On systems of reference involved in spatial memory

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Abstract

The system of reference used by an animal for memorizing the location of a hidden place to which it is liable to return (the goal) can be theoretically defined as being ‘self-centred’, ‘local’, or ‘overall’. According to the system of reference, the goal location is memorized by means of: (1) an egocentric coding that specifies the direction and distance to the goal with respect to the animal’s current position; (2) an exocentric coding that specifies the apparent configuration of nearby landmarks as perceived from the goal; or (3) an exocentric coding based on a global representation of space over the whole range of movement, respectively. A compass provides useful directional information (to the species capable of deriving it) that may be used in the framework of any of the three systems of reference. A goal location may be memorized concurrently in the three systems of reference which are complementary rather than mutually exclusive. In particular, the joint use of the self-centred and local systems of reference has been demonstrated in animals of numerous species that are able to shift from the former to the latter while approaching a goal. In contrast, there is no clear evidence supporting that an animal is able to rely on a global representation of space. © 1997 Elsevier Science B.V.

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1. Introduction

So far, the question of the systems of reference used by an animal to memorize a place to which it intends to return (referred to as the goal; e.g. the home or a food cache) has not been directly addressed but only tackled occasionally. Addressing this question proves to be of major importance to understand how spatial information is processed by an animal during both exploration of the environment and navigation because the animal should express its current location and the memorized goal location in the same system of reference to be able to plan and correct the course to the goal efficiently.

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From a theoretical point of view, three types of system of reference can be distinguished. Indeed, the goal location may be encoded egocentrically as a vector that specifies the head-referred direction and the distance to the goal. This coding requires a self-centred system of reference that is anchored on the animal’s current position (location and heading). The goal location may also be encoded exocentrically with respect to the nearby landmarks that are perceptible from this location. This coding requires a local system of reference that is based on the arrangement of these landmarks. As a third theoretical possibility, the goal location may be encoded within a map-like representation of space over the whole range of movement. This coding requires an overall system of reference that allows all the places within the range of movement to be addressed in a common way. This trichotomy of the systems of reference is only a theoretical proposal and other ones can be imagined (in the last part of this paper I will briefly present an alternative proposal that considers only one single type of system of reference involving a unified representation of space). It is however the most liable way of organizing the vast amount of sometimes contradictory knowledge that has accumulated over numerous decades about spatial memory in several taxa. In this paper, I will present evidence that supports the self-centred and local systems of reference, and show that there is no clear evidence supporting the overall system of reference.

Before discussing each of the three systems of reference in detail, several comments must be made for clarity’s sake about the meaning given to the words egocentric and exocentric in this paper. (1) They are synonymous to the words autocentric and allocentric, respectively (the dichotomy commonly employed in the literature, egocentric vs. allocentric, is etymologically inconsistent). (2) They refer to the way an animal is assumed to encode the goal location in memory, independently of the origin-internal or external-of spatial information used. In particular, that an animal uses allothetic information (i.e. provided by a measure system involving an external reference, e.g. the sun or magnetic compass) does not necessarily mean that the coding is allocentric (exocentric). Symmetrically, that an animal uses idiothetic information (i.e. provided by an internal measure system, e.g. the vestibular system), does not necessarily mean that the coding is egocentric. (3) The coding is said (somewhat abusively) to be exocentric when the system of reference assumed to be involved is provided by the environment but not necessarily centred on a specific location. (4) This paper is not concerned with non-spatial forms of memory that may be involved in reaching a goal, e.g. the memory of locomotor sequences which is often referred to as egocentric memory in the literature.

