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Abstract

During locomotion, mammals update their position with respect to a fixed point of reference, such as their point of departure, by processing inertial cues, proprioceptive feedback and stored motor commands generated during locomotion. This so-called path integration system (dead reckoning) allows the animal to return to its home, or to a familiar feeding place, even when external cues are absent or novel. However, without the use of external cues, the path integration process leads to rapid accumulation of errors involving both the direction and distance of the goal. Therefore, even nocturnal species such as hamsters and mice rely more on previously learned visual references than on the path integration system when the two types of information are in conflict. Recent studies investigate the extent to which path integration and familiar visual cues cooperate to optimize the navigational performance.

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PATH INTEGRATION IN MAMMALS AND ITS INTERACTION WITH VISUAL LANDMARKS

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Summary

During locomotion, mammals update their position with respect to a fixed point of reference, such as their point of departure, by processing inertial cues, proprioceptive feedback and stored motor commands generated during locomotion. This so-called path integration system (dead reckoning) allows the animal to return to its home, or to a familiar feeding place, even when external cues are absent or novel. However, without the use of external cues, the path integration process leads to rapid accumulation of errors involving both the direction and distance of the goal.

Therefore, even nocturnal species such as hamsters and mice rely more on previously learned visual references than on the path integration system when the two types of information are in conflict. Recent studies investigate the extent to which path integration and familiar visual cues cooperate to optimize the navigational performance.

Key words: path integration, dead reckoning, visual landmarks, cognitive map, mammals.

Introduction

Path integration, also termed 'dead reckoning', is a navigational process by which signals generated during locomotion allow the subject to update its position in relation to its point of departure. In animals ranging from ants and bees to small mammals such as rodents, path integration has been studied mainly with respect to homing. The results show that, even if the outward trip takes a sinuous route, the animal returns home by a straight path, along a homing vector that is assessed continuously during the outward trip.

Path integration may occur with or without the help of external references. Hymenopterans, for instance, rely on the solar azimuth (or on correlated skylight patterns) to measure the direction and at least partially on visual flow for assessing the distance of their progression (Wehner, 1992). Night-active rodents, in contrast, measure self-generated information without external references. They combine and 'integrate' vestibular signals, somatosensory and possibly central feedback derived from locomotion and motor commands stored in terms of efference copies. The exclusive dependence on signals from within the organism adversely affects the evaluation of translational as well as of rotational components of locomotion. We shall see that inaccuracies in the measurement of rotations without the help of a compass impose particularly heavy limitations on the computation of position.

The first part of this paper deals with dead reckoning in various mammals tested in the absence of external references. In rodents and carnivores, current research on path integration mainly follows the basic ethological paradigm, in which the subject starts from a fixed point of departure and returns to it.

Human subjects can be induced through verbal instructions to accomplish various tasks that require the estimation of active or passive displacements, such as reproducing changes in direction and/or location, returning to their original position or performing blindfolded the direct route towards a previously presented visual target. The data from different experimental situations will allow us to describe the various inputs to the path integration system. Furthermore, we shall discuss recent models on how path 'integration' is accomplished by this system and how it enables the animal to determine the vector it must follow in order to arrive at a particular location in space.

Considerations on the functional signification of path integration, i.e. its survival value compared with other strategies of navigation, show that path integration is of great importance for central-place foragers, which have to return home even when external references are unavailable or not yet known. However, without the help of external spatial cues, and in particular without an external compass, path integration by itself is not precise enough to be used beyond limited excursions.

This leads us to consider the interplay between path integration and the reliance on stable landmarks which mammals associate on a long-term basis with particular places and/or directions in the familiar environment. Conflict situations between path integration and learned external references allow us to assess their relative importance. The most relevant questions in this context, however, concern the cooperation between these two categories of spatial information. According to a comprehensive view of navigation (Gallistel, 1990), path integration is closely linked with the so-

called cognitive map (for a recent review, see Poucet, 1993), i.e. the representation of familiar space as a system of interconnected landmark–place associations. However, while the connection between path integration and the map optimizes technical navigation systems (Kayton, 1990), it has still to be proved whether it operates at the level of subhuman species. In this paper, we report one recent experiment that tested the hypothesis that rodents update their current position in a known environment not only with respect to their point of departure but also on the level of their map system and, therefore, identify ambiguous landmarks with the help of path integration.

Path integration without external references: input variables

Fig. 1 illustrates the 'homing' performance of golden hamsters, dogs and humans in the classic 'return to the point of departure' task. The subjects were led along an L-shaped path from a point of departure D to a point P, from where they had to return to D. In these experiments, the subjects were prevented from using relevant external cues (visual, acoustic, olfactory) during the outward trip (see legend to Fig. 1). Subjects of all three species still selected approximately the correct direction and travelled on the shortest route. These results suggest that path integration can be accomplished even without the help of external cues such as a sun compass or landmarks. Some errors, however, are evident from these results. The return is never completely precise and, in certain conditions, the three species show similar systematic errors in the return direction, suggesting that they updated the homing vector according to a similar algorithm (Maurer and Séguinot, 1995).

