A comparative analysis of spatial memory processes

Simon Benhamou *, Bruno Poucet
CNRS-LNC, 31 Chemin J. Aiguier, F-13402 Marseille cedex 20, France
Accepted 2 December 1994

Abstract

This paper reviews spatial memory processes in three highly evolved taxa: hymenoptera, birds and mammals. In these three taxa, the goal location can be memorized egocentrically as a vector specifying the head-referred direction and the distance to the goal, and/or exocentrically as a view specifying the spatial layout of the surrounding landmarks perceived by the animal when standing at the goal. The egocentric coding process requires a path-integration mechanism to update the memorized goal location as a function of the animal's current position. Changes of direction are estimated allothetically (by reference to an external compass) in hymenoptera, idiothetically (on the basis of internal movement-related information) in mammals, and probably in both ways in birds. Computer simulations have shown that path-integration is very sensitive to random errors occurring in idiothetic but not in allothetic estimations. When using the exocentric coding process, hymenoptera store the bearings and angular sizes of landmarks in a compass-oriented colour snapshot taken at the goal. They may then return to the goal by moving so as to reduce the discrepancy between the current view of landmarks and the memorized snapshot. In mammals, this process can be accounted for by a neurobiologically plausible model which highlights the fundamental role of exploration of the environment. The way this process is implemented in birds is less clear.

Keywords: Bird; Hymenoptera; Mammal; Model; Spatial memory

1. Introduction

Some animals are able to memorize locations of shelters and food sources. They can therefore restrict their movements around these locations, in order to be more efficient in foraging or escaping predators. The evolution of spatial memory processes is therefore linked to the emergence of home range. Thus, although they are also found in more primitive taxa, spatial memory processes are most efficient in highly evolved taxa such as mammals, birds and hymenoptera. Beyond the advantages of

* Corresponding author.
possessing a well-established home range in terms of foraging or escaping predators, a considerable evolutionary pressure to develop very efficient spatial memory processes is brought to bear on these three taxa by breeding. In most mammal species, the young is not able to follow its mother during the first weeks following birth. The lactating female therefore returns to her den regularly to nurse her pups. In hymenoptera and most bird species, adults collect food in the environment and bring it back to the nest to feed the young. Even in these bird species in which chicks are able to leave the nest just after hatching, parents must return regularly to the nest from laying to hatching to sit on their eggs. It is therefore crucial for these animals to memorize the home location to return to it as directly as possible after a foraging trip.

This paper focuses on the similarities and differences of the spatial memory processes in mammals, birds, and hymenoptera. At the theoretical level, the location of a hidden place to which an animal intends to return (the goal) can be memorized as an egocentric (site-independent) coding or as an exocentric (site-dependent) coding. The egocentric coding process enables the animal to memorize the goal location in relation to its current position (location and orientation). The exocentric coding process enables the animal to memorize the goal location in relation to the spatial layout of landmarks. Both types of processes have been convincingly demonstrated in these three taxa. However, the underlying mechanisms are somewhat different.

2. The egocentric coding process

The egocentric coding process is used by an animal to memorize the goal location as a vector that specifies the head-referred direction of the goal, and the distance between its current location and the goal location. This process involves a path-integration mechanism by which the moving animal updates the memorized goal location using route-based information, that is information about its own movements. This ability to keep track of the goal location during movements has been convincingly demonstrated in mammals (Mittelstaedt and Mittelstaedt, 1980, 1982; Etienne et al., 1985, 1986, 1988, 1991; Séguinot et al., 1993), birds (Von Saint Paul, 1982) and hymenoptera (Von Frisch, 1967; Wehner and Räber, 1979; Wehner and Wehner, 1986, 1990; Müller and Wehner, 1988; Schmidt et al., 1992), and also in some other arthropods (see references in Benhamou et al., 1990). Several mathematical models have been developed to account for it (see Benhamou and Séguinot, 1995, and Maurer and Séguinot, 1995).