2. A taxonomy of systems of reference

2.1. The self-centred system of reference

The self-centred system of reference is, by definition, anchored on the position of a moving animal. It therefore enables the animal to deal with an egocentric representation of the goal location. This location is likely to be encoded as a vector whose orientation, referred to the animal’s body-head axis, specifies the current goal direction, and whose length specifies the current distance to the goal. When moving, an animal must therefore continuously update the goal pointing vector by processing route-based information, i.e. dynamic information collected en route about its changes of direction (rotations) and changes of location (translations). The mechanism by which an animal combines rotational and translational information to update this vector has been modelled in different ways (review in Benhamou and Séguinot, 1995; Maurer and Séguinot, 1995; see also Hartmann and Wehner, 1995; Wittmann and Schwe gler, 1995 for neural network models). It was hypothesized earlier as a kind of dead reckoning (Darwin, 1873), and is now usually referred to as path integration (Mittelstaedt and Mittelstaedt, 1982, 1980). An animal returning to a goal whose location has been memorized by path integration during the outward journey is usually said to perform route-based navigation (Baker, 1981). This term, however, is liable to generate some confusion due to the lack of strict correspondence
between information and navigation terms. Indeed there is now clear evidence that route-based information is also involved in another type of navigation in mammals (Section 2.2). Instead, I will employ the term vector navigation to stress that this process is thought to work directly in a vectorial form (contrary to other navigational processes that are assumed to provide a goal pointing vector only at the final stage of the computation). The ability to perform vector navigation to home has been demonstrated in mammals, birds, and hymenopters (review in Benhamou and Poucet, 1995), and also in other insects (Frantsevich et al., 1977; Beugnon and Campan, 1989), in crustaceans (Hoffmann, 1984) and arachnids (Mittelstaedt, 1985; Moller and Görner, 1994).

Although vector navigation is a site-independent process, the updating mechanism, path integration, was initially formulated in exocentric terms (Mittelstaedt and Mittelstaedt, 1973, 1982). In this framework, the animal is assumed to update its position in an external, home-centred, system of reference, rather than to update the home location in a self-centred system of reference (similarly, dead reckoning is the method by which a human navigator relies on route-based information to update the compass bearing and distance to the boat from the starting point of the journey). The two formulations are mathematically equivalent (note however that the exocentric formulation requires using an external reference direction whereas the egocentric formulation does not). If we are to look at the underlying neurobiological processes, however, it seems better to adopt the animal’s point of view, and hence to consider that path integration involves an egocentric localization system (Potegal, 1982; Benhamou et al., 1990; Wehner and Menzel, 1990; Wehner et al., 1996). In accordance with this view, rats with lesions of the caudate nucleus, a structure known to be involved in egocentric localization, but not rats with lesions of the hippocampal formation, a structure known to be involved in exocentric localization, are impaired in a return task following passive transport along an L-shaped outward path (Abraham et al., 1983). Such results further dismiss the recent claim by McNaughton et al. (1996) that the rat hippocampus would be a path integration system (Section 2.2). Eventually, a definite biological answer should be provided in mammals as well as in other taxa by electrophysiological studies focusing on the resulting neural signal: if path integration works exocentrically, this signal should vary for any movement except when the animal is turning on the spot; in contrast if, as assumed, path integration works egocentrically, this signal should vary when the animal is turning on the spot, but not when it is moving at a fixed distance around the starting point (Fig. 1).

The vectorial representation of the goal location varies accordingly to the mathematical laws of optic flow, except that the apparent movement of the (hidden) goal cannot be directly perceived and must therefore be inferred by the moving animal to update the goal location relative to its own position. As a result, the direction and distance to the goal vary interdependently during an animal’s translation: the change in the goal direction (motion parallax) is proportional to the sine of the direction and is inversely related to the distance, while the distance decreases linearly with the cosine of the direction (Benhamou, 1997). An orientation mechanism in which the direction and distance to the goal are decoupled can therefore be considered only in the particular case of an animal moving straight toward or away from the

![Fig. 1. Vector navigation.](image)
goal (Bovet, 1995). If several goal locations were to be kept in memory at the same time in the self-centred system of reference, each one should be encoded independently from each other. Indeed, the motion parallax of one goal depends on its respective direction and distance, and so provides no information about the motion parallax of another goal: both have to be inferred concurrently but independently from each other by feeding two parallel computing processes with the same route-based information. Hamsters seem capable of memorizing the locations of both the home and a food source at the same time while they simply shuttle back and forth between the two (Etienne et al., 1991). However, the ability of an animal following a sinuous path to memorize several goal locations egocentrically, which involves the simultaneous management of various independent motion parallaxes, has never been demonstrated in any species.

