Psicológica (2002), 23, 3-32.

Navigational strategies and models

T. Rodrigo[*]

University of Barcelona

Many scientists are interested in the different mechanisms and strategies that animals use to navigate. This paper reviews a series of studies and models about the navigational strategies that animals can use to move from one place to another. Studies of long-distance navigation have mainly been focused on how animals are able to maintain a certain orientation across a distance of hundreds of kilometers. These studies have shown the great variety of sources of information that animals can use to orientate themselves, as well as their redundancy. But, for successful navigation to occur, animals not only have to know how to orientate themselves, they also have to know which direction they should be orientated and for how long. Direction and duration have mainly been studied in short-distance navigation. These studies have shown that animals can use a variety of strategies to locate a given goal. Whether an animal uses a specific strategy will depend on its sensory capabilities and also on the conditions imposed by the environment.

Navigation can be defined as the process which enables a course or path from one place to another to be identified and maintained (Gallistel, 1990). The importance of this process for animals that navigate over long distances is obvious. There are many animal that migrate, both to find favourable climatic and nutritional conditions for the adults and to provide the young with the necessary conditions for growth. Navigational errors could take them far from their goal and to a place without the necessary conditions for their survival. However, the apparent ease with which migratory animals return to the same wintering or breeding places has always impressed us, as has the ability of homing pigeons to return to the nest from hundreds of kilometers away. Not only migratory animals and the homing pigeons use navigation. Many animals navigate across short distances during the course of their normal daily activities. Most have to leave their nest or refuge to find food and, as soon as they get it, face the problem of returning there. But animals are not only aware of their nest's position. They also know where they are most likely to find food or to encounter a predator. This means that the ability to move from one place to another in an efficient way is an important factor in their own survival.

The aim of this article is to review the different mechanisms and strategies that animals use in navigation. As we will see, studies of long-

---

[*] Laboratori de Psicologia Animal i Estabulari, Facultat de Psicologia, Universitat de Barcelona, Pg. de la Vall d'Hebron 171, 08035 Barcelona. Spain. E-mail: trodrigo@psi.ub.es

distance navigation, concerned mainly with migratory birds and homing pigeons, have focussed on the different orientation mechanisms. In contrast, studies of short-distance navigation have looked more at how animals know in which direction and how far they should move in order to find a certain goal.

LONG-DISTANCE NAVIGATION

Long-distance navigation encompasses a wide range of animal movements, from the circumglobal migrations of the arctic tern to the return flights to the nest of homing pigeons, covering tens to hundreds of kilometers (Able, 1996). Research interest has centered mainly on how animals are able to maintain a certain orientation across hundreds of kilometers. Studies have shown the great variety of sources of information that animals can use to orient themselves, as well as their redundancy. This redundancy in orientation systems makes it difficult to design experiments to evaluate the role of a certain cue (see Emlen, 1975). Showing that an animal can orient itself in the absence of a certain cue does not imply that it might not use it when it is available. Neither should closely related species be assumed to employ the same means of orientation. It will be useful to look briefly at the main sources of information that animals use to orient themselves (for a detailed review, see Able, 1980).

Main orientation systems

The sun and polarized light. As early as 1911, Santschi demonstrated that the myrmicine ant, *Messor barbarus*, used the sun in returning to its nest. Subsequently, many studies have been carried out aimed at elucidating the sun's role in animal orientation. These have shown that while some animals use the sun essentially as a fixed reference point, others possess a compass system that compensates for changes in the sun's position during the day. For example, Baker (1968,1969) observed that butterflies shifted their flight direction in phase with the sun's azimuth, implying that they were orienting at a constant angle with respect to the sun. However, this strategy is clearly ineffective for those animals which migrate over long distances and who must maintain a constant compass orientation, as this means they have to take into account the apparent movement of the sun during the day. Animals are said to possess a "sun compass" when they use the sun to orient themselves and take into consideration its apparent daily movement. The sun compass was discovered simultaneously by von Frisch (1950) in honeybees and by Kramer (1950) in birds. They observed that animals maintained a constant compass orientation at different times of the day and, therefore, in relation to the different positions of the sun. However, the clearest demonstrations of the existence of a sun compass come from experiments in which the animal's internal clock is phase shifted relative to sun time (see for example, Keeton, 1969, 1974; Matthews, 1961; Schmidt-Koenig, 1960). In these experiments animals are generally maintained in an artificial environment with a light-dark cycle that is out of phase with respect to the external cycle. Results have shown that animals orient themselves with respect to the sun's position and the time of day as indicated by their out-of-phase internal clock. Many animals are able to perceive the polarization plane (the e-vector) of polarized light (Kreithen and Keeton, 1974; von Frisch, 1949; Waterman, 1966) and this provides them with an orientation axis. It can also be used to determine the position of the sun and, therefore, as a means of orienting with respect to the sun when it is not visible. Orientation by polarized light has been studied extensively in bees and ants. Both species use ultraviolet wavelengths (von Frisch, 1967; von Helversen and Edrich, 1974) and both can detect the polarization axis when only a small area of blue sky is visible (von Frisch, 1967).

The stars and the moon. The study of the use of stars for orientation was begun by Kramer (1949,1951) in migratory birds. He carried out experiments in which nocturnal migratory birds were placed in circular cages under star-spangled skies. His observations that birds fluttered and hopped in the appropriate direction during spring and fall have been confirmed in many species (for a review, see Emlen, 1975). The most obvious advantage of using stars as a method of orientation is that since stars maintain a fixed geometric relationship, they can be used independently of the time, season or geographical locality. The classic experiments of Sauer (1957,1961; Sauer and Sauer, 1960) and Emlen with indigo buntings (1967a,b) have shown that nocturnal migratory birds can select migratory directions based only on the stars. However, it seems that early visual experience with stars is necessary for normal migratory orientation (Able and Able, 1996; Emlen, 1969, 1970). The moon can also provide a potential orientation cue for species that move at night. However, as both the size and position of the moon changes from night to night according to the lunar cycle, use of the moon as a compass implies that animals possess an internal clock that is in phase with lunar time. Beach amphipods have been shown to use a moon compass (Enright, 1972; Papi and Pardi, 1963).

The Earth's magnetic field. The idea that terrestrial magnetism could be used as a compass by animals dates back more than century (see Keeton, 1974). Yeagley (1947,1951) applied this idea in birds and, postulating that the Coriolis force could be detected, developed a system of bi-coordinate navigation. However, this hypothesis was not widely accepted and the possibility of magnetic orientation was considered improbable for almost a decade. It was the subsequent work of Merkel and colleagues (Merkel and Fromme, 1958; Merkel, Fromme, and Wiltschko, 1964; Merkel and Wiltschko, 1965) and of Wiltschko and Wiltschko (1972), that provided overwhelming evidence that birds can indeed obtain directional information from terrestrial magnetism (see Wiltschko and Wiltschko, 1996).

Other sources of information. Currents and waves in water provide relatively stable directional information that can be used in conjunction with compass information. Currents enable an animal to maintain the direction of movement. It is known that many classes of fish are able to orient themselves with respect to the direction of currents in streams and torrents (see Leggett, 1977; Royce, Smith, and Hartt, 1968). This simple mechanism is not feasible in the sea, but there is evidence that currents can be important sources of orienting information for migrating fish, as is the case of salmon (Royce et al., 1968). In the ocean, the passage of waves or swells produces horizontal oscillations on the bottom called wave surge. The wave surge direction is constant over long periods of time and is often independent of currents. It is known that migratory spiny lobsters move at angles to both current and wave surge (Herrnkind and Kanciruk, 1978).

For a long time, the wind has been considered to be an important factor in the orientation of migratory birds. Finding them far from their normal ranges has frequently been correlated with winds during the preceding days. In addition, wind direction is an important determinant of whether migratory birds will initiate flight on a certain day (see Richardson, 1978). Because the wind is variable in time and space, it cannot provide absolute compass information, but it can be used in combination with compass information to establish flight orientation.

Although sounds do not provide compass information per se, they might play some role in the orientation of migratory animals. Of particular interest among these acoustic cues, are the variety of sounds emanating from ground sources (D'Arms and Griffin, 1972; Griffin, 1969), the flight calls emitted by birds migrating at night (Griffin, 1969) and infrasounds (Kreithen, 1978).

Similarly, although visual cues cannot provide animals with information about absolute compass direction, landmarks can be used together with compass cues to maintain directionality during oriented movement, or to substitute compass systems in familiar areas. As will be seen later, they become very important in the last homing phases of some species, when the landmarks that define the goal’s position become perceptible.

Models of long-distance navigation

So far, the different mechanisms that animals can use to orient themselves during long distance journeys have been described. However, animals also have to know which direction they should be oriented in and for how long. Gwinner (1972) pointed out the possibility that the direction and duration of migration are largely under endogenous control. But learning must also play a role. Long exposure to stars is essential before indigo buntings will migrate in the correct direction (Emlen, 1970). Experiments with starlings have shown that the knowledge which is acquired during a journey can influence the path of subsequent ones (Perdeck,1958). In addition, experience in wintering or breeding areas appears to be necessary to enable homing to those localities in subsequent seasons (Able, 1980). Experienced individuals of at least some species (e.g. some sea birds and homing pigeons) have the ability to navigate from unfamiliar areas to their home site. Although several models have attempted to explain how homing pigeons perform these feats, none of them has been able to explain satisfactorily the experimental data.

The bicoordinate navigation hypothesis proposed that one means by which a bird might return to its home would involve determining latitude and longitude at the displacement site and comparing these values with home coordinates. This could be carried out using the sun (Mathews, 1961, 1968), stars (Sauer, 1961; Sauer and Sauer, 1960), earth magnetism coupled with the strength of the Coriolis force (Yeagley, 1947, 1951) and smell (for example, Papi, Ioalé, Fiaschi, Benvenuti, and Baldaccini, 1978). However, this hypothesis has been rejected on the basis of numerous tests (see Able, 1980; Gould, 1982; Keeton, 1974).