Animals obviously update the memorized goal location using approximate neural computations rather than solving the problem mathematically in a complete form. In fact, very little is known in this field. In mammals, the caudate nucleus seems to be involved in this process (Potegal, 1972, 1982). Nervous systems of hymenoptera and of vertebrates probably work in very different ways. Systematic errors in goal direction estimates may appear in experimental procedures constraining animals such as ants (Wehner and Wehner, 1986; Müller and Wehner, 1988), hamsters (Séguinot et al., 1993) or dogs (V. Séguinot, unpublished results) to take two-part (L-shaped) outward paths. These systematic errors may be due to an overestimation of the virtual motion parallax of the memorized goal location during animal's translations (Benhamou and Séguinot, 1995). This type of error, evidenced in simple paths, is likely to provide insights on the way the nervous system updates the memorized goal location (Maurer and Séguinot, 1995). In natural conditions, however, movements are much more complex, incorporating numerous changes of direction. In these conditions, neural solutions in hymenoptera and
vertebrates should be reliable approximations of the mathematically correct solution, because natural selection should have improved the neural computing procedures during evolution. Nevertheless, the memorized goal location may differ from the actual goal location because of random estimation errors in route-based information. Consequently, in natural conditions, the updating mechanism should produce a resultant random error but no systematic error.

We have studied the efficiency and limitation of the egocentric coding process using computer simulations (Benhamou et al., 1990). The model animal performs a random search path with a given sinuosity, and memorizes the location of the starting point in relation to its own position. The path is modelled as a sequence of steps (translations) alternating with changes of direction (rotations). The updating mechanism is then modelled using recurrent formula by which the egocentric vector specifies the memorized location after n + 1 steps \((\omega_{n+1};D_{n+1})\) as a function of its previous value computed after n steps \((\omega_n;D_n)\). The route-based information used by the updating mechanism is provided by the measures of the last change of direction \((\alpha_n)\) and of the length of the last step \((P_{n+1})\) made by the animal (Fig. 1). The formulas used to model the updating mechanism are mathematically right, so that no systematic error can occur. Random estimation errors, however, affect either translations or rotations. The memorized location is therefore subject to a resultant random error which tends to increase during the movement because of the recurrent nature of the egocentric coding process. The bivariate statistical distribution of the memorized location is circular and centred on the starting point of the path, and its standard deviation (expressed in the same unit as step lengths) constitutes an accurate measure of the resultant random error.

Results of computer simulations can be summarized as follows (Benhamou et al., 1990):

1. When errors occur only in step length estimations, the accuracy of the egocentric coding remains very high. The resultant random error is proportional to the amount of estimation errors and to the square root of the path length, but does not depend on the path sinuosity. It emerges that the egocentric coding process is not very sensitive to translation estimation errors. Neither in vertebrates nor in hymenoptera do we know of any sensory mechanism able to accurately measure translations, which are probably roughly measured on the basis of proprioceptive information. Computer simulations highlight that an accurate mechanism for measuring translations is not necessary to memorize the goal location with a good accuracy.
(2) When errors occur only in estimations of changes of direction, the accuracy of the egocentric coding depends on the way these estimations are made: either idiothetically, i.e. directly on the basis of internal movement-related information, or allothetically, i.e. indirectly by reference to an external compass (Mittelstaedt and Mittelstaedt, 1982). (a) If rotations are measured idiothetically, the accuracy declines quickly. In most cases, the resultant random error is approximately equal to the product of the path length and the amount of estimation errors, and depends on the path sinuosity only to a slight extent. (b) If rotations are measured allothetically, the accuracy remains fairly good. The resultant random error is approximately proportional to the amount of estimation errors and to the square root of the path length, and inversely proportional to the path sinuosity.

(3) Whichever way rotations are measured (idiothetically or allothetically), translation and rotation estimation errors affect the accuracy of the egocentric coding independently (the variances of the two resultant random errors are additive).