The self-centred system of reference allows the direction and distance to the goal to be directly available at any time. Its weakness, however, is due to the propensity of the updating mechanism to accumulate random estimation errors, which generates increasing inaccuracy in the memorized goal location during large scale movements. In fact, the updating mechanism is very sensitive to errors occurring in the idiothetic estimation of rotations, but not to errors occurring in the allocentric estimation of translations (Benhamou et al., 1990). Hence, translations need only be roughly measured. Translational information can be provided idiothetically by kinaesthetic systems and, at least in hymenopters, by the visual system from the self-induced optic flow from the ground (Ronacher and Wehner, 1995; Esch and Burns, 1996; Schöne, 1996a; Srinivasan et al., 1996). On the other hand, the way rotations are measured is of major importance. Most mammals can acquire rotational information only idiothetically by means of their vestibular and kinaesthetic systems (the visual system is useless because in natural, i.e. heterogeneous, environments, the rotational component cannot be extracted unequivocally from the global self-induced optic flow), while hymenopters are able to use a sun (or polarized skylight) and possibly a magnetic compass to derive this information allocentrically. Thus, hamsters are completely lost after a few turns (Etienne et al., 1988) while desert ants can return very close to their home after a long sinuous outward foraging path (Wehner and Wehner, 1986, 1990). In addition, a systematic error is generated when left and right turns are not balanced in the outward path (Müller and Wehner, 1988; Séguinot et al., 1993; but see Benhamou, 1997). It may be due to an overestimation of the inferred motion parallax of the goal (Benhamou and Séguinot, 1995).

Because of the propensity of the updating mechanism to accumulate random estimation errors, the self-centred system of reference is useful only to reach an area surrounding the goal. Afterwards, the animal should shift to another, nearby landmark-based mechanism (i.e. involving a local system of reference; Section 2.2) to pinpoint the exact goal location. The goal location is therefore likely to be memorized concurrently in (at least) two systems of reference. The way the two systems compete in case of conflicting cues varies among taxa. Probably because path integration is not very reliable in mammals, hamsters tend to home according to a compromise between vectorial and landmark information, even after a very short outward path from home (Etienne et al., 1990a,b, 1995a,b, 1996). In contrast, hymenopters such as bees (Wehner et al., 1990) and ants (Wehner et al., 1996) ignore landmark information until the goal pointing vector has been reset to 0, probably because path integration is very reliable while vision is not very accurate in these species. To discover the invisible burrow entrance in the absence of nearby landmarks, desert ants (Wehner and Srinivasan, 1981; Müller and Wehner, 1994) and desert woodlice (Hoffmann, 1983a,b) perform search loops around the egocentrically memorized home location (see also Frantsevich et al., 1977; Beugnon and Campan, 1989). A similar search loop mechanism may be used by a predator to exhibit a very efficient form of area-concentrated searching around the memorized location of the last prey item detected (Benhamou, 1994).
2.2. The local system of reference

A local system of reference is based on the spatial layout of the nearby landmarks surrounding the location of a given goal. Hence, it enables an animal to deal with an exocentric representation of this location. The animal can therefore return there by processing location-based information, i.e. static information provided on site by the apparent configuration of the landmarks as perceived from its current place. This ability has been shown in mammals, birds and hymenopters (review in Benhamou and Poucet, 1995), and also in other insects (e.g. see Collett and Land, 1975). It is usually called location-based (Baker, 1981) or place (Sutherland and Dyck, 1984) navigation. I will use the latter term because, as mentioned above, both route-based and location-based information are involved in this type of navigation in mammals (see below).

A local system of reference is obviously useful only when an animal is close enough to the goal to perceive the landmarks that define the goal location. Remote landmarks cannot provide reliable locational cues, even if they are perceptible from any distant place, because their apparent configuration remains similar whatever the animal's location (such landmarks, however, can be used as directional cues, i.e. serve as a kind of compass). During large scale movements in the natural habitat, the local system of reference is thus particularly useful to adjust the terminal part of the path to the goal: it enables an animal to correct its course when the nearby landmarks that define the goal location become perceptible from the animal's current location. If several distant goal locations were to be kept in memory at the same time (e.g. food caches), each one should be encoded in its own local system of reference (i.e. based on the same landmarks).

Close goal locations, however, may be encoded, independently from each other, in a common local system of reference. This formalism however seems hardly tenable from a biological point of view. Indeed, simply discarding a single landmark may disrupt such a system of reference. Furthermore, it rests on the unverified assumption that an animal can accurately determine the current metric distances to various landmarks. Zipser (1986) proposed another much simpler and elegant formalism which is subject however to the same criticism. The animal is assumed to give each landmark a relative weight so that the spatial distribution of the weighted landmarks is goal-centred. Then, any current view of the landmarks would enable the animal to derive the direction and distance to the goal using a simple averaging process. A much more biologically plausible solution is to consider that the animal encodes the goal location in a 'content-addressable' memory which stores the panoramic view specifying the apparent configuration of landmarks perceived by the animal when standing at the goal (Collett and Kelber, 1988).

