

## Resetting the path integrator: a basic condition for route-based navigation

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### Summary

During short excursions away from home, some mammals are known to update their position with respect to their point of departure through path integration (dead reckoning) by processing internal (idiothetic) signals generated by rotations and translations. Path integration (PI) is a continuously ongoing process in which errors accumulate. To remain functional over longer excursions, PI needs to be reset through position information from stable external references. We tested the homing behaviour of golden hamsters (*Mesocricetus auratus* W.) during hoarding excursions following a rotation of the arena and nest. In continuous darkness, the hamsters returned to their point of departure at the rotated nest, and therefore depended on PI only. In other trials, the animals were briefly presented with visual room cues

during or at the end of the outward trip, visual cues being pitted by 67° or 98° against the animal's current self-generated position vector. After a fix, the animals headed for the usual (unrotated) nest location, as defined by room cues, independent of the timing of the fix. These results were obtained in two different geometrical settings and showed that, after the fix, the animals update their position, and not merely their head direction or internal compass, in a new reference frame. Thus, episodic fixes on familiar external references reset the PI and therefore greatly enhance the functional signification of navigation that is based on feedback information from locomotion.

Key words: golden hamster, *Mesocricetus auratus*, path integration, internal compass, cumulative error, visual position fix.

### Introduction

Path integration (PI) allows a navigator to update their position with respect to a particular reference point without using external, location-based references. Instead, the navigator assesses changes in direction and distance through signals that are generated by locomotion. Path integration is a continuously ongoing computational process, which may be modelled in discrete form by breaking the path into arbitrarily small steps. Every step yields a particular vector, which is added to the vector that represents the agent's position at the end of the preceding step. Thus, during an excursion, the agent's current position vector results from the summation of the vectors that derive from all preceding steps, and errors which affect the estimation of position get necessarily accumulated.

The accuracy of path integration depends on (1) the precision in estimating and coding rotations and translations and (2) the adequacy of the algorithm according to which new increments in direction and distance are computed and added to the current position vector.

(1) Mammals ranging from rodents to humans are capable of updating their position through internal or idiothetic (Mittelstaedt and Mittelstaedt, 1973) cues exclusively (Berthoz et al., 1999; Etienne and Jeffery, in press). However, without the help of external references, the estimation of the angular and linear components of locomotion is strongly affected by cumulative errors. Inaccuracies in the mainly vestibular

measure of rotations are particularly detrimental. They lead to a progressive shift of the idiothetic directional reference frame itself and thus to angular drift (Benhamou et al., 1990; Etienne et al., 1988, 1996). Furthermore, without the help of a general directional reference such as the sun or geomagnetic field, vector information cannot be stored in short-term memory during pauses in locomotion. To retrieve a stored vector at a resource site in order to return home, the subject needs to relate this vector to a currently perceived, external reference direction. Without the latter, PI has to go on throughout an excursion, a condition which greatly increases the accumulation of noise.

(2) The attempts to formalize PI range from computations that are mathematically correct (Mittelstaedt and Mittelstaedt, 1982; Gallistel, 1990) to approximate algorithms based on the observation of systematic errors in the homing behaviour of various species. In the latter perspective, Müller and Wehner (1988) observed that, after a two-leg outward journey to a food source, homing desert ants overshoot the return angle at the end of the second outward leg and therefore commit an 'inwards' homing error. As the same bias has also been observed in homing through PI by other arthropods and by mammals (for references, see Etienne and Jeffery, in press), a similar PI algorithm may have evolved in different taxa (Maurer and Séguinot, 1995; Müller and Wehner, 1988).

Obviously, the PI system is not a strategy allowing an animal to explore its environment over longer distances and to return home safely unless it is complemented by additional spatial references. Convergent results from unrelated species suggest that all animals with a fixed home base use two very different, but deeply complementary, categories of spatial information to return to their home base and also to proceed to a familiar resource site: landmarks and PI. We may therefore expect that visual landmarks or any other stable familiar cue from the environment can reset PI. Only in this condition will PI remain functional beyond very short excursions.

In navigational terms, the process by which an agent derives position information from the current view of landmarks is named 'taking a position fix'; the agent has to estimate its current position within an allocentric reference frame in spite of viewing familiar landmarks from an egocentric perspective, which depends on its own location and orientation (Gallistel and Cramer, 1996). Furthermore, in the context of PI, the resultant allocentric position coordinates are not just used for place navigation but have to be fed into the path integrator. Thus, after the fix, self-position is updated on the basis of visually computed coordinates.

In our current study on the role of visual fixes during PI by hamsters, the animal hoards food in darkness. During a short time interval, the room lights are turned on, either at the end or during the outward trip to the food source. During the fix interval, there is a 98° conflict between the nest direction as computed from the room cues and the nest direction as derived from PI. In a conflict situation of this magnitude, hamsters (Teroni et al., 1987; Etienne et al., 1990b) and mice (Alyan and Jander, 1994) give priority to vision (and may therefore reset the path integrator through a fix on the landmark scenario).

Preliminary results that were obtained in the above-mentioned conflict situation (Etienne et al., 2000), in our usual experimental set-up with the nest at the arena periphery, left two questions open.