Whether path integration is carried out by insects using the sun azimuth (or correlated skylight patterns) to assess rotations (Wehner, 1992) and optic flow to measure translations (Esch and Burns, 1995; Ronacher *et al.* 1994), or whether path integration is performed by night-active rodents deprived of external references or by self-contained 'technological' inertial guidance systems (Barlow, 1964), the evaluation of both direction and distance is always required. In vertebrates, rotations can be measured unequivocally by the semicircular canals, which respond to angular acceleration only. Otolithic stimulation through linear acceleration may inform the subject about linear distances, provided, however, that the otolithic signals are processed by central mechanisms that differentiate between linear and gravitational acceleration (Mayne, 1974) or are continuously compared with the afferent signals coming from the semicircular canals. (For a recent review of the central processing of inertial signals by the vestibular system, see Wiener and Berthoz, 1993.) Somatosensory information (pressure changes on the skin and proprioceptive reafferences from muscles, tendons and joints) as well as stored motor commands (efference copies) complement vestibular information in the estimation of rotations as well as translations. There is very little analytical evidence on the
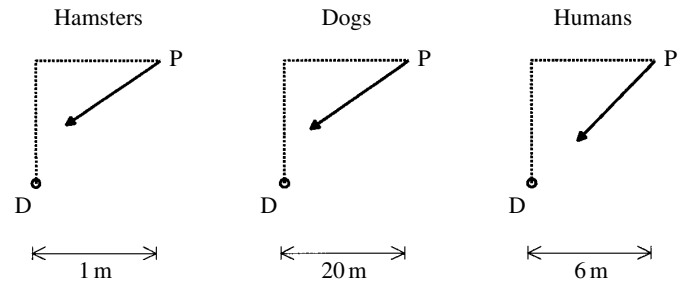

Fig. 1. L-shaped outward journey and direct return in hamsters, dogs and humans. *Hamsters* (*N*=5) followed a bait from their nest (at D) to a food source (at P); there they filled their cheekpouches and then returned home. The entire trial occurred under infrared light, during the diffusion of pink noise and after stirring the sawdust substratum on the experimental floor. The animals were filmed under infrared light and the experimenter was equipped with an infrared viewer to lead the animal during the outward journey (data from Séguinot *et al.* 1993). *Dogs* (*N*=4) were presented with a piece of scentless food at the point of departure (D) and then led to the point P, from where they returned towards D in search of the food. The subjects were blindfolded and earphoned during the outward journey only. The experimental floor was covered with hundreds of food dummies (V. Séguinot, unpublished results). *Human subjects* were guided from point D to point P and then asked to return alone to D. The subjects were blindfolded and earphoned throughout the trial (data from Fujita *et al.* 1993). On the three diagrams, the dotted line represents the guided outward journey and the solid vectors the mean return direction to the point of departure of the entire experimental group.

relative roles of these different categories of signals and, in particular, on how they interact to yield the necessary information for computing position. The available data will be reviewed here first for rodents, the most-studied species in the field of spatial orientation, and then for humans, the ideal subjects for dissociating through behavioural experiments the roles of the various signals pertaining to path integration.

Rodents

The vestibular assessment of *rotations* was demonstrated in homing gerbils. The animals compensated for a brisk passive rotation which they experienced before returning to the nest (Mittelstaedt and Mittelstaedt, 1982). However, non-inertial signals which are generated only during actively performed rotations also play an important role. As illustrated by Fig. 2, golden hamsters were rotated on a platform or had to walk in circles before initiating the return to the nest during hoarding excursions. The greater the number of unidirectional passive rotations or actively performed unidirectional circles, the less they were compensated for and the greater the scatter of the homing direction. Yet, the homing direction was more affected by passive rotations than by walking in circles: on average, the subjects continued to orientate in the general direction of the nest provided they had not been submitted to more than one full rotation; however, if they walked actively, they continued to orient towards the nest even after performing three circles (Etienne *et al.* 1988).

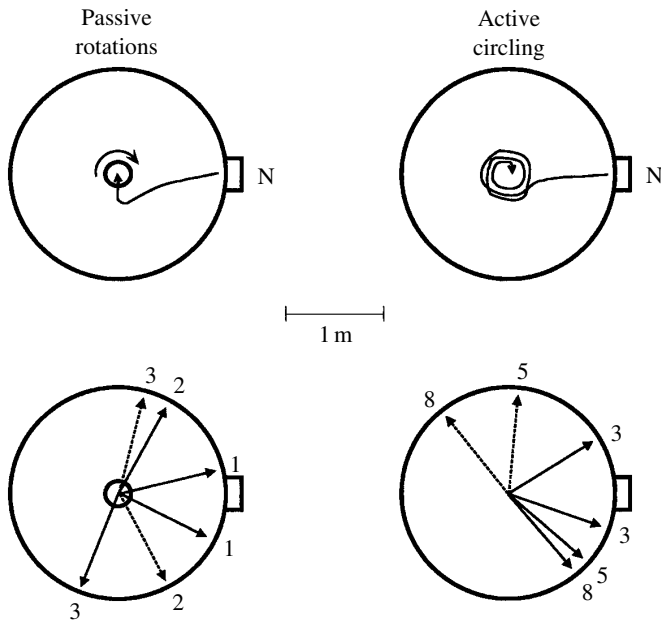In rodents, experiments on the compensation of passive

Fig. 2. Compensation for rotations by hamsters. Upper row, left: the subject was lured from its nest (N) to a food source located on a small platform at the arena centre. While it pouched food, the platform was rotated clockwise or counterclockwise. Upper row, right: the hamster followed a bait from the nest to the central region of the arena, then along a circular path around the arena centre and finally to a food source at the centre. In both situations, the subjects returned fairly directly to the arena periphery and then searched for the nest along the arena wall. All trials occurred under infrared light. Lower row: homing directions. The arrows (solid arrows, *P*<0.05; broken arrows, *P*>0.05; Moore's test) represent the mean orientation of groups of 4–6 subjects just before they reached the arena periphery. Each hamster underwent 15 trials in each experimental situation. The number next to each arrow indicates the number of 360 ° rotations to which the animal had been subjected. Clockwise-biased arrows correspond to clockwise rotations, counterclockwise-biased arrows to counterclockwise rotations. After Etienne *et al.* (1988).
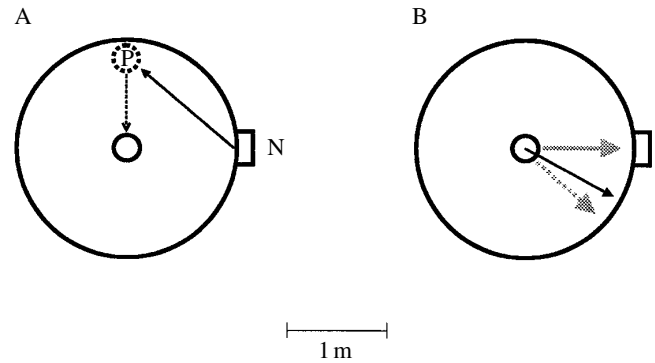