Place navigation is then a process through which an animal returns to a goal by comparing the current view of the environment with the panoramic view memorized at the goal location. This memorized view defines the goal location exocentrically, with respect to surrounding landmarks. The animal should therefore express its current position exocentrically, with respect to the same landmarks, to be able to navigate efficiently toward the goal. The current view of the environment, however, provides the animal with egocentric spatial information, and similarly, the actions that the animal should perform to navigate toward the goal are also programmed egocentrically. Efficient place navigation appears therefore to require that the animal carries out a two-fold conversion of the frame of reference, from egocentric sensory inputs through exocentric localization to egocentric motor outputs.

According to the so-called snapshot model, bees and wasps memorize the goal location by storing the bearings and angular sizes of landmarks in a compass-oriented snapshot taken from the goal (the local system of reference is therefore assumed to be based on both the landmarks surrounding the goal and a reference direction provided by a compass). They may then return to the goal location by moving so as to progressively
reduce the discrepancy between the current retinal image and the stored snapshot (Cartwright and Collett, 1982, 1983, 1987). Colours (Cheng et al., 1986; Gould, 1987) and distances to landmarks (Cheng et al., 1987; Zeil, 1993; Lehrer and Collett, 1994; Brünnert et al., 1994; Lehrer, 1996; Zeil et al., 1996), as well as contextual cues (Collett and Kelber, 1988) are also used in the visual matching process. This process is quite rigid, however, because the snapshot specifying the (exocentric) goal location is a simple copy (but with a lower resolution; Gould, 1987) of the (egocentric) retinal image obtained from this place. The use of retinotopic coordinates compel these insects to orient their body in a predetermined compass direction to be able to return to a goal by computing the discrepancy between the current retinal image and the stored snapshot specifying its location (Collett and Baron, 1994; Collett, 1996). This is why, at early stages of learning, they turn back when leaving the goal and orient transitorily in the compass direction that they will have later on when approaching it (Lehrer, 1993, 1996; Collett and Lehrer, 1993; Zeil, 1993; Zeil et al., 1996; Schöne, 1996b). Insects can thus perform place navigation without really determining their current exocentric position. Rather, they rely on a computational solution that directly relates egocentric inputs to egocentric outputs. This is done at the expense of high rigidity because they are unable to determine the goal direction when they are not oriented in a suitable compass direction.

In contrast, the navigational process used by mammals appears much more flexible thanks to some neurobiological mechanisms specifically designed to allow them to determine their current position with respect to surrounding landmarks. Indeed, electrophysiological studies focusing on the hippocampal formation showed that a rat freely moving in a familiar environment is able to recognize the apparent configuration of landmarks experienced from any place and to deduce its heading (review in Muller et al., 1991). Contrary to what occurs in insects which would memorize only the locations of particular places (those acting as goals or as choice points in well-established routes), mammals appear to store spatial information about numerous places (even those having no special status; review in Poucet, 1993; Poucet and Benhamou, 1997). This exocentric place-heading representation system may reduce the informational burden it bears by filtering out the high spatial frequencies displayed by fine-grain cues. Indeed, small objects whose locations are potentially fleeting, although clearly noticed, would not be used in place navigation by mammals (Alyan and Jander, 1994) and birds (Bennett, 1993; Herz et al., 1994). Hence only coarse-grain cues that outline the geometry of the environment would really act as landmarks (Poucet and Benhamou, 1997). Mammals would therefore encode the location of any place (whether it has a goal status or not) as the panoramic view provided by the apparent configuration (as locally perceived) of a rather small number of landmarks showing stable spatial relations (Biegler and Morris, 1996). Recent evidence obtained in rats further suggests that the landmark identity may be ignored at this level, at least at early stages of learning (Benhamou and Poucet, 1997).