The map and compass hypothesis proposed by Kramer (1953) is based on the idea that a navigating bird performs two tasks analogous to consulting a map and a compass. According to Kramer (1953), homing pigeons possess a map that allows them to determine the direction in which they should fly in order to return to their ranges and a compass that allows them to orient themselves correctly. We have already seen the different orientation mechanisms or compass systems that animals use in their journeys over long distances. However, while the compass component of the hypothesis has been widely accepted, the map component has proved more controversial. Pearce (1997) has argued that it is unlikely that homing pigeons could return to the nest from a unknown place using a map that they hadn't had the opportunity to acquire. Some proposals have been made regarding the map component in long-distance navigation, for example, the olfactory map (Papi et al., 1978) or the gradient map (Wallraff, 1974). However, most navigation models involve a map with some sort of coordinates system and, as will be seen later, these have mainly been interested in explaining homing in short-distance navigation.

SHORT-DISTANCE NAVIGATION

As Shettleworth (1998) points out, all animals who are able to locate their refuge or food places have a feature in common: the acquisition of an internal representation of the goal's location or how to reach it. That is, they show some form of spatial learning. In many of studies of spatial learning, animals have to navigate over short distances in order to solve successfully a certain task. It is not surprising that there has been a great interest in discovering the navigational strategies used by animals and the conditions for using each of them. It will be seen that animals use a variety of strategies to locate a given goal. As with orientation mechanisms, the fact that an animal uses a given navigational strategy in a specific situation does not imply that it can not use another one under different conditions.

Navigation using information based on the animal's own movement.

The desert ant (*Cataglyphis fortis*) wanders here and there, taking a long and tortuous path in search of food, and as soon as it finds a prey, it returns to its nest, which may be hundreds of metres away. The ant does not return to its nest retracing the steps of the outward journey, but rather takes in a direct path (see Figure 1). One might think that ants detect the nest location on the basis of some type of exteroceptive information (scent, landmark, etc.). However, Wehner and Flatt (1972) presented evidence that excluded this possibility. They showed that if an ant was caught when it left the nest and was moved away to a distance of approximately 5 metres, it did not know how to find the nest and behaved as if it were lost. The ability to return to the origin of a path in the absence of exteroceptive information about its location was already observed by Darwin in 1873, who hypothesized that this was achieved by means of dead reckoning. This ability is known as path integration (Mittelsdaet and Mittelsdaet, 1980) or route-based navigation (Baker, 1981). Path integration refers to the process by which animals keep track of their current position in relation to a known position using interoceptive information, that is, information based on their own movement. For this, they have to continuously process information about changes in distance and direction at the different points of their path.

Path integration has been demonstrated in arachnids (Mittelstaedt,1985), crustaceans (Hoffmann, 1984), hymenopterans (von Frisch, 1967; Wehner and Räber, 1979; Wehner and Wehner, 1986, 1990; Müller and Wehner, 1988; Schmidt, Collett, Dillier, and Wehner, 1992), birds (von Saint Paul, 1982) and also in mammals (Mittelstaedt and Mittelstaedt, 1980, 1982; Etienne et al., 1985, 1986, 1988, 1991; Séguinot, Maurer, and Etienne, 1993; Benhamou, 1997b). Mittelstaedt and Mittelstaedt (1982) placed mother gerbils (*Meriones unguiculatus*) and their pups inside a nest that was at the edge of a large circular arena. The pups were then caught and displaced to a hole in another part of the arena. They observed that the mother soon began to search for the pups and that as soon as she found them, picked one up one in her mouth and ran straight back to the nest. The gerbils performed equally well in conditions of total darkness and when the outward path had zigzags and detours.

The most convincing demonstration that animals who use path integration keep track of the distance and direction (what has been called a navigation vector) of their nest from their current position comes from experiments on displacements. Wehner and Srinivasan (1981) trained some ants to search for food in a specific location that was approximately 20 metres away from their nest and on a terrain without distinctive features. The ants were then caught upon leaving the food place and displaced to about 600 metres before being released. The ants went in a direction that corresponded to the direction of the nest from the food place and continued in this direction for a distance that was practically the same as the distance between the food place and the nest. Once they had traveled this distance they began to search for the nest in circles. This observation demonstrates that the ants kept track of the distance and direction of the nest from the food place and that in the homing time, they followed the route indicated by their current navigation vector. Mittelstaedt and Mittelstaedt (1982) rotated the edge of the arena while the mother gerbil was in the hole, so that the nest was displaced. They observed that the mother gerbil returned to the place where the nest had been previously, demonstrating that the homing performance was not based on a cue emanating from the nest, but rather one based on path integration.

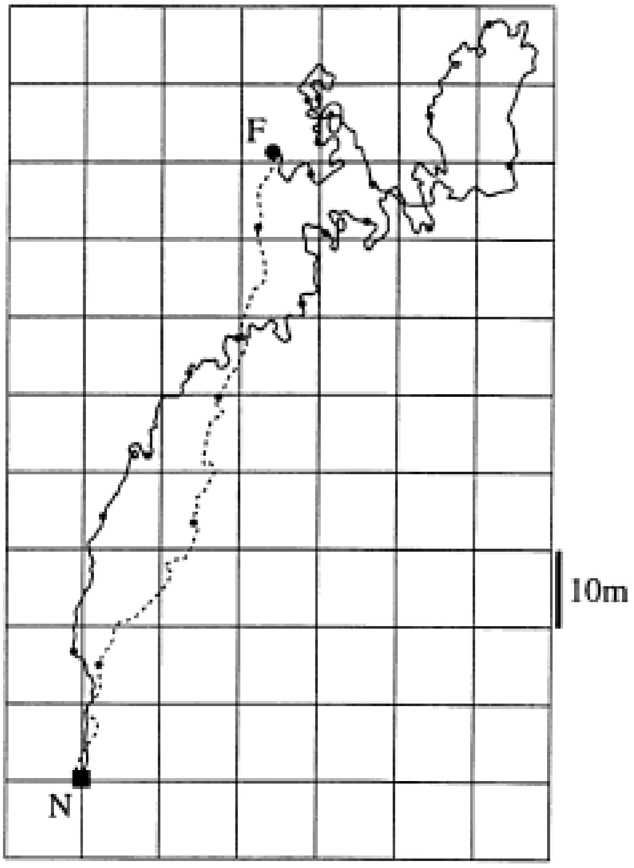

Figure 1. Foraging trip of an individual ant, *Cataglyphis fortis*. When the ant found food (F) after a circuitous search (solid line), it returned on a fairly straight path (stippled line) to the nest (N). From "Path integration in desert ants, *Catagliphys fortis*", by M. Müller and R. Wehner, 1988, *Proceedings of the National Academy of Sciences, 85*, p-5288. Copyright 1988 by Wehner. Reprinted with permission.

They also observed that if the hole was rotated briskly while the mother and their pups were inside, she compensated for the rotation and headed straight back to the nest (see also Bardunias and Jander, 2000). However, if they rotated it or displaced it slowly sideways, the gerbil did not compensate and was misoriented. Similar results have also been obtained with geese (von Saint Paul, 1982) and golden hamsters (Etienne, Maurer, Saucy, and Teroni, 1986).

Although path integration can often be a very effective homing mechanism, it also, as pointed out above, has limitations. In path integration both random errors and systematic errors may ocurr. If ants are forced to take a two-leg outward journey with a controlled turn between the two legs, it has been shown that errors increase in relation to the angle through which they are forced to turn. These systematic errors indicate that ants are not continuously integrating the perceived distance and direction from home, but use a simpler approximate solution (Müller and Wehner, 1988). The effects of rotation at the food site were investigated more systematically by Etienne, Maurer and Saucy (1988). They carried out an experiment with golden hamsters in a circular arena that was completely in the dark. To search for food the hamsters had to go to the center of the arena from their nest box, that was in a given position at the edge of the arena. Once they had collected the food, the efficiency with which they returned to the nest was observed. Under these conditions, the hamsters always showed a high level of accuracy. But if they were rotated before allowing them to pick up the food, 3, 5 or 8 turns, either clockwise or anti-clockwise, their performance was worse and continued to deteriorate as the numbers of turns was increased. Therefore, as the number of turns increased, the degree of error involved in path integration also increased. Apparently, the errors were caused by undercompensation for rotation, because they were in the same direction as the turns. Random and systematic errors have also been demonstrated in dogs (Séguinot, Cattet, and Benhamou, 1998).

Path integration is not exclusive to homing. Animals can also use this method to go to a previously learned place of food (Collett, Collett, and Wehner, 1999; Etienne, Maurer, Berlie, Reverdin, Rowe, Georgakopoulos, and Séguinot, 1998; von Frisch, 1967), to maintain a constant direction in space (Barnwell, 1965; Merkel and Fischer-Klein, 1973), to identify specific points in ambiguous environments (Etienne, Maurer, and Séguinot, 1996; Margules and Gallistel, 1988), to maintain a search path centered on the point of maximal probability (Müller and Wehner, 1994; Wehner and Srivasan, 1981), or to locate two points continually in space (Etienne, Hurni, Maurer, and Séguinot, 1991). It has also been suggested that path integration combines with all modes of spatial information and, as will be seen later, many investigators consider it to be the basis of long-term spatial representations or cognitive maps (Gallistel, 1990; Gallistel and Cramer, 1996; McNaughton et al., 1996; Redish and Touretzky, 1997; Samsonovich and McNaughton, 1997). However, as Maurer (1998) points out, path integration is not a memory process in itself, but rather a computational process that stores in short-term memory the results of a computation that has to be repeated at every step.