Fig. 3. Compensation for passive translations by hamsters. (A) From its nest N, the hamster followed a bait to a peripheral platform P provided with a food source. While the animal pouched food, the platform was pulled to the arena centre. The animal then returned home. All trials occurred under infrared light. (B) The grey arrows correspond to the theoretical homing vectors assuming that the animal compensated fully for the passive translation (solid arrow) or did not compensate for the passive translation at all (broken arrow). The black arrow indicates the observed mean homing direction (*P*<0.01, Moore's test) of eight animals, each of which underwent 15 experimental trials. After Etienne *et al.* (1988).

translations by means of inertial signals led to inconsistent results. Rats were able to return, mostly through short cuts, to a rewarded goal station after having been transported backwards away from it along an L-shaped pathway. Lesions at the level of the vestibular end organs and of more central vestibular relay stations (vestibular nuclei and caudate nucleus) specifically affected their performance (for references, see Potegal, 1987). Thus, the animals remained informed on changes in both direction and position through vestibular signals during their passive transportation.

Gerbils were reported not to compensate for passive translations while homing after an outward journey consisting of an active and a passive leg (Mittelstaedt and Mittelstaedt, 1982). However, they seemed to react to angular as well as to linear inertial signals when induced to walk along a straight line in a rotating arena (Mittelstaedt and Glasauer, 1991).

Golden hamsters carried out a partial compensation for passive translations in the above-mentioned experiment that involved an active and a passive translation during the outward journey (see Fig. 3). By contrast, in certain experiments, where the animals entered a transportation box at the nest exit to be displaced directly to a food source at the arena centre, the subjects seemed to take into consideration only the angular components of the passive outward journey and therefore chose a constant homing direction (Etienne *et al.* 1988). The discovery of 'head direction cells' that fire even in the absence of external stimuli when the head is in a particular spatial orientation suggests the existence of an internal compass (Taube *et al.* 1990*a*,*b*). When viewed in the light of this finding, the results obtained from golden hamsters suggest that the internal compass dominates over the path integration system whenever the output of this system is opposed to the animal's general expectations on the basis of other sources of information.

Humans

Let us now turn to recent results obtained from human subjects required to evaluate their orientation in space, as well as their distance from the starting point or the goal, after either active or passive changes in orientation or position.

Subjects were induced to perform active *rotations* around their vertical axis (45–315 °) and then to reproduce this rotation (Loomis *et al.* 1993) or to rotate back to their initial orientation (Sauvé, 1989). In both studies, the subjects overcompensated for rotations below 180 ° and increasingly undercompensated for rotations of greater amplitude. Furthermore, the greater the turn amplitude, the greater the scatter of the observed responses.

The role of the semicircular canals in the evaluation of rotations was assessed through the reproduction of passive rotations by normal and labyrinthine-defective patients. After passive rotations around the vertical axis (30–180 °) at

controlled velocity, normal subjects were able to rotate themselves back to their initial position fairly precisely, with a slight undershoot and standard deviations increasing from 5 to 15° from the smallest to the largest rotation. While alabyrinthine subjects completely failed the tests, unilateral absence of vestibular function induced undercompensations of rotations towards the side of the lesion and highly variable responses after rotations in the other direction (Metcalfe and Gresty, 1992). In a similar passive rotation task, normal subjects were instructed to rotate themselves (90–360°) and then to return to their initial orientation. The observed responses exhibited the same tendencies as those found by Metcalfe and Gresty (1992). Interestingly, the path integration aspect of this task, namely the return to the starting position, was executed more precisely than the verbally instructed initial rotation, i.e. subjects tended to return to their original position regardless of whether or not they had turned by the exact amount required by the experimenter (Israël et al. 1995).

The contribution of somatosensory signals to the assessment of actively performed rotations was shown by decoupling these signals from vestibular stimulation. Normal subjects, and even more so labyrinthine-defective patients, who walked in circles on a counter-rotating floor and therefore were not submitted to angular accelerations, experienced subjective rotations and performed the corresponding compensatory eye movements (slow phase of nystagmus). However, comparison of the velocity and timing of the slow-phase eye movements in conditions of vestibular stimulation alone, somatosensory stimulation alone and combined vestibular and somatosensory stimulation revealed that vestibular signals outweighed somatosensory information in healthy subjects. In patients suffering from labyrinthine lesions, the role of non-vestibular afferences increased with the degree of vestibular deficiency, somatosensory information compensating for loss of labyrinthine function (Bles et al. 1984).

In the evaluation of *linear* displacement, locomotor tasks in which actively performed translations (2–11 m) had to be reproduced (Loomis et al. 1993) or to be compensated for by returning to the point of departure (Sauvé, 1989) revealed the subjects' tendency to overestimate shorter and to underestimate longer distances. In further analogy with the compensation of active rotations, the range of errors increased with the length of the path.

The long-standing question as to whether passive translations can be assessed on an exclusively vestibular basis has recently been answered in the affirmative in experiments on the otolithic–ocular reflex (Israël and Berthoz, 1989). Furthermore, in a position estimation task, the subjects' responses approached, within certain limits, the position that would be computed on the basis of twofold integration of the otolith response (Israël et al. 1993; see, however, Mittelstaedt and Glasauer, 1993). When the subjects were asked to reproduce a passive forward translation by actively controlling the velocity of their vehicle, they reproduced fairly accurately the distance, duration and velocity profile of the previously imposed passive forward translation (Georges-François et al. 1995).