A biologically plausible model based on place-place and place-direction associative memories (Benhamou et al., 1995) can explain why limiting prior exploration of the environment impairs place navigation in mammals, as observed in rats (Stahl and Ellen, 1974; Ellen et al., 1984; Sutherland et al., 1987; Whishaw, 1991; Arolfo et al., 1994) and mice (Alyan, 1994). This model acknowledges that a mammal extracts its current (exocentric) location and heading based on any (egocentric) current view of the environment. For that purpose, the animal needs first to process route-based and location-based information jointly during an exploration phase that provides it with a dynamic knowledge of the environment (i.e. specifying both the apparent configuration of landmarks from any place and how this configuration is locally bent by moving around). Contrary to insects, most mammals do not seem capable of using a sun or a magnetic compass as an external reference direction. The model shows that they may derive such a reference direction from the apparent configuration of landmarks and rotational information (the major role of rotational information in heading monitoring was
advocated by McNaughton et al., 1991, 1995 who misleadingly referred to this monitoring as dead reckoning or path integration). The model also accounts for the ability of a rat to keep track for a while of its position in the dark (relative to surrounding landmarks seen before) using route-based information (as shown by electrophysiological data; Poucet and Benhamou, 1997). The striking performance of gerbils (Collett et al., 1986) and hamsters (Etienne et al., 1996) searching in the dark for a goal located with respect to an array of landmarks previously experienced in the light may be based on a similar ability.

2.3. The overall system of reference

Contrary to the self-centred and local systems of reference, which involve only basic forms of spatial representation limited to individual places, the overall system of reference rests on a representation of space over the whole range of movement (survey map). So, when several goal locations are to be kept in memory, the overall system of reference enables the spatial relations between them to be derived: there is no independence between locations. For a human navigator, the overall system of reference consists of a system of Earth-based coordinates (latitude and longitude): the location of any place on Earth is defined in this system, and given a set of places, the spatial relations between them can be determined from the coordinates of their locations. The range of most animals is much more limited, however, hence their overall system of reference need not be Earth-based. Two types have been proposed: gradient maps and mosaic maps (Wallraff, 1974).

The gradient map concept has been proposed to account for the navigational performances of animals which prove capable of returning to a goal location through regions containing no familiar landmarks (Wallraff, 1974, 1985, 1990; Wiltschko and Wiltschko, 1978, 1982). The environment is assumed to contain (at least) two stimulation gradient fields, i.e. two physical or chemical factors to which the animal is sensitive and whose intensities vary monotonically in two fairly different directions. To perform the so-called ‘bicoordinate navigation’, the animal is then assumed to determine its current location based on the two current stimulus intensities, and the goal location based on the two stimulus intensities which were previously memorized when it was at the goal. Additionally, the animal should use a compass (that can be provided directly by one of the gradient directions or by an independent means, e.g. the sun compass) to determine the goal direction (the animal is assumed to know the compass orientations of the gradients). A magnetic gradient map has been hypothesized to account for the performances of homing pigeons (Gould, 1982, 1985) and of Pacific salmon (Quinn, 1982, 1984; but see Jamon, 1990) and sea turtles (Lohmann and Lohmann, 1996a,b) during ocean migration (see also Phillips, 1996). Previously, Papi et al. (1972) (review in Papi, 1990; but see Wiltschko, 1996) proposed that homing pigeons may simply rely on the angular distribution of wind-borne odours around the loft, i.e. on an oversimplified (unidimensional) form of olfactory gradient map that does not allow for true bicoordinate navigation (e.g. a pigeon released at a given place P flies southwards because it remembers that, at the loft, odour perceived at P came from north).