Computationally, path integration involves keeping track of a location that is probably coded as a vector whose orientation specifies the current direction of the goal and whose length specifies the current distance to it (Benhamou, 1997a). Whenever the animal moves, it will update the vector taking into account the changes carried out in direction (rotations) and location (translations). The mechanisms by which an animal combines rotational and translational information to update this vector have been modeled in different ways. Most of the models are strictly mathematical in nature and differ fundamentally in three aspects: (i) in the algorithm used, (ii) in whether they use an egocentric (that is, centered on the animal) or allocentric (that is, centered on some external reference point) reference axis (see Figure 2) and (iii) in whether they incorporate variables that can explain errors in the experimental data (for a more detailed review, see Benhamou and Seguinot, 1995; and for a mathematical treatment, see Maurer and Séguinot, 1995). The first models were those of Jander (1957) and of Mittelstaedt and Mittelstaedt (1973, 1982). These models were based on an allocentric reference system, are mathematically exact and, therefore, do not deal with errors. In 1988, Müller and Wehner presented a model in which they abandoned exact trigonometry as the central process in favour of an arithmetical model that tried to explain the occurrence of errors based on an approximate readjustment. This model also relies on an allocentric reference system (although see Benhamou and Séguinot, 1995 for a discussion of this model in egocentric coordinates). In view of the results of neurobiological studies, subsequent models have been presented based on an egocentric reference system. Although these models (such as that of Benhamou, Sauvé and Bovet, 1990; Fujita, et al., 1990, 1993; and Séguinot et al., 1998) still use trigonometry, they incorporate variables that affect the accuracy of computations in an attempt to explain random and systematic errors.

More recently, and due to the increasingly detailed neuroanatomical and neurophysiological data that are available , attempts have been made to model path integration in a biologically plausible way (review in Hartmann and Wehner, 1995; Wittmann and Schewegler, 1995). Hartmann and Wehner (1995) have successfully applied Müller and Wehner's model (1988) to a neural architecture that includes structures which represent coordinates and calculate angular differences. There are two types of model within the neural network approach. On the one hand, there are those models which present a specific structure for computations of path integration, examples being the models of Maurer and Schreter (1990) and Maurer (1998). On the other, there are those more speculative models which see path integration as a building block of spatial knowledge (McNaughton et al., 1996; Samsonovich and McNaughton, 1997; Gallistel, 1990; Touretzky and Redish, 1996; Wan, Touretzky, and Redish, 1994), but which do not provide an explicit model of how computations would be carried out (for a discussion of the various ways in which path integration could be used for navigation, see Biegler, 2000). These latter models will be discussed later.

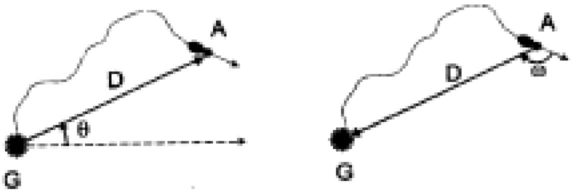

Figure 2. Vector navigation. If path integration works allocentrically (left), the resultant vector (G-A) expresses the direction θ of the animal's current location (A) from the goal location (G) with respect to an arbitrary reference direction (dashed arrow) and the distance (D) between the two locations. This vector varies for any movement except when the animal is turning on the spot. In contrast, if path integration works egocentrically (right), the resultant vector (A-G) expresses the head-referred direcction ω and distance (D) to the goal. This vector varies for any movement except when the animal makes a circular path at a fixed distance around the goal From Benhamou (1997a) with permission.

Navigation using information based on a single landmark.

Because the updating mechanism tends to accumulate errors, path integration is only a reliable navigation strategy for short journeys. This is why most animals often use external landmarks to locate themselves or their goals.

Proximal cues or beacons

Beacons are objects situated so near the goal that the animal simply has to perceive them in order to locate the goal. For example, Morris (1981) trained some rats in a circular pool full of water. They could escape from the water by climbing up onto a black platform that was visible above the water. Under these conditions, the platform functioned as a beacon. Since rats do not like water, they quickly learned to escape by climbing onto the platform, regardless of its location in the pool (see also Redhead, Roberts, Good, and Pearce, 1997; Roberts and Pearce, 1998).

It is clear that in the presence of a beacon, animals only have to orient themselves and approach. For this kind of navigation, animals only need to associate the stimulus-goal (or a stimulus that was immediately adjacent to it) with the reinforcer. It is well known that cues from a desired object draw the animal to it and, in fact, one of the most basic effects of conditioning is that animals approach a CS that has been associated with a positive US (see Shettleworth, 1998).

Distal cues

Navigation using proximal cues is a very simple task. However, although one is sometimes lucky to find cues right beside the goal, landmarks are normally far away. Distal cues are fixed singular objects situated further away from a goal than a beacon is, but which are still close enough to provide some information about the distance to the goal (Collet, Cartwright, and Smith, 1986).

Cartwright and Collet (1983) showed how honeybees could learn to find a sucrose solution placed in a small cup that was situated a few centimetres from a black cylinder in a white room. Once the bees learned to fly directly to the sucrose, the researchers carried out a series of tests. In one of them, they removed the sucrose and were able to observe how the bees searched persistently in the correct location. In another test, they removed the cylinder and observed how the bees failed to search near the goal, indicating that it was used as a landmark for the sucrose.

Collett, Cartwright and Smith (1986) carried out a similar experiment with gerbils. In this experiment, gerbils learned to dig for a sunflower seed buried in bedding, with a cylinder landmark placed at a fixed distance away. As with the bees, the gerbils learned to search in the correct location based on the landmark.

To locate a goal based on a landmark, an animal has to perceive the distance and the direction of their position with respect to the landmark, to remember the distance between the landmark and the goal and its direction, and then to implicitly calculate the distance and direction from their position to the goal. While a single beacon is sufficient to indicate the location of a goal, a single symmetrical landmark, as the one used in these experiments, is not. Such a landmark only indicates the distance to the goal, but not the direction. However, neither the bees nor the gerbils searched the goal in a ring around the landmarks, which is what they should have done if they had used only the information provided by the landmark. Therefore, the animals must have obtained directional information from another source. Given that in both experiments the landmark was moved from trial to trial, but always at the same orientation with respect to the experimental enclosure, one can suppose that both the bees and the gerbils were able to obtain directional information from some other cues (for example, a door or a windows).

With respect to obtaining information about distance, it seems that the bees and the gerbils use different methods. Once the bees had learned to find the sucrose in the correct location, Cartwright and Collett (1983) carried out further tests in which the size of the cylinder was changed. When the landmark was larger than its training size, bees searched for the sucrose at a greater distance from the landmark than its normal location. When the landmark was smaller than the standard, the bees searched nearer to the landmark than the normal sucrose location. Similar results have been obtained in studies with other insects (for a review, see Collett, 1992; Wehner, 1992). Cartwright and Collett (1982, 1983, 1987) proposed that when bees were trained with a single landmark, they did not learn the distance between the landmark and the food source, but rather they used the apparent size of the landmark to locate the goal. They present a model, the *Snapshot or Template Matching Model*, in which they assume that at the goal, bees learned to associate a particular landmark size projected onto their visual receptors with the location of food. Afterwards, the bees reach the goal moving and so progressively reduce the discrepancy between the current perceptual image and the one which they memorized as a snapshot from the goal. Once the discrepancy is at its minimum, the bees will begin to search for the goal (for an application of this model to a neural architecture, see Möller, Maris, and Lambrinos, 1999).

Although the snapshot model can explain the results of the experiments with bees, it is not suitable for gerbils. Collett, Cartwright and Smith (1986) carried out further tests in which they also changed the size of the landmark. They observed that these changes did not affect the place in which the gerbils searched for food. These results showed that, unlike bees, gerbils do take into account the distance between the landmark and the goal, regardless of the landmark's size. Collet et al. (1986) suggested that gerbils' searching behavior could be explained by a *Vectorial Summation Model* (see also Cheng 1988, 1989, 1994 for an application of the model in pigeons). According to this model, when animals are at the goal they learn the specific direction and distance between the goal and the landmark and this is stored as a vector. Thus, when an animal perceives the landmark, it perceives the vector between its current position and the landmark, recovers the stored vector which refers to the landmark and the goal, and then calculates, by means of the sum of vectors, a navigational vector which specifies the distance and direction of the goal from its current position.

Navigation using information based on multiple landmarks

Animals also use multiple landmarks to determine the position of a goal whenever they maintain a constant relationship to it.

Cartwright and Collett (1983) also tested bees with three distinct landmarks. In these experiments the sucrose was situated at the same distance from each of the landmarks, which were separated from each other at an angle of 60 degrees (see Figure 3). As in the previous experiments, the position of the landmarks and the sucrose were moved from trial to trial whilst maintaining a constant orientation. The bees learned to use these landmarks to search in the correct location. Subsequent tests in which the size of the landmarks was changed, but the distance to the goal was held constant, showed that this manipulation did not affect the place in which the bees searched for sucrose. However, the bees' performance was affected in other tests in which the distance of the landmarks from the goal, but not their size, was changed. When the three landmarks were moved close together, bees searched nearer the landmarks than normal and, when the landmarks were moved far apart, they searched farther away than normal. The search locations chosen by bees in these tests were those in which they could perceive the landmarks in the same compass direction as they had found at the goal with the landmarks in their original positions (that is, at 60°, 120° and 180°). Therefore, it seems that when there are multiple landmarks indicating the location of the goal, bees do not use their retinal sizes, but rather the cardinal direction that the landmarks maintain with the goal. Based on these results, Cartwright and Collett (1983) proposed that when bees are trained with several landmarks, they store an instantaneous snapshot of the three cardinal directions of the landmarks. Thus, the bees reach the goal by moving in such a way so as to reduce the discrepancy between the cardinal directions of the perceived landmarks and those they have stored as a snapshot. In order to test this proposal, Cartwright and Collett carried out another very similar experiment in which the orientation of the group of three landmarks varied from trial to trial. This time they found that none of the bees learned to search for sucrose in the correct location. These results show that although bees can identify a goal's location using different landmark characteristics, such as their apparent size or cardinal direction, they are not able to identify a place based on information about the relative position of one landmark to another (for a review, see Collett, 1996).