However, subjects who were tested according to the Thomson paradigm (Thomson, 1983) were able to cover a visually perceived distance without vestibular information. Fig. 4 illustrates a recent experiment (Glasauer et al. 1994) in which normal and bilaterally labyrinthine-defective subjects were shown a target on the floor at a distance of 4 m and were then blindfolded and required to walk slowly towards the target. The two experimental groups differed with respect to the curvature of their path but showed similar distance errors, some of the subjects overshooting the target by more than 1 m. Similarly, normal subjects who walked the estimated distance on a counter-moving conveyor belt, and therefore experienced no inertial signals, behaved as if walking on a stationary substratum, i.e. vestibular input played no role in their estimation of distance (Mittelstaedt and Glasauer, 1993). Somatosensory information and motor commands are therefore sufficient to inform a subject on the distance walked.

The role of motor commands has recently been substantiated by experiments of the following nature. A visual target was presented on a given plane (level, slanting down or slanting up), and then the subject had to walk blindfolded towards the target, but on a plane of different inclination. In these conditions, the subjects tended to make systematic errors in their walking distance, e.g. overshooting in the case of upward viewing and level walking (for references, see Corlett, 1992).

Taken together, these results suggest that the vestibular system plays a prominent role in the uptake and processing of inertial signals derived from rotations. As for translations, experimental evidence from humans has confirmed that mammals can assess short-distance displacements on a purely vestibular basis. During active walking, however, somatosensory reafferences as well as motor commands seem to play a predominant role in the evaluation of distance. Further hypotheses on the possible mechanisms used for distance estimation, such as the energy expenditure hypothesis and the step-counting hypothesis, which were originally formulated with regard to path integration in insects (for references, see Wehner, 1992), have yet to be confirmed.

The evaluation of internal signals derived from locomotion is always affected by noise in the system. Systematic and random errors in the assessment of angular and linear displacement increase with increased magnitude of the displacement. The greater the number of available self-generated cues, the more precisely the subject estimates its position. Finally, particularly good performances are seen in the 'return to the point of departure' tasks, which have a particular functional significance (see below).

Information processing

Neither rotations nor translations, when computed separately, can provide an estimate of position. The measures for angular and linear displacement need to be continuously combined in order to update the homing vector.

Fig. 4. Blindfolded walk to a previously presented visual target by normal and labyrinthine-defective (LD) human subjects. All subjects were shown a target at 4 m distance and then asked to walk at a slow pace, unguided and blindfolded to the target. Abscissa, Distance to target (filled circle); ordinate, deviation from the desired straight start–target direction. The upper graph reproduces the path followed by 10 normal subjects, and the lower graph the path followed by six labyrinthine-defective subjects. The squares indicate the points where the subjects estimated the target position to be. After Glasauer *et al.* (1994).
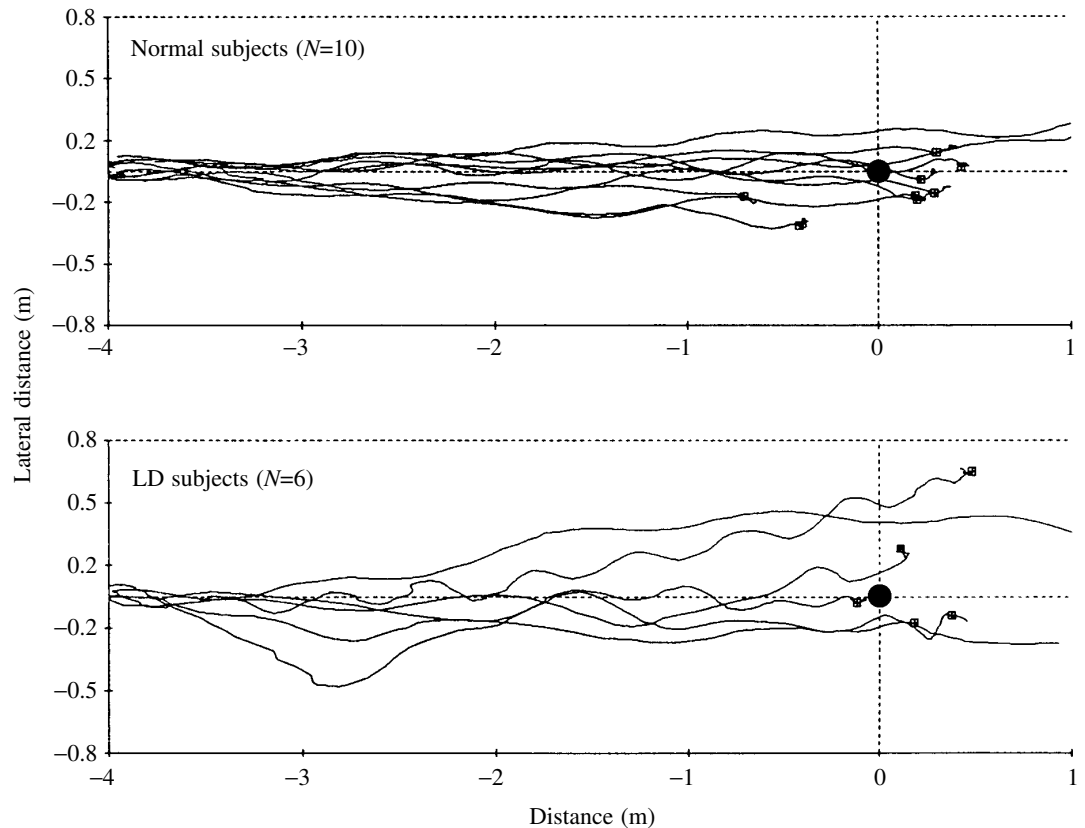
The explicit mathematical description of the computation required is given by trigonometry. Mittelstaedt and Mittelstaedt (1973) used this trigonometric description, without modifying it, as a model of path integration. According to this view, the animal would perform a trigonometric decomposition, within a fixed external reference system, of the elements of its path (any arbitrary, linear segment of the path would be decomposed into its orthogonal – sine and cosine – components) and the resulting components would be summed in order to yield the total positional vector.