Consequently, computer simulations suggest that memorizing the goal location on the basis of idiothetic estimation of rotations will be accurate only if rotations are very accurately estimated, or if the outward path involves a small amount of rotations. In contrast memorizing the goal location on the basis of allothetic estimation of rotations will be accurate over considerable distances involving many rotations. Experimental evidence confirms this point. Mammals measure rotations idiothetically, using information streaming from the vestibular and other proprioceptive systems and possibly from the visual flow. Etienne et al. (1988) have demonstrated that hamsters moving in the darkness are unable to home after more than 3 to 5 full turns. This limitation inherent to the homing process based on idiothetic estimations of changes of direction had been previously pointed out by Barlow (1964), Mittelstaedt and Mittelstaedt (1982) and Potegal (1982). In an experiment on human beings, blindfolded subjects were asked to perform two-part (L-shaped) outward paths (Sauvé, 1989). The first part was 7 meters long, the second part was either 5 or 10 m long, and the turning angle was ranging between 45° and 135°, either clockwise or counter-clockwise. At the end of the outward path, subjects had to return to their starting point. The accuracy of the updating mechanism was fairly bad in this case where rotations could be measured only on the basis of vestibular and proprioceptive information (Fig. 2). When available, visual landmarks may provide an overall reference direction allowing mammals to measure changes of directions allothetically. Such a landmark-based reference direction, however, is likely to be primarily provided by the vestibular system (see paragraph 3). Combining visual and inertial information may limit the random drift of the vestibular system (see McNaughton et al., 1991), and therefore increase the accuracy of the egocentric coding in familiar environments. In contrast, hymenoptera are known to use an Earth-based reference direction, i.e. a ‘true’ compass based on the sun or on the pattern of skylight polarization, and possibly on the Earth magnetic field (see Collett and Baron, 1994). They can therefore measure rotations allothetically as differences in compass headings during movement. Thus, desert ants are able to return almost directly to their nest from a remote feeding site one hundred and thirty meters away, after a sinuous searching path about 600 m long (see Fig. 4 in Wehner and Wehner, 1990).

Path-integration has also been convincingly demonstrated in birds (Von Saint Paul, 1982), but there is little experimental evidence on the updating mechanism used in this taxon. However, most bird species, if not all, are able to use a sun compass, and some species are also able to use a compass based on the Earth magnetic field (e.g. see Wiltshko and Wiltshko, 1993). Furthermore, birds are also endowed with a vestibular system like mammals, and they possess an accurate visual system. Birds are likely to preferentially use their sun compass when available, because the resultant random
Fig. 2. Egocentric coding process in humans during a two-part outward path. In this example, the first part (AB) is 7 m long, the second part (BC) is 10 m long, and the rotation is of 45°. Squares show the end-points of the homeward paths of subjects required to return to the starting point of the outward path (from Sauvé, 1989).

The main function of the egocentric coding process is to enable an animal to return directly to a given location using route-based information. This process may also be used by an animal to perform search loops around a memorized location in order to discover a small hidden target likely to be close to this location. For example, desert ants search for their burrow entrance by performing search loops around the memorized home location at the end of the homing path (Wehner and Srinivasan, 1981). Two spatial memory-based searching mechanisms accounting for this behaviour have been modelled by combining elementary orientation mechanisms with path-integration (Benhamou, 1994). The spatial memory-based searching mechanisms can also apply to the ‘area-concentrated searching’ behaviour exhibited by numerous species when foraging in a patchy environment. In this case, the predator is assumed to memorize the location of the last prey item detected. It then performs search-loops around this location until it detects another prey item or until it has travelled a given distance unsuccessfully. The efficiency of such a predator was computed in four habitat types with different degrees of patchiness. This predator can harvest up to 1.6 times more prey items than if it exhibits optimal area-concentrated searching behaviour without referring to a spatial memory, and almost 3 to 5 times more than if it does not exhibit any area-concentrated searching behaviour but moves in a straight line with an optimal constant speed (Benhamou, 1994).

3. The exocentric coding process

In the exocentric coding process, the goal location is defined by the apparent configuration of landmarks memorized by the animal when it was standing at the goal. Then, the animal can return to
the goal by processing the location-based information provided by the same landmarks as perceived from its current place.