First, hamsters reorient their homing paths less frequently and less accurately when they have the possibility of taking a fix at the end rather than during the outward journey. This result is unexpected. In the first case, the animals may register the visually perceived homing direction in short-term memory and then proceed without sensory feedback along this direction towards the nest. By contrast, in the second case, further updating is needed during the final phase of the outbound trip. In a first experiment, we therefore wished to control our previous data by testing additional subjects according to the same procedures.

Second, during the light interval, the animals may have reoriented the representation of their position, or only the representation of their azimuth, i.e. of their head direction in the horizontal plane (H. Mittelstaedt, personal communication). We assume that head direction is continuously represented by an 'internal compass', which is based on the ensemble activity of head direction cells (Etienne and Jeffery, in press) and may be considered as a subsystem of the path integrator (McNaughton et al., 1996). We

approached this question in a second experiment by changing the geometry of the test space and of the outward journeys, the nest entrance being no longer located at the arena wall but in a more central region of the arena floor. These changes enabled us to create two distinct zones in the arena where the animal may expect the nest to be (1) after a position fix, operating upon the representation of the animal's location and orientation, and (2) after a merely directional fix, acting only upon its internal compass. Testing the animals in an arena with a central nest revealed further features of PI itself.

## Materials and methods

### *Subjects*

Throughout our study, we used only female hamsters (*Mesocricetus auratus* W.) that were at least three months old, females showing a higher motivation for food hoarding than males (Etienne et al., 1983) and getting more easily adapted to our test conditions after a certain age. The majority of subjects came from our own breeding stock. They were isolated from their mother and littermates at the age of one month and each individual lived thereafter in its own home cage, which was provided with a shelter. The animals were always fed *ad libitum* (with hamster pellets, vegetables and fruit), as hoarding is not influenced by food deprivation in this species. The animals were subjected to an artificial light cycle and tested at the beginning of the dark phase (17.00 h to 05.00 h), when these dusk- and night-active animals show the highest activity peak. During the light phase, the experimental room was illuminated by soft, indirect lighting emanating from four tungsten lights fixed at the base of each wall. In test trials with a fix, this 'light phase illumination' was turned on for 10–12 s.

### *Experimental arena and test rooms*

The subjects lived and were tested in a large circular arena (diameter=220 cm). The arena was surrounded by a metal wall (height, 30 cm) and its floor was covered with a thick layer of sawdust (~7 cm deep when flattened). Being mounted on wheels and on a central pivot, the arena could easily be rotated. In experiment I, a nest box, where the animal also established its granary, was attached to the outer side of the arena wall (peripheral nest). The subject could commute between the nest and the arena floor by pushing a door hinged at the top. Three other doors, identical to the nest door but permanently shut, were built at regular intervals into the arena wall. In experiment II, the nest box was located below the arena floor, 50 cm from the arena periphery (central nest). The subject climbed through a hole (diameter=9 cm) onto the arena floor. During the experiments, as soon as the animal started to follow a bait that was presented on the arena floor, the nest exit was covered by a cardboard sheet with a (glued) layer of sawdust. Thus, the animal could identify neither the peripheral, nor the more centrally located nest entrance when the (soft) room lights were turned on. During the experiments, the access to the arena was controlled by shutting the nest exit.



Fig. 1. Experimental room A and apparatus in experiment I. The rectangular room (567 cm×433 cm×220 cm) contained two arenas (diameter: 220 cm) that were equipped with a peripheral nest box. The short walls were either white or black with a grey margin, and the long walls were covered with two-dimensional landmarks. Three landmark objects were located between the two arenas. Normal room lighting was provided by lamps at floor level. An infrared video camera that was surrounded by a ring of infrared diodes (peak emission, 940 nm; bandwidth, 45 nm) was mounted on an optic bench and moved above the centre of the arena where the animal was being tested.

Experiment I took place in room A (Fig. 1), which was located in a country house, and experiment II in room B, in a town building. Both rooms contained two arenas with their centres on a line parallel to the long wall of the room and were richly decorated with landmarks. The white and black patterns of the landmarks were adapted to the visual acuity of hamsters ( $0.5\text{--}0.7\text{ cycles deg.}^{-1}$ ; Emerson, 1980). The shape of the visual configurations was conceived on the basis of a long series of experiments that established their effectiveness as landmarks in conditions of a  $90^\circ$  conflict between vision and PI (Etienne et al., 1990a, 1995a,b; Levy, 1999).

#### *General procedures*

The basic experimental procedures were the same in experiments I and II. However, the geometry of the outward journeys had to be adapted to a number of new conditions in experiment II. For the sake of clarity, we describe here the procedures for experiment I with the peripheral nest box. Specific features of the procedures of experiment II with the central nest box will be mentioned in the Results section for that experiment.

#### *Habituation phase*

Each female hamster was introduced into an experimental arena a few days before the start of the experiments and lived there throughout the test period. Before testing began, the

animals were habituated to the experimental procedures for about two weeks. To be ready for the test trials, they had to show nest-oriented return trips during guided hoarding excursions that took place in different light conditions. Animals that failed to establish their nest and granary within the nest box, to follow a bait in darkness with a strong motivation for hoarding and/or to show nest-oriented homing trips during preliminary trials (see below) were excluded from the experiment.