Again, it seems that the use of landmarks by bees and other insects may be very different to that of vertebrates. An experiment with gerbils indicates that, unlike bees, they can use information about the relative position of several landmarks. In another experiment by Collet, Cartwright and Smith (1986), gerbils were trained to find food in a place that maintained a fixed relationship with the position of two landmarks (see Figure 4). Once they had learned to locate the food, a series of test trials were given. When one of the landmarks was removed, the gerbils searched in two locations whose directions and distances corresponded to those between each of the landmarks and the goal during training. This suggests that the animals knew the direction and distance of the food from the landmarks, but that they did not know which landmark was present. The landmark was treated as if it could have been either of the two training landmarks. In another test the distance between landmarks was doubled and they again found that the gerbils searched in two places defined by the direction and distance of the goal from each of the two training landmarks.

These results suggest that the gerbils calculated the distance and direction of the food from each cue independently. Collett et al. (1986) suggested that gerbils' searching behavior could be explained by a vectorial summation model. Once again, the idea is that gerbils learn specific vectors between the goal and the various landmarks available in the environment. By viewing landmarks from the goal where food is found, the gerbil learns the specific direction and distance between the goal and each landmark. Thus, when an animal enters the arena, it perceives the vector between its current position and the landmarks, recovers the stored vectors which refer to the landmarks and the goal, and then calculates independently, by means of the sum of vectors, navigational vectors that specify the distance and direction of the goal from its current position. All such vector additions converge on the same point in space, the location of food. This idea was further developed by Cheng (1988, 1989) in research on landmark use in pigeons. He trained pigeons to find food in a place that maintained a constant relationship with two landmarks. After training, pigeons were tested with the landmark moved further away. Unlike gerbils, the pigeons did not search in two places. They searched in the middle of the line defined by the two positions of the goal as indicated by the landmarks (see Figure 5). Based on these results, Cheng (1989, 1994) argued that the pigeons were guided by a vector which was the average of all the vectors that indicated the position of the goal with respect to the animal.

Geometrical relationships

In 1986, Cheng presented evidence that rats can use geometrical information to locate a hidden goal. The apparatus consisted of a rectangular box placed inside a sound-attenuating box (see Figure 6). The two short sides of the box and one of the long sides were black, while the other long side was white. Distinctive panels showing different visual patterns were placed in each of the box's corners, two of them being scented with different odors (anise and peppermint). The rats were introduced into the box and had to search for hidden food. The food was buried in one corner of the box. Although rats learned to search in the correct location for the food, they made frequent rotational errors. In other words, the rats searched in the corner diagonally across from the one where the food was hidden. These results show that the rats did not identify the food location based on the information provided by the distinctive panels situated in the corners. Cheng (see also Gallistel, 1990) concluded that the rats used the geometrical framework of the box itself. Thus, what the rats learned was to search for food in the corner that had the long arm to the left and the short arm to the right. This would explain why the animals made rotational errors, since the corner diagonally opposite had the same properties. This experiment clearly shows that rats are sensitive to the geometrical relationships of a test environment.

The distribution of two or more landmarks in space also has geometrical properties. However, the importance of landmark geometry varies considerably among species. As we have seen previously, when landmarks were separated so that each one pointed out a different food position (Cheng, 1989), the pigeons searched in the middle of the line defined by these two positions. A possible explanation for these results is that the pigeons searched for food in terms of the geometrical relationship between the two landmarks, a line. However, we have already seen that gerbils behave differently (Collet et al., 1986). In a similar situation they search in two places, each one corresponding to the place that defined the direction and the distance of the goal from each of the two landmarks.

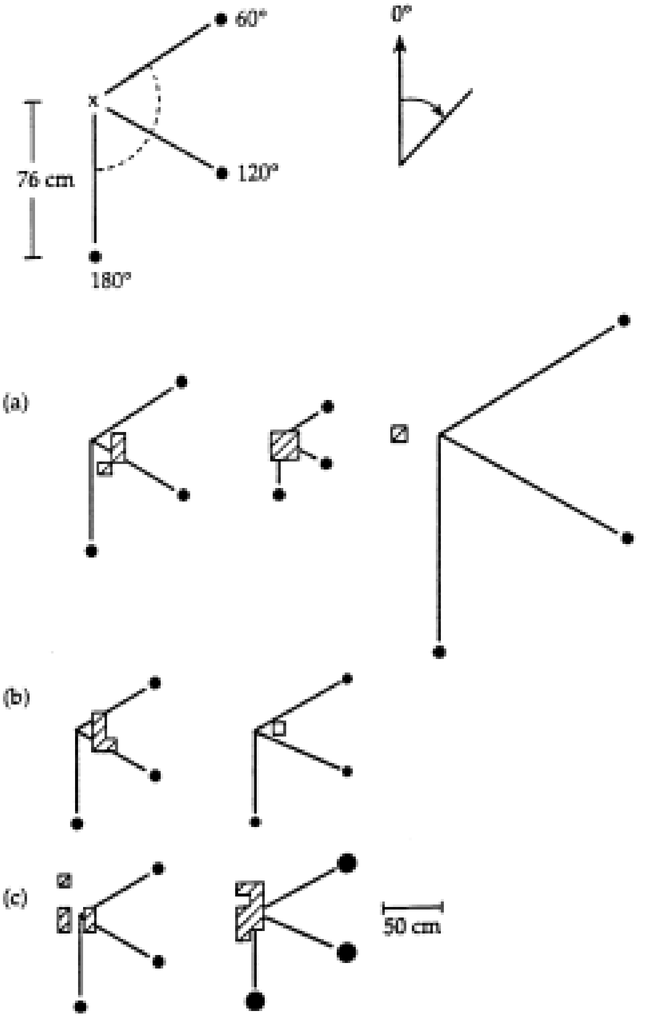

Figure 3. The top diagram shows the angular placements of the three landmarks relative to the goal (x). The lower diagrams show the effects of moving the landmarks closer together or farther apart than during training (a) and the effects of varying the size of the landmarks (b and c). Hatched areas indicate the locations where bees spent the most time searching. From Healy (1998) with permission.

Navigation using information based on the relationship of multiple landmarks. The cognitive map

We have just seen how animals might learn the location of a goal in relation to landmarks. However, animals can learn the position of different objects and its locations with respect to others. Tolman (1948) was the first to propose that animals form sophisticated representations of their environment and called this a *cognitive map*. The results of his experiments with rats in mazes (see Chamizo, 1990; Chamizo, in this edition) led him to suggest that "something like a field map of the environment gets established in the rat's brain" (Tolman, 1948, p.192). Since Tolman introduced the idea of a cognitive map, various forms of evidence have been presented in support of it and theories about the development and neural bases of cognitive maps have been proposed. Although most of the models are based on neurophysiological and neuroanatomical data from the hippocampus, only specific aspects and the use of the cognitive maps will be considered here (for a review of the hippocampus's role in navigation, see Good in this edition).

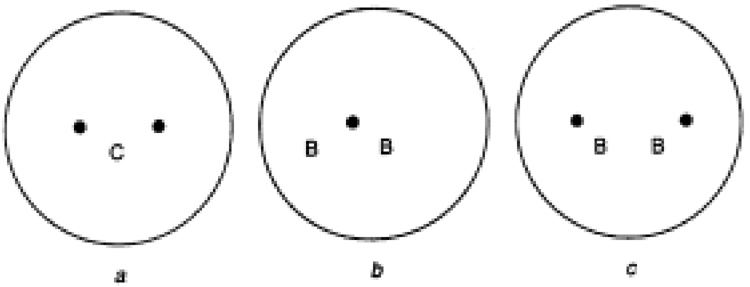

Figure 4. Plane of the test area that Collett et al. (1986) used to study how gerbils use the two landmarks to locate a source of hidden food (C). A circle (to) represents the area that was used during the training. The other two circles represent the place in which they looked for food (B) in the test rehearsals with an only landmark (circle b) or with landmarks most separate that during the training (circle c). From Pearce (1997) with permission.

O'Keefe and Nadel (1978) were the first to present a formal theory of the cognitive map. They define the cognitive map as "the representation of a group of places, some related to others by means of a set of rules of spatial transformation" (pg. 86). When an animal enters a new environment, it forms a representation of the spatial relationships maintained by landmarks or extramaze cues that it perceives from its position. This representation is a place representation. Starting from this initial representation, and as the animal moves around the environment, it begins to incorporate new place representations into the cognitive map. This occurs because of the information coming from the sensory and motor systems with respect to the different distances that the animal perceives; these systems enable space to be represented in a relative way, with reference to the animal. O'Keefe and Nadel called this space relative or egocentric space. Each representation of egocentric space will be incorporated as a place representation within the map, in which the representation of space is absolute, innate and follows a Euclidean metric. Objects are located in cartographic space, but they do not define it: if an object is removed, the space continues to the same. In addition, the animal's motor behavior when moving around the environment is not represented on the map, as it is only instrumental in the map's construction (for a computational approach to this model, see O'Keefe 1991a, 1991b).