The terms used—gradient map, bicoordinate navigation—suggest that the animal builds up a spatial representation of the gradient fields, on which it sets up its current location and the goal location. The ability of an animal to derive locational information from two (or more) gradient fields is a questionable issue by itself (Phillips, 1996). Even if this ability was clearly proved, there is still the need to demonstrate that a spatial representation of the fields is involved. Two intersecting (not necessarily orthogonal) gradient fields undeniably provide a system of reference allowing the coordinates of any place to be determined unequivocally. An animal, however, need not convert the stimulus intensities into spatial coordinates to navigate toward the goal. Indeed, the existence of two gradients in the environment provides several navigational possibilities (depending on what the animal is assumed to know about its environment) that do not involve a mapping of the fields. Thus, if an animal knows the compass orientation of each gradient and the
Fig. 2. Navigation in an environment containing two stimulation gradient fields. In this example, one of the fields is oriented N-S, with a steepness of 0.25°/u while the other is oriented NW-SE, with a steepness of 0.20°/u. (° and ′ are arbitrary intensity units and u is an arbitrary distance unit). The iso-intensity lines of the N-S and NW-SW fields are drawn as full and dashed lines, respectively. The degree of variation of the N-S field intensity along an iso-intensity line of the NW-SE field is 0.18°/u, and the degree of variation of the NW-SE field intensity along an iso-intensity line of the N-S field is 0.14°/u. The values of stimulus intensities currently experienced by the animal (A) are 73° and 15′, and the values memorized at the goal (G) are 68° and 17′. The spatial representation of the two gradient fields shows that the goal is located about 40 u E-NE from the animal's current location. The goal pointing vector A-G, however, can be computed without mapping of the fields simply as the sum of vectors V1 and V2. The vector V1 stands for the N-S field; it is oriented orthogonally to the NW-SE field and its length equals (68 − 73)/0.18 = −27.8 u. The vector V2 stands for the NW-SE field; it is oriented orthogonally to the N-S field and its length equals (17 − 15)/0.14 = 14.3 u. Klinokinesis is another, very simple but rather efficient means of navigating in gradient fields. The sinuous path between A and G was generated (on a computer) by a mechanism of this type using a medium value of the klinokinetic factor (the efficiency is proportional to the value of this factor; Benhamou and Bovet, 1989).

degree with which each stimulus intensity varies along an iso-intensity line of the other field, it can compute the direction and distance to the goal as the sum of two vectors (Fig. 2). Each vector, standing for a given field, is oriented orthogonally to the other gradient direction (i.e. along an iso-intensity line of the other field), and its length equals the difference between the stimulus intensity currently perceived and the stimulus intensity memorized at the goal divided by the degree of variation of the stimulus intensity in the vector direction. This computation, however, may generate large errors due to random fluctuations or anomalies in the actual fields that are not always consistent in direction or steepness. The animal may also return to the goal location by regulating the sinuosity of its path as a function of the variation in the current stimulus intensities (klinokinesis, Fig. 2), or by relying on the local gradient directions (taxis). These elementary orientation mechanisms require no knowledge about the environment and are fairly efficient and robust against random fluctuations (Benhamou and Bovet, 1989, 1992). Wallraff (1989a,b) accounted for homing behaviour of pigeons released far away from their home range by a simple orientation mechanism based on olfactory gradients that looks like a taxis, except that the model pigeon is assumed to know the general compass orientations of the olfactory gradients rather than to rely on the locally perceived gradient directions.

On the other hand, the mosaic map concept has been proposed initially to account for the navigational performances of birds within large regions containing familiar landmarks (Wallraff, 1974, 1985, 1990; Wiltschko and Wiltschko, 1978, 1982). Several experimental studies have also stressed that mammals (Peters, 1973, 1979; Sigg and Stolba, 1981; Fabrigoule and Maurel, 1982; Boesch and Boesch, 1984) and bees (Gould, 1986; Gould and Towne, 1987) may rely on a global representation of space based on familiar landmarks. Numerous theoretical studies have further attempted to show how such a representation may be built up and organized (Kuiipers, 1978; Kuiipers and Levitt, 1988; Yeap, 1988; Gopal et al., 1989; Yeap and Handley, 1991; Yoshino, 1991; Wodden, 1992; Poucet, 1993; Prescott and Mayhew, 1993). These studies have referred to this global representation of space as a cognitive or mental map rather than as a mosaic map, but the two concepts are clearly similar in this context, and eventually derive from the ‘map-in-the-head’ metaphor (Kuiipers, 1982). In this framework, the animal is assumed to be able to mentally organize a kind of global-view-from-above puzzle made of the subsets of landmarks which are locally perceptible from ground-level places. It may thus establish the spatial relations between the salient
landmarks of its environment, including remote landmarks that are momentarily beyond perceptual reach from its current location as they are concealed by nearby landmarks. Consequently, the animal would be able to derive the spatial relations between the goal location and its current location, even when there are no landmarks that can be perceived from both locations. To compute the course to the goal, the animal should further suitably align the ‘map-in-the-head’ with respect to the environment. In the initial formulation of the mosaic map concept, the animal was assumed to use a compass for this purpose (Wiltschko and Wiltschko, 1978). In the absence of compass, the mosaic map may be suitably oriented by putting the landmarks actually perceived and those represented on the map in coincidence.