Whereas Mittelstaedt and Mittelstaedt grafted the trigonometric process onto an earthbound coordinate system, other authors developed models which assumed that the trigonometric computations would be performed in an egocentric (animal-centred) coordinate system. In this case, the animal does not know its own location relative to a fixed external reference system, but only knows the location of the starting point relative to its body.

P. Bovet and his colleagues (Sauvé, 1989; Benhamou *et al.* 1990) developed such an egocentric trigonometric model. However, the model was probabilistic, i.e. movement was not measured precisely, but only estimated; the estimators for both rotation and linear displacement were affected by errors drawn from an unbiased Gaussian distribution. This was chosen in order to assess the influence of noise in the system. The simulations based on the model have shown that random noise in the measure of linear displacement (i.e. step length) has a limited effect on the overall computation of position; this is also true for rotations if they are measured with the help of an external compass. However, if rotations are measured without a compass, the errors influence the outcome of the positional calculation in an adverse way, by increasing the scatter of the homing vectors.

Fujita *et al.* (1990) started with the same assumptions. Basically, path integration is trigonometry in an animal-centred coordinate system. However, they simplified the equations, considering that, if the animal were sufficiently far away from the starting point, the effects of some variables would become negligible and they could be eliminated from the computations. In a further step, they replaced the sine and cosine functions by linear approximations. They found that the computation was remarkably robust to these manipulations. Later (Fujita *et al.* 1993) they developed another model assuming that the errors in the estimation of position originate from errors in encoding rotations and linear displacements: the errors would be due to the existence of 'deforming' functions in the process of encoding the values for rotation and displacement.

Müller and Wehner (1988), in contrast, did not assume that trigonometry was at the core of the computation. They proposed that the latter relies on simpler arithmetic that can be described as a weighted average: the successive changes in direction, relative to the vector computed so far, are weighted by the distance to the target and averaged. The model is strikingly successful in accounting for the homing behaviour of ants and can even be applied with some success to mammals (see Séguinot *et al.* 1993).

As a last trend in the modelling of path integration, some authors have put forward the idea that the underlying functions

can be realized by neuronal primitives. For example, McNaughton *et al.* (1991) have modelled a neuronal look-up table that would update the orientation of the animal on the basis of its rotations. One of us (Maurer, 1993) has constructed connectionist networks which were trained to compute path integration for a simulated animal. The outcome of the training process applied to these networks led to the conclusion that the computation has to be centred more on rotational than on translational components of locomotion: the networks kept track of the direction of the home vector fairly well, but did not update its length (distance to start). Apparently, only the overall scale of the working space (average distance to start, as experienced during the training process) was used by the network in the function that updated the direction of the vector during linear translations. For further information on models of path integration, see Maurer and Séguinot (1995).

Functional considerations

Path integration that occurs without external references seems to depend on a prewired system of information processing which functions automatically, whenever the subject locomotes. Its functional significance is especially important in the context of homing, i.e. in the case of sedentary and therefore 'domicentred' (Trowbridge, 1913) animals that have to return home, even when landmarks cannot be used or are novel.

In contrast, modelling the consequences of noise in the evaluation of the angular and/or the linear components of locomotion has shown that path integration is open to rapid drift when the assessment of direction occurs without an external compass (Benhamou *et al.* 1990). Only short excursions around the point of departure can therefore occur on the basis of path integration based on internal references alone.

Whether mammals navigate over *longer* distances through compass-aided path integration remains a theoretical possibility that has not been supported by empirical evidence (Bovet, 1992). In our short-distance homing experiments, hamsters took little notice of a spotlight that they could have used as a temporary compass reference for assessing direction (Etienne *et al.* 1990).

However, according to a recent model by J. Bovet on long-distance homing in mammals, the subjects may gain directional information by means of visual cues perceived during the outward journey. The homing direction may then be based on course reversal. By contrast, distance information is not derived from the outward journey, but from the subject's previously acquired, long-term knowledge of the home range size. Thus, after their release in homing experiments with a passive outward journey, red squirrels progressed in a given route-based direction only over a 'critical distance'. They then returned to the release point, from where they tried out new homing directions (for references, see Bovet, 1992).

One limitation of path integration without external references is its effectiveness on relatively short routes only. There is, however, a second drawback. Using the sun as a stable external reference, hymenopteran insects, for instance, can memorize the direction of their homing vector beyond the time-span of a particular foraging trip and use vector information in both directions while commuting between the nest and a given foraging site. But if a central-place forager were to use path integration without a compass to return to a temporary food source, it ought to perform a twofold path integration process: while the outward journey from the nest exit to a new feeding place yields the homing vector, the return from this feeding place to the nest might yield the 'return to the last feeding site' vector. A series of experiments tested this hypothesis on hamsters and showed that the animals were able to return to a previously visited, new feeding site irrespective of the availability of relevant directional references from the test environment. However, the outward direction to the food source was much less precise than the homing direction the subjects usually follow in our experimental conditions. This observation casts some doubt on the possibility that, in natural conditions, the animals might return to a recently discovered feeding site on the basis of path integration alone (Etienne *et al.* 1991).