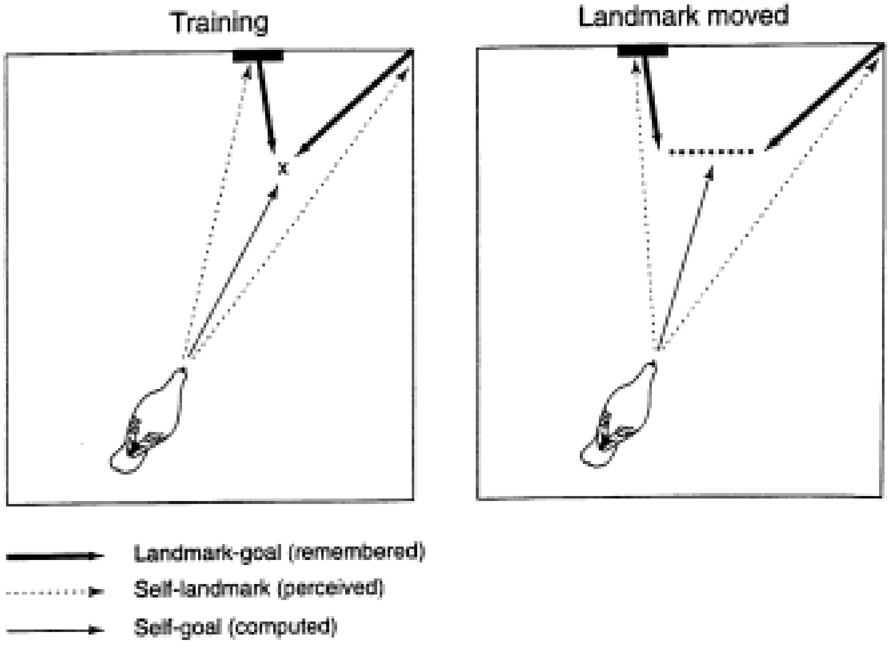

Figure 5. Hypothetical vectors involved in computation of the distance and direction to a goal (x) during training with a conspicuous landmark (black bar). The corner of the search space is treated as a second landmark. The self to landmark and landmark to goal vectors sum to produce the self to goal vector (the distance and direction resulting from summing two vectors is found by placing them head to tail). When the landmark is moved the animal will search somewhere along the dotted line, searching further toward the left the more heavily the black bar landmark is weighted relative to other objects in the box. From Shettleworth (1998) with permission.

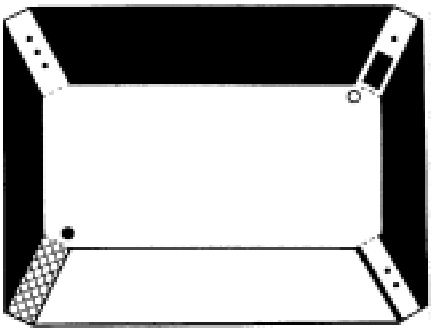

Figure 6. A plain view of the rectangular box used by Cheng (1986). Three walls are black while one is white. Panels differing in visual, tactile, and olfactory characteristics are in the corners. The filled circle represents the location of hidden food. From Cheng (1986) with permission.

When an animal is introduced into a given environment, the landmarks that it perceives will have a certain spatial relationship, and this enables it to locate where it is in the map. No particular landmark is required to locate the animal in the map; any landmark or group of landmarks can be removed without preventing the remaining ones from indicating, on the basis of their relationship, a particular place (O'Keefe and Conway, 1978). Once situated, the next step is locating the goal. When an animal is in a familiar environment, the activation of a place representation will allow it to predict what will appear and where, without the need to move around the environment or to perceive landmarks directly. Thus, the animal will be able to locate the goal in its map and the direction of the goal from its current location. Finally, it only has to choose the most appropriate path, normally the shortest one.

Since Tolman’s (1948) original work, the main characteristic of cognitive maps had already been considered to be their great flexibility. Once an animal has built a map, it can use the information to solve a variety of problems. If animals are introduced into the environment from a new starting point or the previous path is blocked, they will be able to deduce the most direct trajectory from this place to a well-known goal (Morris, 1981; Tolman, Ritchie, and Kalish, 1948).

One of the studies which has presented evidence of a cognitive map in rats has been the work of Morris using a swimming pool (1981). He trained rats in a circular pool full of opaque water, from which they could escape by climbing up onto a platform that was submerged 1 cm below the water level and thus could not be seen by the animals. The platform maintained a fixed position with respect to landmarks or objects in the experimental room. The results showed that the rats learned how to find an object that they could not see, smell or hear, locating their position based on their spatial relationship to landmarks in the experimental room.

There is extensive evidence that rats and others animals use complex relationships of landmarks or extramaze cues to locate a goal (Gould, 1987, 1990; Morris, 1981; Rodríguez, Durán, Vargas, Torres, and Salas, 1994; Suzuki, Augerinos and Black, 1980). As we have seen in the experiment of Morris (1981), rats can swim directly even toward a platform that is completely invisible. In studies of spatial learning in mazes, when rats have learned the location of a goal-box on the basis of extramaze cues in the experimental room, their performance deteriorates if the position of these landmarks is changed (Suzuki et al., 1980), but not when they are rotated or when a number of extramaze cues are removed, even those that are located immediately behind the box-goal (Barnes, Nadel and Honing, 1980; Chamizo, Sterio and Mackintosh, 1985; O'Keefe and Conway, 1978). These results clearly show that the animals learned these tasks based on the spatial relationships between these landmarks.

The most controversial claim of O’Keefe and Nadel’s (1978) theory is that navigation based on a cognitive map (what they call cartographic strategy) is different from and independent of other navigational strategies (called taxon strategies). These researchers argued that taxon learning was associative or incremental whereas they considered cartographic learning occurred in an all-or-nothing way and could be identified with different brain structures, the hippocampus being the structure controlling cartographic learning. Following this claim, a great number of studies aimed at investigating whether cartographic strategy was really different and independent of taxon strategies were carried out. The results failed to support this assumption and although it is assumed that there are different degrees of complexity in solving spatial tasks, these cannot be attributed to different and independent mechanisms (see Chamizo, in this edition).

In 1990, Gallistel also suggested that animals use cognitive maps. However, the definition of cognitive map used here was different to that of O'Keefe and Nadel (1978). For Gallistel, any orientation based on implicitly computing distances and directions is evidence of a cognitive map. Thus, except for navigation based on beacons or proximal cues, all the strategies described above could be considered as evidence of a cognitive map. According to Gallistel, since an animal can only perceive a part of its environment from any one vantage point, the construction of a cognitive map requires the integration of positional information derived from different views of the environment made at different times (Gallistel and Cramer,1996). The construction of a map for navigation involves combining two sorts of position vectors: egocentric vectors which specify the locations of landmarks in a body-centered coordinate system, and geocentric vectors which specify the animal’s position in an earth-centered coordinate system. The egocentric vectors are constituted by the perceived directions and distances of landmarks in the coordinate system, defined with respect to the animal’s body. The geocentric vectors are calculated by path integration and specify the animal’s position in a coordinate system based on the path’s starting point. Gallistell

(1990) suggested that maps are constructed by the egocentric position vector of landmarks being rotated by the geocentric orientation of the animal, and this rotated vector being added to the animal's geocentric position vector (see Figure 7). This process enables the position of notable terrain features perceived at different times and from different points of view to be represented in a common coordinate system, the geocentric system.

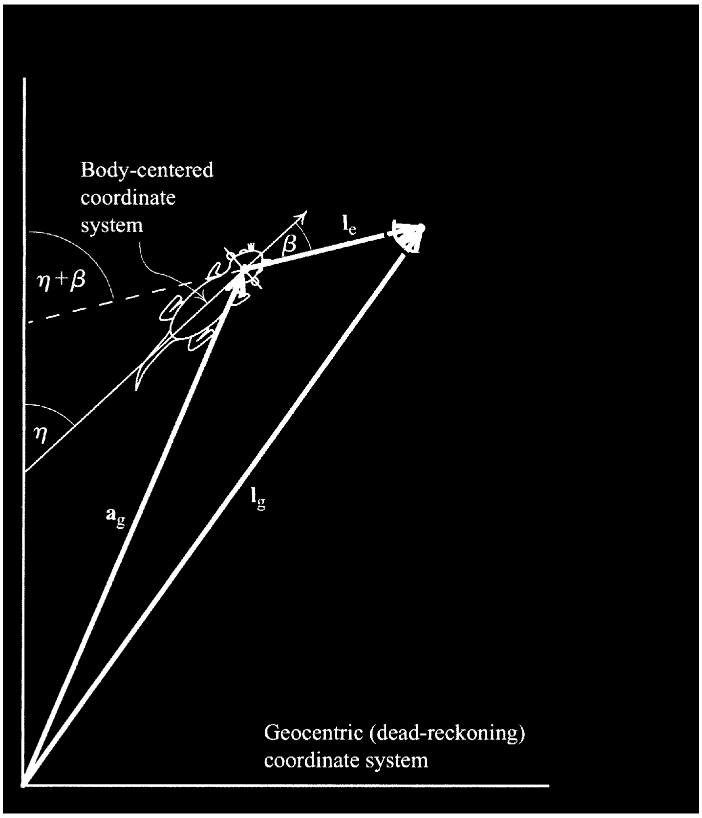

Figure 7. The animal's geocentric position vector is computed by the dead-reckoning mechanism. The egocentric position vector for the landmark – its direction (or bearing, β) and distance from the animal – is computed by the animal's perceptual system. Rotating the egocentric vector by the animal's geocentric orientation (its heading, η) gives a vector of the same length with orientation $\eta+\beta$ (heading+bearing). Adding that vector to the animal's geocentric position vector a_g gives the landmark's position in the geocentric coordinate gramework established by dead reckoning. From Gallistel and Cramer (1996) with permission.

Poucet (1993) presented a model emphasizing a hierarchical organization of space based on the steps required to build cognitive maps. This approach assumes that studying the intermediate stages of spatial learning provides an insight into the various ways in which animals solve spatial problems before reaching the highest level of spatial competence.