#### *Experimental phase*

At the beginning of each test session, the animal was locked up in its nest, and the sawdust substrate was thoroughly stirred up and flattened out again. Before trials in which the subject was expected to cross a zone where it had already been during the previous hoarding excursion, the sawdust was again rapidly mixed at the corresponding location. These precautions were taken to eliminate intra-arena references, either olfactory or tactile.

#### *Test trials in experiment I*

Each test trial (see Fig. 2) consisted of a complete hoarding trip. The subject (1) left the nest, followed a baited, dimly illuminated spoon to a location where the spoon was emptied (outward trip), (2) remained at the food source for  $\sim 20$  s to fill its cheek pouches and (3) returned home to deposit the food in

its granary (return or homing trip). The shape of the outward journey varied between different types of trials. Except for trials 'with a (visual) fix', the complete hoarding excursion took place under infrared light within a wavelength band ( $940\pm 45$  nm) that was well above the limits (740 nm) of the hamsters' visual responsiveness to red and near infrared (Vauclair et al., 1977).

Before starting an experimental session, we tested each subject in two categories of reference trials. 'Uncontrolled reference trials', involving a fairly linear outward journey to a variable location on the arena floor, examined whether the animal returned to the point of departure of its excursion in continuous darkness, updating its position during a simple outward journey. Next, 'controlled reference trials' tested the animals' homing performance in conditions where they could rely on PI as well as on familiar visual references. The rationale of these trials was to habituate the subjects to the sudden illumination of the experimental room and to consolidate the uptake of location-based information when the arena, and therefore the nest entrance, was located in its standard position. Furthermore, these trials allowed us to estimate the effect of the fix and possible variations in its influence. Finally, before the animals left the nest to start the hoarding excursion, the arena (with nest) was rotated by  $180^\circ$  and then back in its standard orientation. This precaution was taken to neutralize possible side effects due to the fact that the arena was always rotated in the experimental trials. Note that albeit passive rotations necessarily stimulate the animals' vestibular system by angular acceleration and are therefore perceived as such; hamsters (Etienne et al., 1986, 1988) and mice (Alyan, 1996) seem to dismiss inertial signals which, during the rotation of the nest, are contradicted by intra-nest references.

In the four types of experimental trials (Fig. 2), the arena and nest box were rotated by  $135^\circ$ , clockwise or counterclockwise, so that the hamster initiated PI at the rotated nest exit. 'Baseline' and 'baseline-with-circling trials' tested the animals' homing performance in continuous darkness after a two-leg outward journey. In baseline trials, the animal paused after the first outward segment, at P1, and in baseline-with-circling trials it had instead to walk in circles at P1. The imposed circling behaviour at P1 was meant to inject additional noise into the PI system.

In the two categories of fix trials, the hamsters were led to P1, where they followed the baited spoon in circles, first in darkness and then (in the opposite direction) under room light. In 'fix-without-translation trials' (where translation refers to the second leg of the outward journey), the fix took place just before the animal filled its cheek pouches at point P1, from where it returned home. By contrast, in 'fix-with-translation trials', the subject had to update its position after the fix, during a second outward translation to the feeding place, which occurred in the dark. Fix-with-translation trials were therefore crucial for analysing whether a visual fix was just kept in short-term memory or acted on the state of an integrator.

In all trials with a controlled outward journey, the animal

was made to approach the food source at point P1 or P2 from a particular direction, being orientated either towards or  $180^\circ$  away from the standard nest location. Furthermore, in trials with a fix, care was taken not to counteract the subject's expectation to find the nest in case it proceeded towards the standard nest location. Thus, the arena was rotated back in its standard orientation and the lights were turned on as soon as the subject had reached the arena's peripheral annular zone. Following the visual cues, the animal compensated automatically for the arena rotation and found the nest box without any difficulty.

A further precaution concerned the possibility that the animals used the experimenter as a reference. To prevent this, the experimenter moved herself while guiding the animal to the food source, reaching different positions at the end of the animal's outward journey and remaining immobile during the subject's homing trip, which always occurred under infrared light. During the light-on interval of fix trials, the animal could see the experimenter at varying positions near the arena border without seeming to be influenced by her.

#### *Expected homing directions in experiment I*

In experimental trials without a fix, the animals could rely on PI only and therefore were expected to return towards the rotated nest (see dotted arrows in the arena circles of Fig. 2). Furthermore, the return directions were expected to be more dispersed in baseline-with-circling trials than in baseline trials.

In experimental trials with a fix, three theoretical homing patterns could be expected. (1) A return to the rotated nest (dotted arrow) would mean that the animal either had not taken a fix or that it had taken up visual position information but then nevertheless followed the PI vector that is anchored to the rotated nest location (Georgakopoulos and Etienne, 1997). (2) If the animal returned towards the standard nest location (dashed arrow), the fix was taken and, in fix-with-translation conditions, the animal's PI system was reset with respect to the standard nest location. (3) The hamster may finally follow a compromise direction, not shown in the corresponding graphs, or switch from one reference point to the other during the performance of the homing trip. In this case, overt behaviour is controlled simultaneously or in succession by the initially established PI vector and the brief presentation of the room cues (Etienne et al., 1990b; Georgakopoulos and Etienne, 1997).