The animal’s current location may be expressed in a local system of reference defined by the nearby landmarks surrounding the animal, while the goal location may be expressed in a local system of reference defined by the nearby landmarks surrounding the goal. In nature, there are often many obstacles (including the landmarks themselves) between the goal location and the animal’s current location (e.g. when the animal is far from the goal). Under these circumstances, there is no overlap between these two local systems of reference (Fig. 3). Consequently, the animal cannot navigate to the goal by relying on them. By specifying the spatial relations between the various landmarks over the whole range of movement, a mosaic map enables the animal to determine its current location and the location of a distant goal in a common, overall system of reference, even when only the nearby landmarks surrounding its current location but not those surrounding the goal location are currently perceptible. However, the ability of an animal to perform place navigation in this situation (that is likely to be common in nature) has not yet been unequivocally demonstrated in any non-human species. Thus, Cartwright and Collett (1987) and Dyer and Seeley (1989) showed that the impressive long-distance orientation abilities of bees reported by Gould (1986) and Gould and Towne (1987) can be accounted for without evoking a global representation of space. Furthermore, recent well controlled experiments dismissed the use of such a representation by bees (Wehner and Menzel, 1990; Wehner and Wehner, 1990; Wehner et al., 1990, 1996; Dyer, 1991, 1996; Dyer et al., 1993; Kirchner and Braun, 1994; Menzel et al., 1996). There is also no real need to refer to this concept to account for the way mammals and birds drive their large scale movements in their home ranges. Their orientation abilities can be accounted for more simply by route-following based on visual piloting, and possibly by punctual transfers from the self-centred system of reference to several local systems of reference (Section 3). Mammals may further rely on olfactory mechanisms based on scent-marking (Benhamou, 1989; Jamon, 1994). In addition, recent laboratory experiments failed to provide any evidence supporting the existence of a global representation of space in mice (Alyan, 1994) and rats (Benhamou, 1996). The very existence of a ‘map-in-the-head’

![Fig. 3. Mosaic map. The animal (A) can determine its current location in a local system of reference defined by the landmarks it perceives currently, while it can have previously memorized the goal location (G) in a local system of reference defined by the landmarks it perceived when it was at the goal. The set of landmarks perceptible from each of the two places is encompassed by a dashed ellipse. If the animal can gradually build up a mosaic map of its environment by relating the various sets of landmarks it perceives from the various places it visits, it will be able to determine the current direction and distance to the goal even when there is no overlap between the set of landmarks currently perceived and the set of landmarks perceptible from the goal. To date, no clear evidence supports this hypothesis.](image-url)
(gradient or mosaic type) can therefore be considered only as a working hypothesis.

3. Discussion

The systems of reference used by an animal to memorize a goal location obviously relate to its ability to build a spatial cognitive map. Since the studies by Tolman (1948) and O'Keefe and Nadel (1978), a growing literature has been published on spatial cognitive mapping in several species, but this concept has been employed with various, somewhat contradictory meanings (see Bennett, 1996). For clarity’s sake, I have therefore avoided to refer to this concept in the present paper. In fact, cognitive mapping is an ambiguous term because the word map refers both to a topographic picture of the environment, and more generally, to any relation between two sets of items (in both spatial and non-spatial contexts). The term ‘spatial cognitive mapping’ may therefore ambiguously refer to the building of different types of spatial representation, be it a global representation of space, i.e. a topographic map-in-the-head, or simpler forms of spatial representation limited to individual places enabled by the self-centred and local systems of reference. In fact, the self-centred system of reference appears so far not to be concerned because the term spatial cognitive mapping usually refers to the building of exocentric representations only. The existence of a spatial cognitive map with a rather strong topographic meaning has often been advocated in the literature based on the ability of an animal to take novel short-cuts. Up to now, however, experimenters failed to eliminate simpler explanations accounting for such an ability (Bennett, 1996).