In hymenoptera, the exocentric coding process has been studied in ants (Wehner and Räber, 1979; Wehner and Müller, 1985; Pastergue-Ruiz et al., 1995), and in bees and wasps. Bees are assumed to join the goal by moving so as to progressively reduce the discrepancy between the current retinal image and that which was memorized as a ‘snapshot’ taken from the goal location (Anderson, 1977; Cartwright and Collett, 1982, 1983, 1987). This discrepancy is measured by pairing landmarks in the current image and the snapshot. The local direction of movement is then computed for one step, and the operation is resumed until the goal is reached. The low angular resolution of the snapshot (Gould, 1987) leaves a chance for mistakes in pairing. Since bees see colours, however, only spots of the same colour are likely to be paired (Cheng et al., 1986). Both colours and shapes (Collett and Kelber, 1988), and distances (Cheng et al., 1987; Zeil, 1993; Lehrer and Collett, 1994; Brünert et al., 1994) of nearby landmarks from the goal can also be used. Furthermore, hymenoptera can use a compass based on the sun and the polarized skylight, or possibly on the Earth magnetic field, which serves as an overall reference direction. In fact, location-based information processing in hymenoptera seems rather rigid because the memorized bearings of landmarks defining the goal location are encoded in retinotopic coordinates (Collett and Baron, 1994). During the early stages of learning, wasps and bees must therefore turn back and orient transitorily in the same direction when leaving as when approaching the goal (Lehrer, 1993; Collett and Lehrer, 1993; Zeil, 1993). This limits the risk of mistakes in pairing because only spots with the closest bearings are assumed to be paired in the current view and in the snapshot.

Many studies have focused on the exocentric coding process in mammals. Thus, rats and other species quickly learn to memorize the location of a hidden platform in a swimming pool by relying on distal visual cues. After a short learning phase, they are able to swim almost directly towards the platform from any starting place in the swimming pool (Morris, 1981; Sutherland and Linggard, 1982; Sutherland and Dyck, 1984; Whishaw and Mittleman, 1986; Schenk, 1987; Kavaliers and Galea, 1994; Kimble and Whishaw, 1994; Sawrey et al., 1994). However, limiting the opportunity to explore impairs navigation (Sutherland et al., 1987; Whishaw, 1991; Arolfo et al., 1994; see also Stahl and Ellen, 1974, and Ellen et al., 1984). Food-storing rodents have also been shown to memorize the locations of several food caches (Vander Wall, 1991; Jacobs and Liman, 1991; Jacobs, 1992). In mammals, the exocentric coding process is much more flexible and cannot be simply accounted for by the snapshot model developed for bees. Thus, gerbils can plan their journey to the goal from the starting place (Collett et al., 1986; Collett, 1987). According to the vector-sum model (Collett et al., 1986), mammals would determine the direction and distance to the goal as the difference between a ‘memorized’ vector specifying the direction and distance to any given landmark when the animal was standing at the goal, and a ‘seen’ vector specifying the current direction and distance to the same landmark. However, this model does not explain how mammals process location-based information.

Two types of electrophysiological data obtained from freely moving rats provide some hints as to how mammals could process this information. First, in the hippocampus, there are neurons called ‘place cells’ because their firing rate depends on the animal’s current location (O’Keefe and Dostrovsky, 1971; O’Keefe and Speakman, 1987; Wilson and McNaughton, 1993; review in Muller et al., 1991). The place field, that is the region of space where a given place cell fires (Fig. 3A), is controlled by the environment, and the firing rate is usually independent of the direction the rat is facing (Fig. 3B). Second, in the postsubiculum, a cortical area close to the hippocampus, there are
other neurons called 'head-direction cells' because their firing rate depends on the current head orientation of the animal, independently of its current location (Taube et al., 1990). The activity of head-direction cells is also controlled by the spatial layout of landmarks. Nevertheless, their firing pattern depends on the absolute head orientation in space (i.e. the animal's heading) and not simply on the direction of a given landmark. This demonstrates that mammals, although they seem unable to use a ‘true’ compass (i.e. an Earth-based reference direction), can rely on an overall reference direction provided by the spatial layout of landmarks.