#### *Organisation of experiments*

After a habituation phase of about two weeks, each subject was tested at least five times per week in the following conditions. At the beginning of an experimental session, the animal had to be oriented homewards in two uncontrolled reference trials and then in two controlled reference trials. If the subjects failed one of the first two trials of either category, they were submitted to a third trial. If they failed this trial again, the test session was postponed to the next day.

A test session was subdivided into sequences of three experimental trials. After each of the first two experimental

trials within such a triplet, the subject had to pass one uncontrolled reference trial, and after the third experimental trial, one controlled reference trial. If the animal was not oriented homewards in the first control trial of each category, the trial was repeated. In the case of a second failure, the session was interrupted. In general, the animals passed one to two sequences of three experimental trials per session and sometimes up to three sequences.

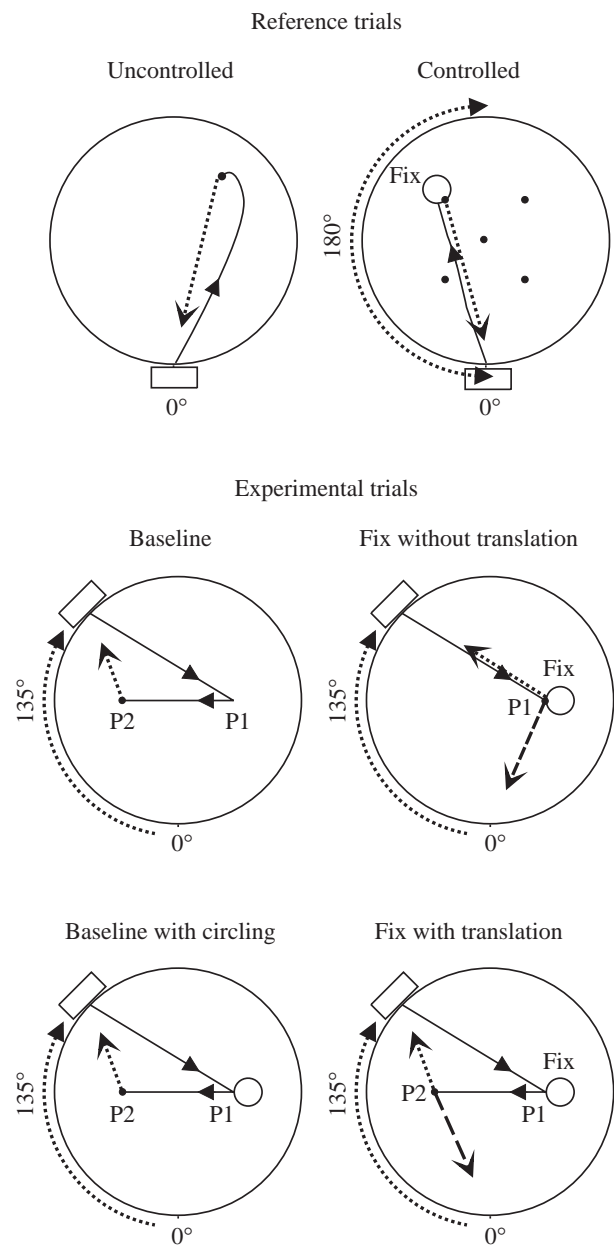
The timeline of a particular test session may be illustrated by the following example: two (successful) uncontrolled reference trials – two (successful) controlled reference trials – one experimental trial (e.g. clockwise fix-without-translation) – two uncontrolled reference trials (the animal fails the first and succeeds the second trial) – one experimental trial (e.g. counterclockwise baseline) – one (successful) uncontrolled

reference trial – one experimental trial (e.g. counterclockwise fix-with-translation) – one (successful) controlled reference trial – one experimental trial (e.g. clockwise baseline-with-circling) – etc.

During an experimental session, each independent variable (e.g. sense of rotation of arena, type of controlled reference trial or experimental trial, initial sense of spoon-guided circles around P1, orientation at the food source) was varied according to a pseudo-random order.

Altogether, a hamster underwent 10–12 (and exceptionally up to 14) clockwise trials and the same number of counterclockwise trials in each of the four basic experimental situations. Assuming that a subject was successful in all reference trials and passed 80 experimental trials altogether in nine sessions only, it underwent 72 uncontrolled and 45