In conclusion, path integration without external references appears to be mainly a safeguarding strategy, which allows humans as well as other animals to return to a known place after short exploratory excursions. Its value must be especially high for inexperienced, young individuals or after dispersal, when the subject is not yet familiar with its environment. Furthermore, path integration may also be initiated elsewhere than at the home. Myomorph rodents, for instance, are likely to follow olfactory and tactile trails within their home range (Jamon, 1994). They may leave these trails at any moment for short exploratory excursions, resorting to path integration to update their location and then to return to the trail. This possibility has been well documented for ants that mainly follow pheromone trails but also use phylogenetically older mechanisms for astronavigation (Wehner, 1981).

Interaction between path integration and learned visual references

Among mammals, even night-active species such as myomorph rodents are in general well-equipped to perceive and memorize visual landmarks (see Etienne *et al.* 1995). Within their home range, the subjects associate particular visual references with particular places and may then pilot within a system of interconnected landmark–place associations. Experiments on mice (Alyan and Jander, 1994) and hamsters (Etienne *et al.* 1990) have shown that in minor conflict situations between (distant) familiar visual references and path integration, the animals give priority to stable visual references. In the situation illustrated by Fig. 5A, for example, hamsters were exposed throughout the dark phase of the light:dark cycle to a weak light spot located opposite their nest. In test trials, the animals were lured to a food source at the arena centre, in total darkness. As soon as they started pouching food, the light spot appeared in a new position, where it remained until the end of the hoarding excursion. If the

animals depended on the familiar light spot as a stable directional reference, they ought to move away from it during their return to the nest; path integration, in contrast, would lead them back to the point of departure of their excursion, i.e. to the nest entrance in our experimental conditions. In the case of a 90° conflict, the animals' homing direction depended mainly on the light spot. However, a 180° conflict between path integration and the familiar light spot, or repeated shifts of the light spot within the same trial, induced a much greater variance in the results and a mean homing vector pointing towards the nest. These findings suggest that during minor conflicts, external references, stored in long-term memory, dominate over the path-dependent homing vector, which is stored in short-term memory. However, in conflict situations that exceed certain limits, the subjects no longer rely on learned references and some of them change over to predominant dependence on path integration.
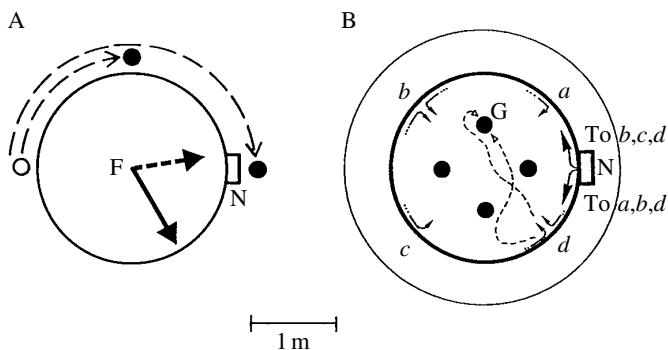

Fig. 5. (A) Conflict and (B) cooperation between path integration and learned visual references. (A) In its standard position, a weak light spot (open circle) is located opposite the nest box (N). During experimental trials, the hamster follows a bait from the nest to a food source (F) at the centre. While it pouches food, the light spot (filled circle) appears in a position which is shifted by either 90° or 180°. The solid vector represents the mean homing directions of 12 hamsters during a 90° rotation of the spot (*P*<0.01, Moore's test); the hatched vector represents the mean homing direction of five subjects during a 180° rotation of the spot (*P*<0.05). All trials took place under infrared light (data from Etienne *et al.* 1990). (B) The arena (inner circle) is surrounded by an optical enclosure (outer circle) and contains four identical cylinders (filled circles) forming a symmetrical array around the centre. The goal cylinder (G) contains a hidden food source. During training, the hamster learns to proceed through two fixed routes to G. It is led under infrared light from its nest (N) along the periphery either to point *a* or to point *c*, through the shortest route. The arena is then lit by ordinary room light, and the animal is induced to proceed by itself to G. In test trials, the animal is led in darkness along six new routes (for clarity, only the initial and final parts of the routes are shown by arrows) to one of four different points (*a–d*) at the arena periphery, from where it has to proceed alone to the correct cylinder within the fully lit arena. The same experiment was repeated in exactly the same way, except that the training and test trials took place in continuous darkness. The two broken lines illustrate the routes towards the goal cylinder taken by two animals after a counterclockwise journey from the nest to point *d*, without seeing the landmarks (J. Berlie, A. S. Etienne, J. Georgakopoulos, R. Maurer, B. Reverdin and V. Séguinot, unpublished results).

Whether path integration *cooperates* with the use of familiar landmarks has, to our knowledge, been examined so far only in insects and humans. Ants establish a link between their homing vector and known landmarks towards the end of a foraging excursion only when their path integrator tells them to match nearby landmarks with the corresponding stored snapshot image in order to pinpoint the invisible nest entrance (Collett *et al.* 1992). At the other extreme, blindfolded human subjects trained to point from a given reference place to various target objects, pointed with ease and fairly precisely to the same objects from a new location to which they had been guided through active locomotion (Rieser *et al.* 1986; Loomis *et al.* 1993). These results suggest that, in a known environment, humans automatically relate path integration to changes in the location of targets with respect to their own position. The perspective under which target objects are expected to be viewed from a new location is therefore updated without concurrent visual input.

Recent experiments on hamsters examine a related question: can rodents identify a particular landmark within a symmetrical array of identical landmarks with the help of positional information from path integration? An experimental method for testing this question on hamsters is illustrated in Fig. 5B. During preliminary training sessions, the animal learns to reach a goal cylinder with a hidden food source by following either of two fixed routes from the nest exit. When the subject leaves the nest, the arena is briefly illuminated. The animal then follows a bait along the arena periphery to point *a* or *c*, in darkness; finally, the arena is again illuminated, and the animal is induced to proceed by itself to the goal cylinder. The latter belongs to a set of four identical cylinders located at symmetrical positions around the arena centre; its identification therefore depends on its location with respect to a fixed reference point (in our conditions the nest exit).