By scanning the environment during exploration, and integrating the rotation movements of the eyes, the head and the whole body on the spot (as estimated from kinesthetic, vestibular, and visual information), the animal would interlink the various local views (i.e. the subsets of landmarks appearing in its visual field) seen in various directions from the same given location into a panorama. A panorama is therefore a circular view of the environment and constitutes a kind of place representation (see Poucet, 1993). It depends on the animal’s current location but not on the animal’s current orientation. Panoramas which are different enough to be clearly distinguished (given the animal’s visual resolution) make it possible to structure the space as a mosaic of adjacent places. The panorama experienced from any place of the environment may be memorized in the hippocampal network (latent learning). The hippocampus would therefore produce a specific firing pattern when a given panorama is experienced (whatever the current heading), whereas the postsubiculum would produce a specific firing pattern when the animal perceives a given local view corresponding to a specific heading (whatever the current location). The overall reference direction allowing headings to be computed may be primarily updated using inertial information provided by the vestibular system and then associated with the current panorama (see McNaughton et al., 1991, 1995, and below).

We have developed a navigation model for mammals, based on the existence of hippocampal place cells and postsubicular head-direction cells (Benhamou et al., 1995). Although not conclusive, some evidence suggests that the metric distances are not precisely coded by mammals (see Poucet, 1993).
Consequently, only the angular sizes and the bearings of landmarks, which can be easily determined at the retinal level, are taken into account in the model. A panorama is then defined independently of the animal’s heading by expressing bearings of landmarks relative to each other (bearings are primarily head-referred in local views). The model works step by step, and involves two phases: exploration and navigation. The navigation process requires that some fairly nearby landmarks are perceptible from both the goal and the animal’s current location. It is therefore assumed to operate only over small distances.

During exploration, the animal forms associations between the current panorama and both the panoramas experienced from the places adjacent to the current place and the overall reference direction which is transferred from place to place. Let us consider the animal moving at random from place to place (Fig. 4A). When the animal was standing at the previous place, the overall reference direction was linked to the panorama experienced from this place using a Place-Direction Associative Memory. When leaving the previous place, the animal saw a particular local view which specified its head orientation relative to the panorama, i.e. to a local reference direction. Its heading was then deduced by referring its head orientation to the overall reference direction. When arriving at the current place, the animal sees a slightly different local view, defining a new local reference direction. First, the previous local view is linked to the current local view by means of a Place-Place Associative Memory. Thereafter, the current local view is integrated into the current panorama. As the animal is facing the same absolute direction when leaving the previous place and arriving at the current place the current heading is equal to the previous one, which enables the animal to determine the overall reference direction at the current place. The overall reference direction is thus transferred from the previous place to the current place, and then linked to the current panorama by means of the Place-Direction Associative Memory.

During navigation, the goal direction is then estimated on the basis of the distribution of the discrepancies between the panoramas experienced from the places adjacent to the current place and the panorama experienced from the goal. The discrepancy between a given panorama and the goal panorama is computed on the basis of the ratio of the angular sizes and of the difference in bearings expressed with respect to the overall reference direction for each common landmark. Assume that the animal is at a given place and attempts to determine in which direction it should move at the next step to approach the goal (Fig. 4B). The goal panorama incorporating the overall reference direction was stored in a long-term memory, so that it can be remembered at any time. The specific panorama experienced from the current place activates the Place-Direction Associative Memory to recall the overall reference direction. Additionally, the current panorama activates the Place-Place Associative Memory, to recall the panorama experienced from each place adjacent to the current place, corresponding to a possible movement direction. The comparison between the two panoramas enables the animal to determine the change in the local reference direction. Bearings of landmarks, as perceived from the current and adjacent places, are then expressed with respect to the overall reference direction. The animal can therefore compute the discrepancies between these panoramas and the goal panorama. By moving at each step in the direction in which the panorama tends to become closer to the goal panorama, it reaches the goal along a fairly straight path.