Fig. 2. Test trials and expected homing directions in experiment I. The large circles with a small rectangle represent the experimental arena and peripheral nest box, respectively. The dotted arrows along the arena circle indicate that the arena has been rotated before the start of the trial. The continuous lines with an arrow within arena circles represent the outward journey to the food source. The small circles indicate that the animal walks in circles (diameter=30 cm). Trials without a fix (left) take place under infrared light only, and the subjects can only home through path integration (PI) that is anchored to the current nest position (dotted arrows). In trials with a fix (right), the room lights are turned on for 10–12 s during or at the end of the outward trip, when the subject is located at P1. During a fix, the homing directions based on PI on the one hand, and on visual references on the other hand, diverge by 98°. The arrows starting at P1 or P2 represent the expected homing directions depending on PI that is reset by a visual fix (dashed arrows) or is not reset (dotted arrows). (In controlled reference trials, the two expected homing directions lead to the nest at 0°). In uncontrolled reference trials, the arena is not rotated and the animal is guided from the nest exit at 0° to any point on the arena floor, where it is offered food, and then returns to the nest. In controlled reference trials, the arena and nest box are rotated by 180° and then rotated back to the standard 0° position. From the nest exit at 0°, the hamster is led to one of five different locations (dots), where it walks along 2.5 full circles (small circle) in the dark, and then along a further circle in the opposite direction, the room lights being turned on. The animal is then offered food and returns home, in darkness. In both reference trials, homing is considered to be successful if the animal deviates by no more than 45° from the correct homing direction when reaching the arena periphery. Before the start of each experimental trial, the arena (with nest box) is rotated by 135° clockwise or counterclockwise. Only clockwise trials are presented here. In baseline trials, the hamster is guided to P1, where it picks up some food, and then to P2, where it fills its pouches completely and initiates the homing trip. Baseline-with-circling trials follow the same pattern, but the animal walks along 2.5 full circles near P1 instead of pouching food. In fix-without-translation trials, the animal is led to P1, walks along 2.5 full circles in the dark and then along a further circle in the opposite direction in the fully lit environment, fills its cheek pouches at P1 and returns towards the arena periphery. Fix-with-translation trials follow the same procedures; however, after the fix interval, the animal is led from P1 to P2, where it fills its pouches and starts the homing trip.



controlled reference trials. In fact, these numbers were always higher, and each subject was tested over several weeks.

#### *Recording and evaluation of behaviour in experiment I*

Except for the uncontrolled reference trials, the complete hoarding trips were recorded by an infrared video system. The coordinates of the subjects during their returns from the feeding place to the arena periphery were subsequently computed (every 200 ms) from the recordings by means of a videotracking system (EthoVision version 1.90; Noldus Information Technology, Wageningen, The Netherlands).

The subjects' orientation in controlled reference trials and in the four types of experimental trials was assessed with respect to two different reference systems (Fig. 3): (1) the animal's position at the end of the homing trip was recorded in the coordinates of the real arena floor and (2) the animal's position

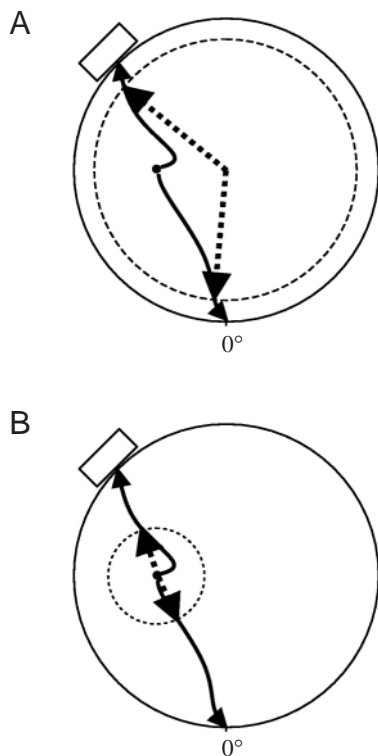


Fig. 3. Evaluation of homing directions in experiment I. For each trial, the homing direction was measured in two coordinate systems. (A) The animal's position at the end of the homing trip, when it reached the 15 cm-wide peripheral annular zone of the arena (dashed circle) was coded with respect to the real arena floor, which was subdivided into  $10^\circ$  sectors. The  $0^\circ$  reference direction was the radius vector pointing from the centre of the arena to the standard nest location; positive values corresponded to clockwise angles. As the return to the nest (curved path) does not start at the arena centre, this measure entails a bias (see text). (B) The animal's orientation was therefore assessed by a second measure, at a distance of 35 cm from the start of the return, with a mobile grid (dotted circle), also subdivided into  $10^\circ$  sectors. The grid was centred on the start of the return at P2 (or P1), and its  $0^\circ$  reference direction was aligned with the standard position of the nest entrance.

at a distance of 35 cm from the start of the homing trip was recorded in the coordinates of a mobile grid.

In the first reference system, we coded the subject's position at a distance of 15 cm from the arena wall, with respect to the arena floor, the  $0^\circ$  reference direction being the radius vector pointing to the standard position of the nest entrance. This type of presentation of the results shows how the animal finalises homing in the coordinates of the arena but leads to slightly biased measures, as the return trips do not start at the centre of the arena (see Fig. 3A). For example, if the animal headed from P1 or P2 exactly towards the standard position of the nest entrance, the true direction measured in the coordinate system of the arena was  $4^\circ$  (instead of  $0^\circ$ ). If the animal headed from the two points of departure to the rotated nest position, the direction measured was  $131^\circ$  (instead of  $135^\circ$ ). These angular shifts were not taken into consideration in the evaluation of the results (the return directions to the standard and rotated nest were coded as  $0^\circ$  and  $135^\circ$ , respectively).