Poucet assumes that two types of information are acquired about space: topological information and metric information. He suggests that initial cognitive maps of an environment may take the form of crude topological maps, which then become refined by the acquisition of metric information through exploratory experience with the environment. According to Poucet, the basic units of cognitive maps are place representations. Place representations are abstract products that are based on the collection of local views of the environment from specific locations. It is assumed that the spatial relationships between different places are coded in polar coordinates as vectors, that is, a pairing of information about distances and directions. This enables local charts to be formed which specify the relationships between places and in which vectorial information is initially conveyed by location-dependent reference frameworks. The next step involves the computation of an overall (location-independent) reference direction for each local chart. This would allow the animal to determine direction from any one point to another. Finally, in order to form an overall representation of an environment, local charts are linked together. Poucet (1993) suggested two possible mechanisms for combining local charts. One is via a common or linking place; the other uses a general reference direction common to both areas by which different local charts can be oriented. This final stage in the formation of a global representation re-emphasizes the point that cognitive maps are established gradually and hierarchically through travel and exploration. Topological and metric information are gradually woven together to form an increasingly sophisticated understanding of an animal's environment. One of the most attractive characteristics in Poucet’s (1993) theory is that even at their highest level, cognitive maps cannot be a complete representation of the environment, and there are privileged places inside the map that are more processed than others. This seems to depend on the individual experience within a given environment.

All the above models are based on the existence of an internal representation of an independent absolute space of objects or sensory events, but within which such experiences can be located. Such an internal model does not depend on body orientation but is assumed, in some abstract way, to maintain its orientation with respect to the external world with rotation of the animal. Other models have been presented (Kuipers 1978,1982; McNaughton, 1988; McNaughton, Leonard and Chen, 1989; Leonard and McNaugton, 1990) that differ from the previous models in that they do not postulate the existence of an overall coordinate system. These models are based on simple associative processes that combine current sensory input with motor outputs in order to predict the resulting pattern of sensory inputs. Here, a spatial structure is nothing more than a listing of completely independent events and the local relations that connect them. The notion that space is represented as a linked list of events is called the “local view” hypothesis (McNaughton, 1987, 1988). In these models, cognitive maps consist essentially of the storage of local views of the environment, which are connected together by codifying the representations of the movement (or series of movements) required to go from one local view to another (McNaughton, Leonard, and Chen, 1989). The main criticism of these models has been that they cannot explain the observed behavioral flexibility, for example, planning new trajectories. However, Leonard and McNaughton (1990) have argued that, as with a cognitive map, computations operating on the local-view/movement representation could allow the rat to plan new trajectories between two locations previously reached only on separate occasions from some common point. However, the cognitive map and local view hypotheses would differ in terms of their predictions about the length of time that the computation would take. While in a coordinate system the computation of the path should be independent of the animal's exploratory experience, in the local-view hypothesis the time needed would be related to the minimum length of the series of movements that connects one view to the other. This conclusion is supported by those experimental results which show that limiting the exploration of a specific area reduces the effectiveness of subsequent navigation from this area (Keith and McVety, 1988).

Models have also been proposed that try to explain how animals use complex landmark relationships to locate a goal. Zipser (1986) developed a model for navigation that he called coefficient β. This model requires the codification of relationships between a group of landmarks and the goal. This codification can be carried out when the animal is at the goal and the information can be used later to locate the goal from any location provided the landmarks are visible. However, Zipser's (1986) theory suffers from two major drawbacks. The first is that it requires a minimum of three landmarks for the localization of a fourth point (the goal) and it is known that animals only need two landmarks to find a goal (O'Keefe and Conway, 1978; Prados and Trobalon, 1998; Rodrigo, Chamizo, McLaren, and Mackintosh, 1997). The second drawback is that it requires that the position of each landmark relative to the current position be accurately estimated and this is not always possible. Collett, Carwright and Smith (1986) and Collett (1987) demonstrated that rodents were able to navigate with one proximal landmark in conjunction with distal cues that served to establish the animals orientation in that environment. These two drawbacks of the model have been overcome in a later reformulation by McLaren (1995), enabling the model to be applied with only two landmarks, even when one of these is so far away that it is difficult to carry out a precise estimate of its coordinates. These models are appropriate for those tasks that require goal localization with landmarks that can be perceived both from the starting point and the goal location. However, it is not clear that they can be used for tasks in which the landmarks that define the goal's position are not directly perceived from the starting point.

Cognitive map or global representation of space?

Historically, the concept of a spatial cognitive map has been important because, as Tolman (1948) argued, it suggests that animals do not merely base their actions on specific stimulus-response associations, but that they also internally reorganize acquired spatial information to form cognitive representations of the environment. One important property of such representations is that they allow animals to react to stimuli that are not immediately present because the relationship of such stimuli to those actually perceived is maintained in a cognitive representation, in other words, a map. However, as Poucet (1993) points out, demonstrating that an animal forms some internal pattern of its environment is not sufficient to prove the cognitive map hypothesis. In fact, the construction of a spatial representation implies that the information sequentially acquired (as a result of the animal's movements) must be integrated into a map-like structure allowing simultaneous access to all relevant information. An additional step is to show that such information can be manipulated in order to produce novel solutions to novel spatial problems.

Whether or not animals have a cognitive map similar to an overall representation of space is something that has been repeatedly debated and has led to much controversy (Shettelworth, 1998). The justification for the postulation of a cognitive map has been based mainly on animal's ability to take novel short-cuts. But as Bennet (1996) points out, there are simpler explanations of apparent novel short-cutting that must be ruled out before one can conclude, as O'Keefe and Nadel do, that animals have a cognitive map. The first explanation that must be ruled out is that based on the fact that the apparently novel short-cut is not truly novel. The second alternative to rule out is that animals are not using path integration which, as has already be seen, allows them to return to the starting point of a journey in a direct path.The third alternative to consider is the possibility that familiar landmarks are being recognised from a new angle, followed by movement towards them (as for example Zipser, 1986; McLaren, 1995). However, in a review of existing data, Bennet (1996) failed to find any case in which the three alternatives had been ruled out. Consequently, Bennett (1996) argued that "no animals have been shown to have a cognitive map" (p. 222).

Furthermore, Benhamou (1997a) argued that there is no evidence which demonstrates that an animal is really able to mentally build up a global representation of space. He presented an alternative process in which, contrary to what happens in a global representation of space, the animal is considered not to know the spatial relationships between important places of the territory, regardless of its location. He states "it is only when the animal is standing in the vicinity of a given important place that the directions and distances to the other important places may be recalled from memory in response to the current view of the local environment" (Benhamou, 1997a, p. 159).

In conclusion, it has been seen that animals can use different orientation mechanisms and different strategies to find the location of a goal. Whether an animal uses one or the other depends on its sensory abilities and the conditions imposed by the environment. However, the suggestion that there is a cognitive map similar to a global representation of space seems to be unjustified given that simpler mechanisms are able to explain the experimental results. It remains to be seen if future research will provide experimental data in support of it.

REFERENCES

Able, K.P. (1980). Mechanisms of orientation, navigation, and homing. In S.A. Gauthreaux (Ed.), *Animal migration, orientation, and navigation.* London: Academic Press, 283-373.

Able, K.P. (1996). Large-scale navigation. *Journal of Experimental Biology, 199*, 1-2.

Able, K.P. and Able, M.A. (1996). The flexible migratory orientation system of the savannah sparrow (*Passerculus sandwichensis*). *Journal of Experimental Biology, 199*, 3-8.

Baker, R.R. (1968). Sun orientation during migration in some British butterflies. *Proc. R. Entomol. Soc. London, Ser. A, 143*, 89-95.

Baker, R.R. (1969). The evolution of the migratory habit in butterflies. *Journal of Animal Ecology*, 703-746.

Baker, R.R. (1981). *Human navigation and the sixth sense*. London: Hodder and Stoughton.

Bardunias, P.M. and Jander, R. (2000). Three dimensional path integration in the house mouse (*Mus domestica*). *Naturwissenschaften, 87*, 532-534.

Barnes, C.A., Nadel, L., and Honing, W.K. (1980). Spatial memory deficit in senescent rats. *Canadian Journal of Psychology, 34*, 29-39.

Barnwell, F.H. (1965). An angle sense in the orientation of a millipede. *Biological Bulletin, 128*, 33-50.

Benhamou, S. (1997a). On systems of reference involved in spatial memory. *Behavioural Processes, 40*, 149-163.

Benhamou, S. (1997b). Path integration by swimming rats. *Animal Behaviour, 54*, 321-327.

Benhamou, S., Sauvé, J.P., and Bovet, P. (1990). Spatial memory in large scale movements: Efficiency and limitations of the egocentric coding process. *Journal of Theoretical Biology, 145*, 1-12.

Benhamou, S. and Séguinot, V. (1995). How to find one's way in the labyrint of path integration models. *Journal of Theoretical Biology, 174*, 463-466.

Bennett, A.T.D. (1996). Do animals have cognitive maps?. *Journal of Experimental Biology, 199*, 219-224.

Biegler, R. (2000). Possible uses of path integration in animal navigation. *Animal Learning and Behavior, 28*, 257-277.

Cartwright, B.A. and Collett, T.S. (1982). How honey bees use landmarks to guide their return to a food source. *Nature, 295*, 560-564.

Cartwright, B.A. and Collett, T.S. (1983). Landmark learning in bees: Experiments and models. *Journal of Comparative Physiology, 151*, 521-543.

Cartwright, B.A. and Collett, T.S. (1987). Landmark maps for honeybees. *Biological Cybernetics, 57*, 85-93.

Chamizo, V.D. (1990). Ratas en el laberinto: memoria espacial y mapas cognitivos. En L. Aguado (Ed.), *Cognición Comparada.* Madrid: Alianza Editorial, 177-199.

Chamizo, V.D., Sterio, D., and Mackintosh, N.J. (1985). Blocking and overshadowing between intra-maze and extra-maze cues: A test of the independence of locale and guidance learning. *Quarterly Journal of Experimental Psychology, 37B*, 235-253.

Cheng, K. (1988). Some psychophysics of the pigeon's use of landmarks. *Journal of Comparative Physiology, 162*, 815-826.

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes, 15*, 366-375.

Cheng, K. (1994). The determination of direction in landmark-based spatial search in pigeons: A further test of the vector sum model. *Animal Learning and Behavior, 22*, 291-301.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149-178.

Collett, M., Collett, T.S., and Wehner, R. (1999). Calibration of vector navigation in desert ants. *Current Biology, 9*, 1031-1034.