Food-storing birds can memorize the locations of numerous food caches in relation to the spatial layout of landmarks (Sherry et al., 1981; Vander Wall, 1982; Sherry, 1982, 1984; Shettleworth and Krebs, 1982, 1986, 1988; Balda and Kamil, 1989, 1992; Kamil et al., 1993; Bennett, 1993; Herz et al., 1994). Similarly, non-storing birds are also able to memorize some locations (e.g. Cheng, 1988,
Fig. 4. Exocentric coding process in mammals. (A) Exploration from the previous place to the current place; (B) Navigation: determining to which adjacent place to move from the current place to approach the goal. ORD: Overall Reference Direction; LRD: Local Reference Direction; P.D.A.M.: Place-Direction Associative Memory; P.P.A.M.: Place-Place Associative Memory. (Simplified from Benhamou et al., 1995).

1989, 1990, 1994; Cheng and Sherry, 1992; Spetch et al., 1992). The dorsomedial forebrain region of birds is called the avian hippocampal complex because of its homology with the hippocampal formation of mammals. Some studies have related the size of the avian hippocampal complex to spatial memory performances, by comparing food-storing and non-storing birds (Krebs et al., 1989; Sherry et al., 1989; Healy et al., 1994). Other studies have shown that hippocampal lesions impaired
navigation in pigeons (Bingman et al., 1987, 1988, 1990; Bingman, 1992). It seems likely that the hippocampus of mammals and birds have a common origin in the telencephalic region of the reptilian brain of their common ancestor. They may play similar roles in place recognition on the basis of visual panoramas. Nevertheless, birds may return more easily than mammals to a given location which has been memorized in relation to the spatial layout of surrounding landmarks. First, birds can use a sun compass as an overall reference direction (Wiltschko and Balda, 1989; Balda and Wiltschko, 1991). Second, they have a good visual resolution and they have many opportunities to see their environment from a fairly large height. In mammals, places have been defined in terms of two-dimensional panoramas, with no direct access to the third dimension, that is the environmental depth. This is because the height from which a terrestrial mammal perceives its environment is assumed to be negligible in comparison to the distances to landmarks. Birds, in contrast, can perceive the environmental depth when perching or flying. Contrary to terrestrial mammals, birds could therefore directly determine the goal location based on the relative distances between the goal and the landmarks (e.g. a given landmark A is twice as close to the goal as another given landmark B).

4. Conclusion

Orientation mechanisms appeared very early in the history of life. Thus, bacteria are able to orient efficiently in chemical gradient fields using taxis or klinokinesis (Benhamou and Bovet, 1992). Orientation mechanisms based on spatial memory have emerged much more recently. They are most efficient in highly evolved taxa, such as hymenoptera, modern mammals (Eutheria) and birds, which appeared very recently, about sixty to seventy million years ago. The last common ancestor of birds and mammals was a primitive reptile living about three hundred million years ago, and the last common ancestor of vertebrates and hymenoptera lived more than six hundred million years ago. Based on these phylogenetic considerations, it is clear that the spatial memory processes originated independently in these three taxa. Nevertheless, those of mammals and birds may be based on a common root found in the organization of their common reptilian brain. In spite of their independent origins, and therefore in spite of considerable differences in sensori-motor equipment and brain organization, spatial memory processes share numerous characteristics in these three taxa, probably because all have to cope with the same geometrical constraints. This is a striking example of evolutionary convergence. Spatial memory processes have emerged to answer the following question: ‘where is a given place with respect to me?’ The question is simple but the answer is not. Two complementary processes are used (and some experimental conditions are liable to generate conflict between them; e.g. see Teroni et al., 1987, Etienne et al., 1990a, b, and Alyan and Jander, 1994). The egocentric coding process is designed to answer that question directly, but it tends to accumulate errors during large scale movements. The exocentric coding process is designed to provide an indirect answer by subdividing the question into two parts: ‘Where is the goal in the environment?’ and ‘Where am I in the environment?’. This process can work only if some fairly nearby landmarks are perceptible from both the goal and the animal’s current location, because the panoramas based on remote landmarks are similar whatever the animal’s location. Thus, the exocentric coding process is efficient when the animal is approaching the goal, while it is perceiving those landmarks that are fairly close to the goal location: this is a short scale process used in the natural habitat to adjust the last part of the path to the goal.
References