To avoid the above-mentioned bias, we took a second measure by means of a mobile grid (Fig. 3B). The grid was centred on the starting point of the return trip, and its  $0^\circ$  reference direction pointed to the standard position of the nest entrance. This reference system allowed us to measure, at a constant distance from the starting point of the return, the animal's exact angular deviation from the direction of the standard nest location. (A direction of  $0^\circ$  and  $-176^\circ$  means that the animal is heading towards the standard and rotated nest location, respectively.) In general, the orientation data based on both types of evaluations will be presented together.

The main question as to whether the animals had taken a fix in each of the two conditions with a fix was assessed by circular statistics and also quantified in terms of the ratio of trials in which the animals returned in the general direction of the standard nest location. We used the following criterion to determine whether the animal had taken a fix in a particular trial. From the starting point of the return, a first line was drawn to the rotated nest box, and a second line to the standard position of the box. The two lines determined an angle of which we drew the bisector. If the animal reached the peripheral annulus of the arena in the region between the bisector and the standard location of the nest box, we considered that it had taken a fix.

A number of temporal parameters of the outward and return journeys were measured. We report four of them. (1) The 'outward plus pouching time' includes the duration of the outward trip plus the time the animal takes to fill its cheek pouches, i.e. the interval between the moment the animal left the nest exit and the start of the return. This measure covers the total time during which the animal has to update its position before the return, including the duration of the food uptake, where the animal often turns around the food source. (2) In trials with a fix, the 'fix-return interval' corresponds to the interval between the moment the room lights are turned off and the start of the return. Furthermore, two time variables were measured with respect to the return trip: the time the animal takes to return from the food source (3) to the peripheral

annular zone of the arena and (4) to the nest door. In fix trials, variable 4 was not measured, as the fix oriented the subjects towards the virtual standard nest location.

*Statistics*

Circular statistics (Batschelet, 1981; Fisher, 1995) were used throughout. On the first order level, we used the Rayleigh test to determine whether the observed homing directions from particular subjects were significantly orientated, and the Mardia–Watson–Wheeler test to see whether the return directions in two different experimental conditions differed significantly from each other.

On the second order level, Moore’s non-parametric test for directionality assessed the statistical significance of second order vectors, and the Mardia–Watson–Wheeler tested the differences in the orientation of the subjects in two different experimental situations. Furthermore, for each experimental condition, the Hotelling confidence interval test established whether the mean orientation of an experimental group differed from the expected (or any alternative) homing direction.

Non-circular statistics were used to assess the significance of a number of variables in the results from repeatedly tested animals. The ratios of trials in which the animals took a fix were compared with the Wilcoxon matched-pairs signed-ranks test. This test also allowed us to compare the length of the homing vectors and the average values of the above-mentioned return times shown by the same subjects in two different experimental conditions.

**Results**

*Experiment I*

We tested our hamsters in optimal conditions to let them take a visual fix and to maintain significantly orientated homing trips. Two sets of data are presented here. Eight hamsters were submitted to the complete experimental series and performed at least 10 trials in each experimental condition. The results from these subjects are presented in the form of the mean orientation of each subject and of the total experimental group, i.e. on the level of first and second order statistics. To