Six test trials follow the same procedures as the training trials, except that the animal is led along six new routes to four different points at the arena periphery, from where it again has to proceed alone to the goal cylinder. So far, nine hamsters have undergone 52 test trials; in 41 (79%) of these trials, the subjects proceeded directly to the goal cylinder without exploring any other cylinder. After having filled their cheekpouches, they returned fairly directly to the nest.

There are two possible explanations for these results. One possibility is that the animal solved the task by translating its current position, as inferred from the path integration process, onto an internally established map that represents the familiar environment in terms of an interrelated set of landmark–place associations. Our hamsters may thus be able, in darkness as well as in light, to relate their instantaneous position to the relative position of the landmarks within the landmark array as represented on their map. When the animal has accomplished its guided journey along the arena periphery and the light is turned on, the subject can compare the perceived appearance and bearing of particular cylinders with their expected appearance and bearing inferred from its own current location. This comparison allows the animal to select the cylinder which

best matches the anticipated appearance and bearing of the goal cylinder.

The other possibility would be that the animal combines the information on its own current position relative to the nest, known through path integration, with the position of the target cylinder relative to the nest, which is also inferred from path integration, but stored in long-term memory. This computation amounts to vector subtraction. It could occur independently of visual input and would not require the use of a map. In contrast to recently proposed models where vector subtraction occurs between seen and stored vectors which are associated with particular landmarks (Cheng, 1989; Collett *et al.* 1986; McNaughton *et al.* 1991), principles of vector addition could be applied to places defined by path integration, independently of any visual input.

To test these alternative explanations, six of the above-mentioned animals underwent the same test series as before; however, the entire trials occurred under infrared light. In these conditions, the subjects very frequently refused to proceed from the periphery to the goal region and instead returned to the nest. Yet, in 24 trials where the subjects decided to proceed to the landmark array, they proceeded along a fairly direct path towards the goal and chose the correct cylinder 23 times (the broken lines on Fig. 5B show two of these paths).

It seems, therefore, that whatever the visual test conditions, the hamsters solve the task by combining the long-term nest-to-goal vector with the current nest-to-self position vector. In this context, seeing the goal cylinder would (1) confirm the route planned ahead through vector information, and therefore induce the animal to leave the arena periphery, and (2) allow the subject to pinpoint more precisely the goal location. In contrast, in the tests conducted under light conditions, the presence of four identical cylinders visible to the animal resulted in more errors than in the tests conducted in darkness. This is because, in the former case, each of the four identical cylinders may have attracted the trained animal. By contrast, in darkness, only the path integration system could be used for inferring the correct location of the food from a distance.

These results open up new perspectives. Can hamsters store vector representations of more than one place to proceed to a series of different foraging sites? If they can, do hamsters use each outward vector independently from the other vectors? Or are the vectors interrelated, so that the animals can proceed along the most economical route from one foraging site to another, without being guided by directly perceived external references? If this last assumption turns out to be correct, it will necessarily lead us back to the much debated map concept, since a map may, among other possibilities, take the form of a vector map, i.e. consist of a set of interrelated vectors (Cartwright and Collett, 1987).

References

Alyan, S. and Jander, R. (1994). Short-range homing in the house mouse, *Mus musculus:* Stages in the learning of directions. *Anim. Behav.* **48**, 285–298.

Barlow, J. S. (1964). Inertial navigation as a basis for animal navigation. *J. theor. Biol.* **6**, 76–117.

Benhamou, S., Sauvé, J.-P. and Bovet, P. (1990). Spatial memory in large scale movements: Efficiency and limitation of the egocentric coding process. *J. theor. Biol.* **145**, 1–12.

Bles, W., de Jong, J. M. B. V. and De Wit, G. (1984). Somatosensory compensation for loss of labyrinthine function. *Acta otolaryngol.* **97**, 213–221.

Bovet, J. (1992). Mammals. In *Animal Homing* (ed. F. Papi), pp. 321–361. London: Chapman & Hall.

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

Cheng, K. (1989). The vector sum model of pigeon landmark use. *J. exp. Psychol.: Anim. Behav. Proc.* **15**, 366–375.

Collett, T. S., Cartwright, B. A. and Smith, B. A. (1986). Landmark learning and visuo-spatial memories in gerbils. *J. comp. Physiol.* A **158**, 835–851.

Collett, T. S., Dillmann, E., Giger, A. and Wehner, R. (1992). Visual landmarks and route-following in desert ants. *J. comp. Physiol.* A **170**, 435–442.

Corlett, J. (1992). The role of vision in the planning and guidance of locomotion through the environment. In *Vision and Motor Control* (ed. L. Proteau and D. Elliott), pp. 375–397. Amsterdam: Elsevier.

Esch, H. and Burns, J. E. (1995). Honeybees use optic flow to measure the distance of a food source. *Naturwissenschaften* **82**, 38–40.

Etienne, A. S., Hurni, C., Maurer, R. and Séguinot, V. (1991). Twofold path integration during hoarding in the golden hamster? *Ethol. Ecol. Evol.* **3**, 1–11.

Etienne, A. S., Joris-Lambert, S., Maurer, R., Reverdin, B. and Sitbon, S. (1995). Optimizing distal landmarks: horizontal versus vertical structures and relation to background. *Behav. Brain Res.* **68**, 103–116.

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

Etienne, A. S., Teroni, V., Hurni, C. and Portenier, V. (1990). The effect of a single light cue on homing behaviour of the golden hamster. *Anim. Behav.* **39**, 17–41.

Fujita, N., Klatzky, R. L., Loomis, J. M. and Golledge, R. G. (1993). The encoding-error model of pathway completion without vision. *Geogr. 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. *Geogr. Analysis* **22**, 326–335.

Gallistel, C. R. (1990). *The Organization of Learning.* Cambridge, MA: MIT Press.