Collett, T.S. (1987). The use of visual landmarks by gerbils: Reaching a goal when landmarks are displaced. *Journal of Comparative Physiology A, 160*, 109-113.

Collett, T.S. (1992). Landmark learning and guidance in insects. *Phil. trans. R. Soc. Lond B, 337*, 295-303.

Collett, T.S. (1996). Insect navigation *en route* to the goal: multiple strategies on the use of landmarks. *Journal of Experimental Biology, 199*, 227-235.

Collett, T.S., Cartwrigth, B.A., and Smith, B.A. (1986). Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Physiology A, 158*, 835-851.

D'Arms, E. and Griffin, D.R. (1972). Balloonists' reports of sounds audible to migration birds. *Auk, 89*, 269-279.

Darwin, C. (1873). Origin of certain instincts. *Nature, 7*, 417-418.

Deutsch, J.A. (1960). *The structural basic of behavior*. Cambridge: Cambridge University Press.

Emlen, S.T. (1967a). Migratory orientation in the indigo bunting, *Passerina cyanea.* I. Evidence for use of celestial cues. *Auk, 84*, 309-342.

Emlen, S.T. (1967b). Migratory orientation in the indigo bunting, *Passerina cyanea. Auk, 84*, 463-489.

Emlen, S.T. (1969). Bird migration. Influence of physiological state upon celestial orientation. *Science, 165,* 716-718.

Emlen, S.T. (1970). Celestial rotation: Its importance in the development of migratory orientation. *Science, 170*, 1198-1201.

Emlen, S.T. (1975). Migration, orientation and navigation. In D.S. Farner and J.R. King (Eds.), *Avian Biology,*Vol 5. New York: Academic Press, 129-219.

Enright, J.T. (1972). When the beachhopper looks at the moon: The moon compass hypothesis. In S.R. Galler, K. Schmidt-Koenig, G.J. Jacobs, R.E. Bellevile (Eds.), *Animal orientation and navigation*. NASA US Government Printing Office, Washington, DC, SP- 262, 523-555.

Etienne, A.S., Hurni, C., Maurer, R., and Séguinot, V. (1991). Twofold path integration during hoarding in the golden hamster?. *Ethology, Ecology, and Evolution, 3*, 1-11.

Etienne, A.S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J. and Séguinot, V. (1998). Navigation through vector addition. *Nature, 396*, 161-164.

Etienne, A.S., Maurer, R., and Saucy, F. (1988). Limitations in the assessment of path dependent information. *Behaviour, 106*, 81-111.

Etienne, A.S., Maurer, R., Saucy, F., and Teroni, E. (1986). Short distance homing in the golden hamster after a passive outward journey. *Animal Behaviour, 39*, 696-715.

Etienne, A.S., Maurer, R., and Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology, 199*, 201-209.

Etienne, A.S., Teroni, E., Maurer, R., Portenier, V., and Saucy, F. (1985). Short distance homing in a small mammal: The role of exteroceptive cues and path integration. *Experientia, 41*, 122-125.

Fujita, N., Klatzky, R.L., Loomis, J.M., and Golledge, R.G. (1993). The encoding-error model of pathway completion without vision. *Geographical Analysis, 25*, 295-314.

Fujita, N., Loomis, J.M., Klatzky, R.L., and Golledge, R.G. (1990). A minimal representation for dead-reckoning navigation: Updating the homing vector. *Geographical Analysis, 22*, 326-335.

Gallistel, C.R. (1990). *The organization of behaviour*. New York: Wiley.

Gallistel, C.R. and Cramer, A.E. (1996). Computations on metric maps in mammals: Getting oriented and choosing a multi-destination route. *Journal of Experimental Biology, 199*, 211-217.

Gould, J.L. (1982). The map sense of pigeons. *Nature, 296*, 205-211.

Gould, J.L. (1987). Landmark learning by honey bees. *Animal Behaviour, 35*, 26-34.

Gould, J.L. (1990). Honey bee cognition. *Cognition, 37*, 83-103.

Griffin, D.R. (1969). The physiology and geophysics of bird navigation. *Quarter. Rev. Biol. 44*, 255-276.

Gwinner, E. (1972). Endogenous timing factors in bird navigation. In S.R. Galler, K. Smichmidt-Koenig, G.J. Jacobs, and R.E. Belleville (Eds.), *Animal orientation and navigation*. Washington, NASA Spec. Publi. 262, 321-338.

Hartmann, G. and Wehner, R. (1995). The ant's path integration system: A neural architecture. *Biological Cybernetics, 73*, 483-497.

Healy, S. (1998) (Ed.). *Spatial representation in animals*. Oxford: Oxford University Press.

Herrnkind, W.F, and Kanciruk, P. (1978). Mass migration of spiny lobster, *Panulirus argus* (Crustacea:Palinuridae); synopsis and orientation. In K. Schmidt-Koenig and W.T. Keeton (Eds.), *Animal migration, navigation, and homing*. Berlin/New York: Springer-Verlag, 430-439.

Hoffmann, G. (1984). Orientation behaviour of the desert woodlouse *Hemilepistus reaumuri*: adaptations to ecological and physiological problems. *Symposium of the Zoological Society of London, 53*, 405-422.

Jander, R. (1957). Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa). Zeitschrift für vergleichende Physiologie, 40*, 162-238.

Keeton, W.T. (1969). Orientation by pigeons: is the sun necessary? *Science, 165*, 922-928

Keeton, W.T. (1974). The orientational and navigational basis of homing in birds. *Adv. Study Behav., 5*, 47-132.

Keith, J.R. and McVety, K.M. (1988). Latent place learning in a novel environment and the influences of prior training in rats. *Psychobiology, 16*, 146-151.

Kramer, G. (1949). Über richtungstendenzen bei der nächtlichen zugunruhe gekäfigten vögel. In E. Mayr and E. Schüz (Eds.), *Ornithologie als biologische Wissenschaft*, Heildelberg: Winter, 269-283.

Kramer, G. (1950). Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. *Naturwissenschaften, 37*, 377-378.

Kramer, G. (1951). Eine neve methode zur erforsching der zugorientierung und die bisher damit erzielten ergebnisse. *Proce. Xth. Inter. Ornithol. Congre.*, Upsala, 271-280.

Kramer, G. (1953). Die sonnenorientierung de vogeln. *Versh. dt. zool. ges.*, 72-84.

Kreithen, M.L. (1978). Sensy mecanisms for animal orientation- Can any new ones be discovered? In K. Schmidt-Koenig and W.T. Keeton (Eds.), *Animal migration, navigation, and homing*. Berlin/New YorK: Springer-Verlag, 25-34.

Kreithen, M.L. and Keeton, W.T. (1974). Detection of polarized light by the homing pigeon, *Columbia livia. Journal of Comparative Physiology, 89*, 83-92

Kuipers, B.J. (1978). Modeling spatial knowledge. *Cognitive Science, 2*, 129-153.

Kuipers, B.J. (1982). The "map in the head" metaphor. *Environmental Behaviour, 14*, 202-220.

Leggett, W.C. (1977). The ecology of fish migrations. *Annu Rev Ecol Syst., 8*, 285-308.

Leonard, B. and McNaughton, B.L. (1990). Spatial representation in the rat: Conceptual, behavioral and neurophysiological perspectives. In R.P. Kesner and D.S. Olton (Eds.), *Neurobiology of comparative cognition*. Hillsdale, NJ: Erlbaum, 363-422.

Margules, J. and Gallistel, C.R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning and Behavior, 16*, 404-410.

Matthews, G.V.T. (1961). "Nonsense" orientation in *mallard anas platyrhynchus* and its relation to experiments and bird navigation. *Ibis, 103*, 211-230.

Matthews, G.V.T. (1968). *Bird Navigation.* Cambridge: Cambridge University Press.

Maurer, R. (1998). A connectionist model of path integration with and without a representation of distance to the starting point. *Psychobiology, 26*, 21-35.

Maurer, R. and Schreter, Z. (1990). Sensori-motor spatial learning in connectionist artificial organisms. In F. Heylighen, E. Rosseel, and F. Demeyere (Eds.), *Self-steering and cognition in complex systems: Towards a new cybernetics.* New York: Gordon and Breach Science Publishers, 160-182.

Maurer, R. and Séguinot, V. (1995). What is modelling for? A critical review of the models of path integration. *Journal of Theoretical Biology, 175*, 457-475.

McLaren, I.P.L. (1995). A better beta model of navigation. *British Journal of Mathematical and Statistical Psychology, 48*, 51-55.

McNaughton, B.L. (1987). Neural association of movement and space: Preliminary steps toward a noncartographic theory of spatial representation and learning. *Neuroscience Letters, (Suppl. 29*), S143-S144.

McNaughton, B.L. (1988). Neural mechanisms for spatial computation and information storage. In L. Nadel, L.A. Cooper, P. Culicover, and R.M. Harnish (Eds.), *Neural connections and mental computations*. Cambridge: MIT Press, 285-350.

McNaughton, B.L., Barnes, C.A., Gerrard, J.L., Gothard, K., Jung, M.W., Knierim, J.J., Kudrimoti, H., Qin, Y., Skaggs, W.E., Suster, M., and Weaver, K.L. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology, 199,* 173-185.

McNaughton, B.L., Leonard, B., and Chen, L.L. (1989). Cortical-hippocampal interactions and cognitive mapping: A hypothesis based on reintegration of the parietal and inferotemporal pathways for visual processing. *Psychobiology, 17*, 230-235.

Merkel, F.W. and Fromme, H.G. (1958). Untersuchungen über das Orientierungsvermögen nächtlich ziehender Rotkehlchen, Erithacus rubecula. *Naturwissenschaften, 45*, 499-500.

Merkel, F.W., Fromme, H.G., and Wiltschko, W. (1964). Nichtvisuelles orientierungsvermögen bei nächtlich zugunruhigen rotkelchen. *Vogelwarte, 22*, 168-173.