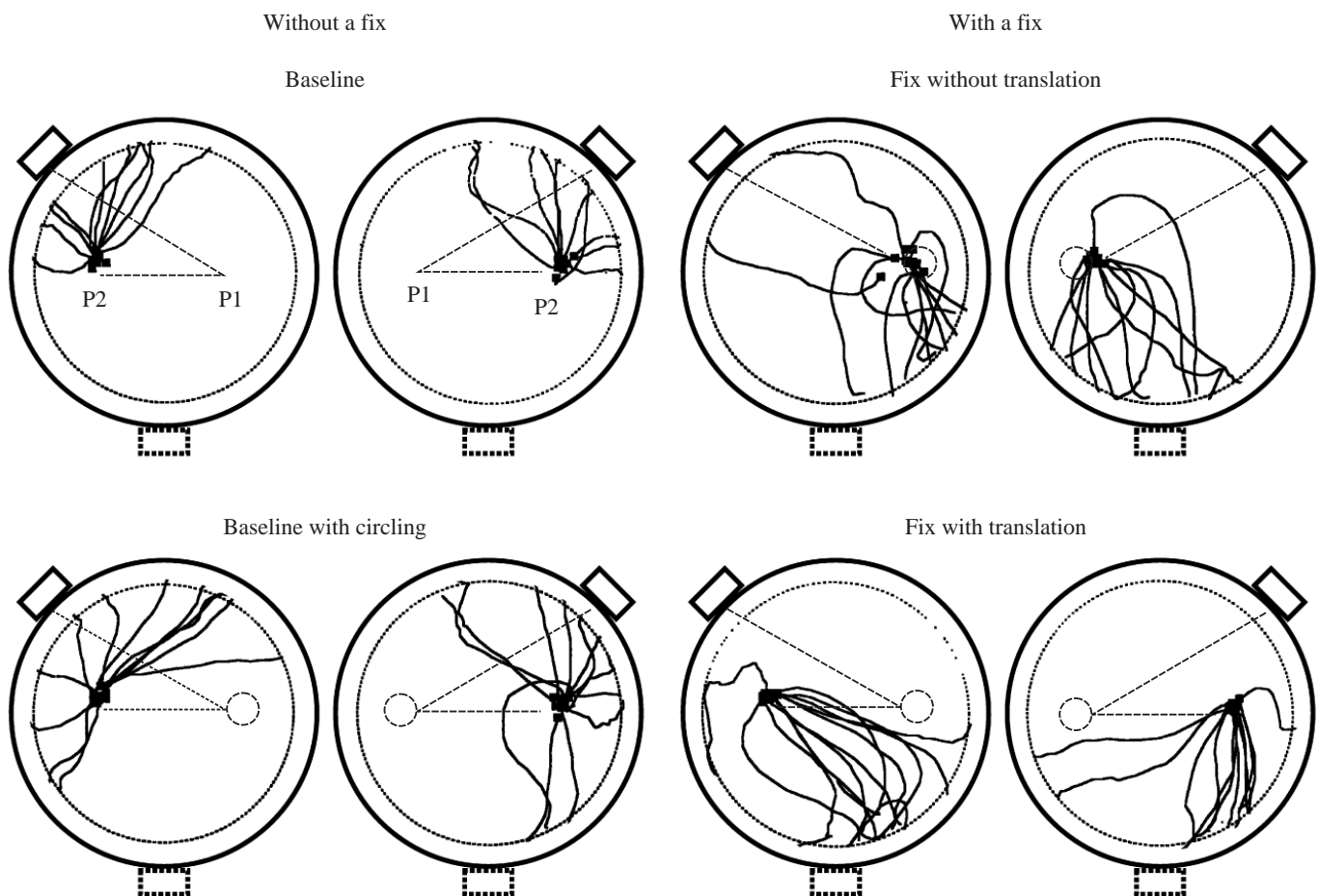


Fig. 4. Homing paths of one subject in the four classes of experimental trials of experiment I. The large circles represent the experimental arena with the nest box in its standard 0° position (dashed rectangle) and in its rotated position (continuous rectangle) during the experimental trials. The 15 cm-wide peripheral zone is shown by a dotted circle. The dashed lines (and circles) represent the outward journey to points P1 and P2. The return journeys from the feeding place at the end of the outward journey to the peripheral annular zone of the arena are drawn for the four different (clockwise and counterclockwise) experimental trials.

Table 1. *Homing directions: experiment I*

	Experimental conditions															
	Without a fix								With a fix							
	Baseline				Baseline with circling				Fix without translation				Fix with translation			
	+135°		-135°		+135°		-135°		+135°		-135°		+135°		-135°	
	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$
Subject																
I 1	+137	0.86**	-142	0.86**	+160	0.47	-145	0.68**	-61	0.69**	-27	0.49	+6	0.63**	-47	0.63**
2	+147	0.72**	-105	0.45	-167	0.64**	-122	0.76**	+60	0.23	+7	0.66**	+49	0.58*	-20	0.73**
3	+160	0.84**	-152	0.96**	-174	0.73**	-133	0.74**	-23	0.49	+19	0.82**	-25	0.90**	+7	0.90**
4	+146	0.85**	-140	0.83**	+157	0.50*	-106	0.43	-42	0.61*	+13	0.89**	-13	0.82**	-19	0.80**
5	+125	0.87**	-176	0.71**	+113	0.39	-160	0.48	+35	0.44	-7	0.52*	+12	0.53*	-40	0.4
6	+146	0.86**	-131	0.74**	+175	0.37	-132	0.72**	+24	0.49	+19	0.62**	-18	0.67**	+12	0.72**
7	+136	0.90**	-108	0.85**	+131	0.70**	-87	0.81**	-44	0.72**	-8	0.44	+20	0.31	-50	0.85**
8	+157	0.94**	-167	0.80**	+135	0.74**	-141	0.31	-38	0.42	+29	0.67**	+45	0.66**	-26	0.59*
II 1	-176	0.69**	+161	0.75**	-155	0.61**	+163	0.66**	-50	0.66**	-10	0.51*	+12	0.74**	-43	0.52*
2	-167	0.72**	-127	0.31	-148	0.79**	-159	0.68**	-30	0.54	+9	0.52	+28	0.68**	-11	0.70**
3	-145	0.76**	+136	0.74**	-113	0.73**	+173	0.60**	+22	0.37	+11	0.39	-36	0.76**	+18	0.81**
4	-164	0.70**	+176	0.71**	-121	0.35	+175	0.29	-12	0.57*	-6	0.68**	-26	0.73**	-21	0.82**
5	-170	0.81**	+144	0.64*	-118	0.35	+117	0.29	-3	0.83**	-8	0.41	+20	0.34	-42	0.36
6	-155	0.76**	+168	0.84**	-127	0.29	+169	0.39	+31	0.84**	-2	0.57*	-14	0.75**	+19	0.65**
7	-176	0.74**	-130	0.61*	-160	0.51*	-122	0.52*	-31	0.60*	-1	0.51*	+15	0.58*	-58	0.81**
8	-134	0.87**	+136	0.88**	-167	0.58*	+91	0.32	-36	0.72**	-2	0.72**	+36	0.63**	-53	0.57*
Mean vectors																
I	+144.3	0.98**	-140.2	0.92**	+156.4	0.90**	-128.5	0.93**	-13.4	0.76**	+5.8	0.96**	+9.3	0.90**	-23.1	0.93**
II	+199	0.97**	+171	0.81**	-139	0.94**	+166.8	0.75**	-14.1	0.89**	-1.1	0.99**	+4.7	0.91**	-24.4	0.88**

