respectively). In all versions of experiments A and B performed at two localities by two research groups, the bees highly significantly selected the compass rather than the map courses (Figures 2, 3).

In this context one additional result is extremely interesting. At release site R_1 of Figure 3, the behavior of bees released under sunny and overcast conditions is compared. Under the overcast sky the bees could see neither the sun nor parts of the pattern of polarized light (as indicated by control experiments not described here). In spite of this lack of celestial information the bees selected the compass course much in the same way as they did under sunny conditions. It is already known from the elegant experiments of Dyer (Dyer & Gould 1981, Dyer 1987) that bees can infer the azimuthal position of the sun on completely overcast days from familiar landmark panoramas, which they have originally used as frames of reference for learning the sun’s daily course. Thus it follows that in those of our experiments which were performed under a fully overcast sky, the bees did use landmark information, but they used this information not to compute the true position of the release site within some kind of mental map; they used the landmarks merely to determine the compass course $c_H$ that normally would have led them back to the hive.

One further observation is worth mentioning. The bees displaced from either the feeding station or the hive certainly realized that they had been displaced and that they had been released at an unusual site, because after release they circled around for a short while, spiraling higher and higher up in the air, before they flew off along a straight course. Such circling was never observed when the trained bees, prior to displacement, left either the hive or the feeding station. Notwithstanding this often intensive circling behavior, the displaced bees finally selected the proper compass course and never showed any sign of map-based behavior. In conclusion, all the results of our displacement experiments — of which Figures 2 and 3 provide only some examples — are at variance with both Gould’s data and his conclusion (Gould 1986, Gould & Towne 1987).

Even if the bees, as reported by Gould (1986), had finally selected what looked like a map course rather than a compass course, this would not conclusively demonstrate that the bees had used landmark-based mental maps to reach their intended goal. Dyer & Seeley (1989), one of whom (F. C. D.) is well familiar with Gould’s study area, clinch a strong argument...
against Gould's interpretation by stressing that "it would be well within the visual abilities of bees to see a forested upland on being released in a pasture, or vice versa. Bees and many other insects can find a specific familiar site relative to a small array of landmarks by moving to get a better match between their current visual image, and the image learned with previous experience at the site (Wehner 1981, Collett & Cartwright 1983). This matching process can be performed by bees no matter how they enter the array (for example via novel routes)."

Cartwright & Collett (1987) add another point by arguing that novel routes might be generated by manipulating vectors rather than by referring to a landmark-based topographic map.

In a second paper Gould goes even one step further in assuming that mental maps of the landscape form the frame of reference for the honeybee's dance communication system, and that the communication dances performed by successful foragers within the hive have evolved "to provide a direct readout" of landmark-based maps (Gould & Towne 1987). In their rebuttal of Gould's argument, Dyer & Seeley (1989) convincingly show that a communication system based on landmark maps rather than on vector information obtained via the bee's path integration system would be very inefficient indeed. As the arrangement of landmarks around any particular hive is unpredictable to bees starting their foraging lives, a map-based communication system would first require numerous flights to assemble the landmark-map, and would then require that the maps of dancers and recruits overlap. In the context of the present account, we note that a map-based communication system in the way proposed by Gould & Towne (1987) is not supported by experimental evidence.

Let us finally turn to displacement experiment C (Figure 1c). This experiment was designed in such a way that the bees had returned to the hive and therefore had reset their path integration system to zero before being displaced. Left with no compass information, they must now resort exclusively to landmark cues. Many classical experiments dating back even to the last century (Fabre 1879, Romanes 1885) have been performed in this way, but general conclusions are difficult to draw from the results. The homing success rates calculated on the basis of the times taken by the bees to return, or on the basis of the number of successful returns, varied widely even among individuals of the same colony. These variations are mainly due to the fact that the bees' foraging experiences prior to the displacement experiments were neither controlled nor known. In only one study has at least the age dependence of the homing success rate of honey bees been investigated to some extent (Lewtchenko 1959; for studies of other hymenopterans see Rau 1929, Ugolini 1986). Nevertheless, taken together, the results of all type-C experiments cited in the literature (for summary see Wehner 1981) are consistent with the hypothesis that after release the bees first perform extensive circling flights until they reach what has been called (Cartwright & Collett 1987) the catchment area of the snapshot they have taken at the hive. Thus searching behavior and mechanisms of matching-to-memory as outlined in the beginning of this chapter are entirely adequate to explain the results of the type-C experiments.
Recent investigations, in which the foraging range of the colony and the foraging experience of individually marked bees were known (R. Wehner, unpublished), also clearly showed that the bees pick a straight path to the hive, and return quickly, only when the release site R is positioned along the line HF. Angular deviations from that line result in a dramatic increase of the flight times needed for return. It seems as though the bees had become familiar only with a pattern of landmarks they had experienced while traversing specific routes. This conclusion is in full accord with similar experiments performed with ants, in which, unlike bees, the search trajectories can be recorded in detail (Wehner & Flatt 1972, Wehner et al 1983).