I would like now to examine an alternative proposal that stresses that animals may use only one single type of system of reference rather than two or possibly three, according to the taxonomy I introduced in this paper. This proposal stems from the conjunction of two views. On the one hand, according to the hypothesis advocated by O'Keefe and Nadel (1978), animals (at least mammals) may deal with an Euclidean representation of space. On the other hand, according to the initial formulation of path integration provided by Mittelstaedt and Mittelstaedt (1973, 1982), animals may update their current location with respect to a Cartesian system of reference defined by the starting point of the journey and an arbitrary reference direction. Early navigators used this method, called dead reckoning, to update their current location on a nautical chart, on which they indicated the locations of the new lands they encountered as they went along. As a result, they were able to build up more and more detailed charts serving in return as a background for marking their current location. The recent theoretical account made by Gallistel (1990), and Gallistel and Cramer (1996) about the way mammals may mentally represent space by using concurrent route-based and location-based information is a simple transposition of the way early navigators built nautical charts. An animal is thus assumed to express its current location, the locations of the landmarks (including those that are beyond perceptual reach) and the goal location in a single (overall) Cartesian system of reference over a global representation of space. Contrary to what occurs with a mosaic map that involves a relative (landmark-based) representation of space, landmarks are not parts of the system of reference that rests on an absolute representation of space. The arbitrary origin and reference direction of such a representation may be provided by any starting point and starting direction with respect to which the animal computes its current location for a while by dead reckoning.

Several authors seem to share this view, either to analyse their experimental results (Arolfo et al., 1994; Georgakopoulos and Etienne, 1994; Etienne et al., 1996) or to model some neurophysiological mechanisms involved in spatial information processing (McNaughton et al., 1991, 1995, 1996; Wan et al., 1994; Touretzky and Redish, 1996), in spite of the lack of evidence that an animal is really able to mentally build up a global representation of space. In particular, this view primarily rests on a route-based representation of space that has been so far demonstrated only in humans (e.g. Péreux and Lapin, 1993). Recently, Moghaddam and Bures (1996) attempted to properly test the existence of such a representation by overtraining
rats to navigate in the water maze in complete darkness. They interpreted the ability of the rats to navigate fairly efficiently during a transfer test in which the platform was moved to a new location as clear supporting evidence. However, that the overtrained rats proved capable of navigating toward the new platform location in the first trial (i.e. before being aware that the goal location was changed) may rather indicate that they had learned to use some cues emanating from the platform (e.g. the reflection of water waves) to locate it in the dark. A global representation of space built on both landmark-based and route-based information can of course account for the striking ability of rats to be aware of their position in space with respect to landmarks previously seen when moving in the dark for a while. This ability, however, can be explained more simply by the use of route-based information in the framework of a local system of reference (Poucet and Benhamou, 1997).

To end this paper, I would like to advocate a process that presents a high flexibility but rests on actual demonstrated mechanisms, and so constitutes a full alternative to the existence of a global representation of space. This process consists in associating with any important place (e.g. home, shelters, or food sources) the directions and distances to the other important places located beyond perceptual reach. Each of these vectorial representations is assumed to be primarily expressed egocentrically in the animal’s self-centred system of reference by means of path integration, and later on, stored exocentrically in the local system of reference defined by the landmarks surrounding the important place that the animal has reached (using simple place-vector associative memories). This generates a set of multiple local systems of reference, each one coding for the directions and distances to the others (Benhamou et al., 1990; Poucet, 1993). The animal is therefore not assumed to know the spatial relations between the important places of its home range independently of its location (contrary to what occurs in a global representation of space): 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. Similarly, Cartwright and Collett (1987, see also Collett, 1996; Menzel et al., 1996; Wehner et al., 1996) proposed that bees may associate the direction and distance to the hive with the snapshots taken from some foraging places. In mammals, the reference direction used at a given important place to express the vectorial representations of the other important places is assumed to be provided locally by the apparent configuration of landmarks, whereas in bees, the reference direction used at a given foraging place to express the vectorial representation of the hive would be provided by a compass. The homing behaviour of pigeons released at distant familiar sites (Fül Featured: et al., 1983; Luschi and Dall’Antonia, 1993) may also be accounted for by the association of the compass bearing of the loft with each of the familiar release sites.

There is thus no doubt that an animal’s brain can form egocentric and exocentric spatial representations about individual places (and possibly about some spatial relationships between them, such as neighbourhood relationships). However, there is so far no clear evidence that it is able to form a global, unified representation of space. The navigational performance of animals over large spaces, i.e. when the nearby landmarks surrounding the goal are beyond perceptual reach from the animal’s current location, can be accounted for by elementary orientation mechanisms or by fairly simple memory processes rather than by a global representation of space. The biological reality of such a representation remains therefore to demonstrate experimentally, and its evolutionary necessity can be questioned.

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References