Merkel, F.W. and Wiltschko, W. (1965). Magnetismus und richtungs finden zugunruhigen rotkelchen (*Erithacus rubecula*). *Vogelwarte, 23*, 71-77.

Merkel, F.W. and Fischer-Klein, K. (1973). Winkelkompensarion bei Zwergwacnteln (Excalfactoria chinensis) [Angle compensation in Indian blue quails (Excalfactoria chinensis)]. *Die Vogelwarte, 27*, 39-50.

Mittelstaedt, H. (1985). Analytical cybernetics of spider navigation. In F.G. Barth (Ed.), *Neurobiology of Arachnids.* Berlin: Springer-Verlag, 298-316.

Mittelstaedt, H. and Mittelstaedt, M.-L. (1973). Mechanismen der Orientierung ohne richtende Aussenreize. *Fortschr. Zool., 21*, 46-58.

Mittelstaedt, H. and Mittelstaedt, M.-L. (1982). Homing by path integration. In F. Papi and H.G. Wallraff (Eds.), *Avian navigation.* Berlin: Springer-Verlag, 290-297.

Mittelstaedt, M.-L. and Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturweissenschaften*, *67*, 566.

Möller, R., Maris, M, and Lambrinos, D. (1999). A neuronal model of landmark navigation in insects. *Neurocomputing, 26-27*, 801-808.

Morris, R.G.M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation, 12*, 239-260.

Müller, M. and Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis. Proceedings of the National Academy of Sciences USA, 85*, 5287-5290.

Müller, M. and Wehner, R. (1994). The hidden spiral: Systematic search and path integration in desert ants, *Cataglyphis fortis*. *Journal of Comparative Physiology A*, 175, 525-530.

O'Keefe, J. (1991a). The hippocampal cognitive map and navigational strategies. In J. Paillard (Ed.), *Brain and Space*. London: Oxford University Press, 273-295.

O'Keefe,J. (1991b). An allocentric spatial model for the hippocampal cognitive map. *Hippocampus, 1*, 230-235.

O'Keefe, J. and Conway, D.H. (1978). Hippocampus place units in the freely moving rat: Why they fire where they fire. *Experimental Brain Research, 31*, 573-590.

O'Keefe, J. and Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Claredon Press.

Papi, F. and Pardi, L. (1963). On the lunar orientation of sandhoppers (amphipoda talitridae). *Biol. Bull (Woods Hole, Mass), 124*, 97-105.

Papi, F., Ioalé, P., Fiaschi, V., Benvenuti, S., and Baldaccini, N.E. (1978). Pigeon homing: Cues detected during the outward journey influence initial orientation. In K. Schmidt-Koenig and W.T. Keeton (Eds.), *Animal migration, navigation, and homing*. Springer-Verlag, Berlin and New York, 65-77.

Pearce, J.M. (1997). *Aprendizaje y cognición*. Barcelona: Ariel.

Perdeck, A.C. (1958). Two types of orientation in migrating starlings *Sturnus vulgaris* and chaffinches *Fringilla coelebs*, as revealed by displacement experiments. *Ardea, 46*, 1-37.

Poucet, B. (1993). Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychological Review, 100*, 163-182.

Prados, J. and Trobalon, J.B. (1998). Locating an invisible goal in a water maze requires at least two landmarks. *Psychobiology, 26*, 42-48.

Redhead, E.S., Roberts, A., Good, M., and Pearce, J.M. (1997). Interaction between piloting and beacon homing by rats in a swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes, 23*, 340-350.

Redish, A.D. and Touretzky, D.S. (1997). Cognitive maps beyond the hippocampus. *Hippocampus, 7*, 15-35.

Richardson, W.J. (1978). Reorientation of nocturnal landbird migrants over the Atlantic Ocean near Nova Scotia in autumn. *Auk, 95*, 717-732.

Roberts, A.D.L. and Pearce, J.M. (1998). Blocking in the Morris swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes, 25*, 225-235.

Rodrigo, T., Chamizo, V.D., McLaren, I.P.L. and Mackintosh, N.J. (1997). Blocking in the spatial domain. *Journal of Experimental Psychology: Animal Behavior Processes, 23*, 110-118.

Rodríguez, F., Durán, E., Vargas, J.P., Torres, B., and Salas, C. (1994). Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Animal Learning and Behavior, 22*, 409-420.

Royce, W.F., Smith, L.S., and Hartt, A. (1968). Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. *Fishery Bull. Fish Wildl. Serv. U.S., 66*, 441-462.

Samsonovich, A. and McNaughton, B.L. (1997). Path integration and cognitive mapping in a continuous attractor neural network. *Journal of Neuroscience, 17*, 5900-5920.

Santschi, F. (1911). Observations et remarques critiques sur le mécanisme de l'orientation chez les fourmis. *Rev. Suisse Zool, 19*, 305-338.

Sauer, E.G.F. (1957). Die sternenorientierung nächtlich ziehender grasmücken (*Sylvia atricapilla, borin and curruca*). *Zeit. Tierspsychol., 14*, 29-70.

Sauer. E.G.F. (1961). Further studies and the stellar orientation of nocturnally migratory birds. *Psychol. Forsch., 26*, 224-244.

Sauer, E.G.F. and Sauer, E.M. (1960). Star navigation of nocturnal migrating birds. Cold Spring Harbor Symp. *Quant. Biol., 25*, 463-473.

Schmidt-Koenig, K. (1960). Internal clocks and homing, In L. Frisch (Ed.), *Biological clocks*. Cold Spring Harbor, NY: The Biological Laboratory, 389-393.

Schmidt-Koenig, K. (1975). *Migration and homing in animals*. Berlin/New YorK: Springer-Verlag.

Schmidt, I., Collett, T.S., Dillier, F.X., and Wehner, R. (1992). How desert ants cope with enforced detours on their way home. *Journal of Comparative Physiology A, 171*, 285-288.

Séguinot, V., Maurer, R., and Etienne, A.S. (1993). Dead-reckoning in a small mammal: The evaluation of distance. *Journal of Comparative Physiology A, 173*, 103-113.

Séguinot, V., Cattet, J., and Benhamou, S. (1998). Path integration in dogs. *Animal Behavior, 55*, 787-797.

Shettleworth, S.J. (1998). *Cognition, evolution and behavior*. Oxford: Oxford University Press.

Suzuki, S., Augerinos, G., and Black, A.H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation, 11*, 1-18.

Tolman, E.C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*, 189-208.

Tolman, E.C., Ritchie, B.F., and Kalish, D. (1946). Studies in spatial learning: I. Orientation and short-cut. *Journal of Experimental Psychology, 36*, 13-24.

Touretzky, D.S. and Redish, A.D. (1996). Theory of rodent navigation based on interacting representations of space. *Hippocampus, 6*, 247-270.

von Frisch, K. (1949). Die Polarisation des Himmelslichts als orienterender factor bei den tanzu. *Experientia, 5*, 142-148.

von Frisch, K. (1950). Diesonne als kompas im leben der bienen. *Experientia, 6*, 210-221.

von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, Mass.: Belknap Press of Harvard University Press.

von Helversen, O. and Edrich, W. (1974). Der Polarisationsempfänger im Bienenauge: ein Ultraviolettrezeptor. *J. Com Physiol., 94*, 33-47.

von Saint Paul, U. (1982). Do geese use path integration for walking home?. In F. Papi and H.G. Wallraff (Eds.), *Avian navigation*. Berlin: Springer-Verlag, 298-307.

Wallraff, H.G. (1974).*Das Navigationssystem der Vogel*. Oldenbourg, Munich and Vienna.

Wan, H.S., Touretzky, D.S., and Redish, A.D. (1994). Towards a computational theory of rat navigation. In M. Mozer, P. Smolensky, D. Touretzky, J. Elman, and A. Weigend (Eds.), *Proceedings of the 1993 Connectionist Models Summer School*. Hillsdale, NJ: Lawrence Erlbaum Associates, 11-19.

Waterman, T.H. (1966). Systems analysis and the visual orientation of animals. *American Science, 54*, 15-45.

Wehner, R. (1992). Arthropods. In F. Papi (Ed.), *Animal homing*. London: Chapman and Hall, 45-144.

Wehner, R. and Flatt, I. (1972). The visual orientation of desert ants, *Cataglyphis bicolor*, by means of terrestrial cues. In R. Wehner (Ed.), *Information Processing in the Visual Systems of Arthropods*. Berlin/Heidelberg/New York: Springer, 295-302.

Wehner, R. and Räber, F. (1979). Visual spatial memory in desert ants, *Cataglyphis bicolor*. *Experientia, 35*, 1569-1571.

Wehner, R. and Srinivasan, M.V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of Comparative Physiology A, 142*, 315-338.

Wehner, R. and Wehner, S. (1986). Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. *Monitore Zool. Ital., 20*, 309-331.

Wehner, R. and Wehner, S. (1990). Insect navigation: use of maps or Ariadne's thread?. *Ethology, Ecology, and Evolution, 2*, 27-48.

Wiltschko, W. and Wiltschko, R. (1972). Magnetic compass of European Robins. *Science, 176*, 62-64.

Wiltschko, W. and Wiltschko, R. (1996). Magnetic orientation in birds. *Journal of Experimental Biology, 199*, 29-38.

Wittmann, T. and Schewegler, H. (1995). Path integration- a network model. *Biological Cybernetics, 73*, 569-575.

Yeagley, H.L. (1947). A preliminary study of a physical basis of bird navigation. *Journal of Applied Physiology, 18*, 1035-1063

Yeagley, H.L. (1951). A preliminary study of a physical basis of bird navigation II. *Journal of Applied Physiology, 22*, 746-760.

Zipser, D. (1986). Biologically plausible models of place recognition and goal location. In J.L. McClelland and D.E. Rumelhart (Eds.), *Parallel Distributed Processing, II.* Cambridge, M.A.: Bradford Books, 432-470.