Georges-François, P., Grasso, R., Berthoz A. and Israël, I. (1995). Self-controlled reproduction of passive linear displacement: distance, duration and velocity. In *Multisensory Control of Posture and Movement* (ed. F. Hlavacka and T. Mergner). London: Plenum (in press).

Glasauer, S., Amorim, M.-A., Vitte, E. and Berthoz, A. (1994). Goal-directed linear locomotion in normal and labyrinthine-defective subjects. *Expl Brain Res.* **98**, 323–335.

Israël, I. and Berthoz, A. (1989). Contribution of the otoliths to the calculation of linear displacement. *J. Neurophysiol.* **62**, 247–263.

ISRAËL, I., CHAPUIS, N., GLASAUER, S., CHARADE, O. AND BERTHOZ, A. (1993). Estimation of passive horizontal linear whole-body displacement in humans. *J. Neurophysiol.* **70**, 1270–1273.

ISRAËL, I., SIEVERING, D. AND KOENIG, E. (1995). Self-rotation estimate about the vertical axis. *Acta otolaryngol.* **115**, 3–8.

JAMON, M. (1994). An analysis of trail-following behaviour in the wood mouse, *Apodemus sylvaticus*. *Anim. Behav.* **47**, 1127–1134.

KAYTON, M. (1990). *Navigation: Land, Sea, Air and Space*. New York: IEEE Press.

LOOMIS, J. M., KLATZKY, R. L., GOLLEDGE, R. G., CICINELLI, J. G., PELLEGRINO, J. W. AND FRY, P. A. (1993). Nonvisual navigation by blind and sighted: assessment of path integration ability. *J. exp. Psychol.: Gen.* **122**, 73–91.

MAURER, R. (1993). L'intégration du chemin ou navigation à l'estime chez l'animal. Formalisation de modèles neuromimétiques. Doctoral thesis, University of Geneva.

MAURER R. AND SÉGUINOT, V. (1995). What is modelling for? A critical review of the models of path integration. *J. theor. Biol.* **175,** 457–475.

MAYNE, R. (1974). A systems concept of the vestibular organs. In *Handbook of Sensory Physiology*, vol. VI/II (ed. H. H. Kornhuber), pp. 493–580. Berlin: Springer.

McNAUGHTON, B. L., CHEN, L. L. AND MARKUS, E. J. (1991). 'Dead reckoning', landmark learning and the sense of direction: a neurophysiological and computational hypothesis. *J. cogn. Neurosci.* **3**, 190–202.

METCALFE, T. AND GRESTY, M. A. (1992). Self-controlled reorienting movements in response to rotational displacements in normal subjects and patients with labyrinthine disease. *Ann. N.Y. Acad. Sci.* **656**, 695–698.

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 *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 290–297. Berlin: Springer Verlag.

MITTELSTAEDT, M. L. AND GLASAUER, S. (1991). Idiothetic navigation in gerbils and humans. *Zool. Jb. Physiol.* **95**, 427–435.

MITTELSTAEDT, M. L. AND GLASAUER, S. (1993). Contribution of inertial and substratal information to the perception of linear displacement. *Proceedings of the XVIIth Barany Society Meeting*, Prague, pp. 102–105.

MÜLLER, M. AND WEHNER, R. (1988). Path integration in desert ants, *Cataglyphis fortis. Proc. natn. Acad. Sci. U.S.A.* **85**, 5287–5290.

POTEGAL, M. (1987). The vestibular navigation hypothesis: a progress report. In *Cognitive Processes and Spatial Orientation in Animal and Man*, vol. II (ed. P. Ellen and C. Thinus-Blanc), pp. 28–34. Dordrecht: Martinus Nijhoff Publ.

POUCET, B. (1993). Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychol. Rev.* **100**, 163–182.

RIESER, J. J., GUTH, D. A. AND HILL, E. W. (1986). Sensitivity to perspective structure while walking without vision. *Perception* **15**, 173–188.

RONACHER, B., MANETSCH, D. AND WEHNER, R. (1994). Self induced optic flow cues influence the assessment of travel distance in the ant *Cataglyphis fortis. Göttingen Neurobiology Report.* Stuttgart, New York: Thieme.

SAUVÉ, J.-P. (1989). L'orientation spatiale: Formalisation d'un modèle de mémorisation égocentrée et expérimentation chez l'homme. Doctoral thesis, University of Aix-Marseille II.

SÉGUINOT, V., MAURER, R. AND ETIENNE, A. S. (1993). Dead reckoning in a small mammal: The evaluation of distance. *J. comp. Physiol.* A **173**, 103–113.

TAUBE, J. S., MULLER, R. U. AND RANCK, J. B. J. (1990a). Head direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *J. Neurosci.* **10**, 420–435.

TAUBE, J. S., MULLER, R. U. AND RANCK, J. B. J. (1990b). Head direction cells recorded from the postsubiculum in freely moving rats. II. Effect of environmental manipulations. *J. Neurosci.* **10**, 436–447.

THOMSON, J. A. (1983). Is continuous visual monitoring necessary in visually guided locomotion? *J. exp. Psychol.: Human Perception and Performance* **9**, 427–443.

TROWBRIDGE, C. C. (1913). On fundamental methods of orientation and 'imaginary maps'. *Science* **38**, 888–897.

WEHNER, R. (1981). Astronomischer Kompass bei duftspurlegenden Ameisen (Messor). *Jb. Akad. wiss. Lit. Mainz* **81**, 112–116.

WEHNER, R. (1992). Arthropods. In *Animal Homing* (ed. F. Papi), pp. 45–144. London: Chapman & Hall.

WIENER, W. AND BERTHOZ, A. (1993). Forebrain structures mediating the vestibular contribution during navigation. In *Multisensory Control of Movement* (ed. A. Berthoz), pp. 427–456. Oxford: Oxford University Press.