When bees and ants do not assemble and use mental topographic maps, what kind of internal representation of their foraging terrain should we attribute to them? One of us (R.W.) has published a survey of various ways whereby central place foragers might assemble spatial representations of their foraging sites (Wehner et al 1983). Let us briefly review these ways in the light of more recent data.

**Vector information** The predominant piece of spatial information bees and ants acquire and use is vector information. By referring to the sky as a directional reference (Wehner 1989), measuring flight and walking distances, and integrating directions and distances, the insect obtains information about the radial coordinates of a foraging site as well as how to return from that foraging site to the starting point (home). For example, desert ants (*Cataglyphis*) can leave the nest and proceed along circuitous routes for more than 200 meters. After having located a food item they do not retrace their outward path, but walk directly back to the nest. They locate the nest entrance with fair precision by using only their path integration system (Wehner 1982, Wehner & Wehner 1986, Müller & Wehner 1988). Path integration and the use of vector information have been described for bees (von Frisch 1967) and other arthropods as well (Goerner & Zeppenfeld 1980, Seyfarth et al 1982, Hoffman 1983, Goerner & Claass 1985, Mittelstaedt 1985, Ugozini 1987).

**Route information** Depending on the degree of patchiness of the food supply within their nest environs, many central place foragers frequently revisit the same foraging site (Rosengren 1971, Fresneuf 1985, Seeley 1985, Wehner 1987, Harkness & Isham 1988). In these cases the vector course leading to that site can become increasingly "decorated" with snapshots of landmarks, i.e. with landmark-based route information added to the original vector information (Rosengren & Parno 1978, David & Wood 1980, Kaul 1983, Fourcassie 1986, Klotz 1987). In their final approaches toward the nest, walking *Ammophila* wasps (Barends 1941) and *Cataglyphis* ants (Wehner 1987) often select idiosyncratic and stereotyped routes, which differ slightly from the straight vector courses, and which can be changed experimentally by manipulating the arrangement of landmarks around the routes. Further evidence for the use of landmark-based route information comes from the marked trap-lining behavior of many solitary bees (Barrows 1976), bumble bees (Haas 1967, Heinrich 1976), and orchid bees (Janzen 1971). The latter two have been shown to visit the same set of plants day after day in the same order along a feeding route that may extend up to 23 km from the nest.

With this additional piece of evidence, we can now extend the snapshot model introduced above. Let us propose that the homing insect uses a stack of snapshots activated sequentially as the insect approaches its nesting site. As recent experiments in *Cataglyphis* show (R. Wehner, unpublished), these snapshots are not completely unprocessed retinal images. The snapshots pertaining to points along the route that are far away from the nest contain only distant landmarks. As the ant moves closer to its final destination, it progressively refers to nearby landmarks. For simple geometrical reasons, the functional implications of this behavior are easy to understand. While distant landmarks guide the ant to the broad area of the goal, close landmarks allow for finally pinpointing the exact position of the goal. Model bees using just two snapshots (the one used first with the close landmarks filtered out) behave in exactly this way (Cartwright & Collett 1987), and real bees have been shown to discriminate between nearby and remote landmarks of equal angular (retinal) size. In their final search for the goal, they weigh near landmarks more heavily than distant ones (Cheng et al 1987). Although insects seem to be unable to measure the absolute sizes of objects, and do not resolve the optical size-distance ambiguity (Cartwright & Collett 1979, Wehner & Rauber 1979), they can obtain information about relative distances by exploiting motion parallax cues (Collett 1978, Eriksson 1980, Goulet et al 1981, Lehrer et al 1988).

**Vector maps** When a bee forages at more than one feeding site (von Frisch 1967) and thus possesses vector information about, say, sites A and B, it could in principle devise the novel route AB through vector addition. Furthermore, if the two routes were linked with snapshots taken at A and B (Cartwright & Collett 1987, for birds Wallraff 1974, Fueller et al 1983), the bee could define the direct trajectory AB even after displacement from the hive to A or B (Figure 1c). No data are available that support this hypothesis in any insect. Furthermore, it might be worth mentioning in this context that even in path integration ants do not perform what could be called vector addition (Müller & Wehner 1988). The way they integrate their paths would be completely inadequate for assembling a vector map.
Topographic maps  Similarly to constructing a vector map from individual vectors, the animal could combine landmark-based routes within a geocentric system of coordinates and thus form the analogue of a topographic map as defined in the beginning. However, the results and discussions presented in this chapter make it quite clear that the question posed in the title cannot be answered in the affirmative. At present there is no convincing evidence for map-based behavior in insects. Certainly, bees cannot "make use of novel and efficient routes on the basis of map-like cognitive representations" (p. 863 in Gould 1986). The insect's navigational system is able to cope with many different ecological situations, e.g., obscured sun (Wehner & Rossel 1985, Rossel & Wehner 1986), overcast sky (Dyer 1987), apparent movement of the sun (New & New 1962, Wehner & Lanfranconi 1981, Dyer 1987), and drift by wind (Herna & Lindauer 1963), but unexpected displacements in dark boxes carried by human experimenters have obviously not been an evolutionary force that has shaped the insect's navigational system.

Literature Cited

Rau, P. 1929. Experimental studies in the homing of carpernter and mining bees. J. Comp. Psychol. 9: 75–87