Part I refers to the subjects' mean orientation on the arena floor at the end of the return to the arena periphery, at a distance of 15 cm from the arena border. The 0° reference direction is the radius vector of the arena that points towards the standard nest location; positive values are measured clockwise. Part II reports the animals' mean orientation at a distance of 35 cm from the start of the return. The 0° reference direction points from the point of departure of the homing trip towards the standard nest position. The mean orientation of each subject in 10–14 trials is indicated by first order vectors ( $\theta$  and  $r$  = angle and length of vector, respectively). One or two asterisks indicate that  $r$  is significant at the 0.05 or 0.01 level, respectively (test of Rayleigh). The last two rows report the angle ( $\theta$ ) and length ( $r$ ) of second order vectors that represent the mean orientation of the whole experimental group. All second order vectors are significant at the 0.01 level (Moore's test).  $N=8$ .



facilitate the reading of our results, which are based on elaborate test procedures, we start by presenting the results of one repeatedly tested subject on a descriptive rather than quantitative level.

Fig. 4 illustrates the return itineraries of one hamster (subject 4 in Table 1) in the complete set of experimental trials. Trials without a fix imply that homing occurs through PI only. This is well illustrated by baseline trials (which involve no circling), in which the animal returns very significantly, but with a slight inward bias (see Introduction), towards the current nest location. In baseline-with-circling trials, the mean homing direction again points towards the point of departure of the hoarding excursion. However, the particular homing directions are much more scattered than in the baseline trials, due to the strong increase of the angular component of the outward trip.

The opportunity of taking a brief visual fix reorients the mean homing direction in both fix conditions. In fix-without-translation trials, however, the animal does not always take a fix and shows more convoluted homing paths than in fix-with-translation trials. In the latter conditions, the subject clearly updates its position with respect to the standard nest location during the second outward translation. Thus, the fix does not just allow the subject to keep visual references in short-term memory but changes the reference frame for PI.

As in all our homing experiments with a peripheral nest box, the majority of the observed homing trajectories tend to be fairly direct. However, some homing paths seem clearly goal directed but at the same time show a certain sinuosity. This is also the case in controlled reference trials, where PI and briefly presented visual references confirm and therefore consolidate each other. Furthermore, the convolution and dispersion of the return itineraries increase with the length and sinuosity of the outward journey and the degree of conflict between self-generated and external spatial cues.

#### *First and second order data from main experimental group*

Table 1 and Fig. 5 report the first and second order vectors from the eight subjects that underwent the complete test series. In trials without a fix, the mean orientation of each particular subject points towards the rotated nest location. Among all test conditions, homing occurred most precisely in baseline trials, where the hamsters performed a relatively short outward plus pouching time (mean duration, 35.3 s), having already been offered some food at P1 instead of walking in circles. In clockwise trials all first order vectors are very significant, and in counterclockwise trials only one subject was non-significantly orientated.

In baseline-with-circling conditions, by contrast, four animals were non-significantly orientated in clockwise and/or counterclockwise trials. On the whole, seven out of 16 first order vectors that refer to the subject's orientation at a short distance from the starting point of the return, and six out of 16 vectors that pertain to the animals' orientation at the arena periphery, are non-significant. This increase in the dispersion of the homing directions was due to the sinuosity and also to the longer duration (mean duration, 40.7 s) of the outward plus

pouching duration. The statistical comparison between the first order vector lengths showed that the homing directions were more dispersed in clockwise baseline-with-circling than in clockwise baseline trials (orientation at 35 cm from start,  $N=8$ ,  $T=2$ ,  $P<0.05$ ; peripheral orientation,  $N=8$ ,  $T=0$ ,  $P<0.01$ ; Wilcoxon matched-pairs signed-ranks test).

On the second order level, the mean orientation of the whole experimental group was very significant throughout the two test conditions without a fix. Note that in baseline conditions, the second order vectors express a very slight inwards error (see Introduction). Statistically, the mean (peripheral) orientation differed between clockwise baseline and clockwise baseline-with-circling trials (orientation at 35 cm from start point,  $B=15.9$ ,  $P>0.05$ ; peripheral orientation,  $B=26.3$ ,  $P<0.01$ ; Mardia-Watson-Wheeler test). Furthermore, the animals' mean orientation near the arena periphery differed from the expected homing direction towards the rotated nest box in clockwise baseline-with-circling trials ( $P<0.05$ , Hotelling's confidence interval test). In all other conditions without a fix, the mean return direction was not different from the expected orientation towards the rotated nest entrance, where the animals had initiated the outward journey.

In trials without a fix, the animals returned rapidly to the arena periphery; the less accurate their homing direction, the longer they then had to search for the nest entrance. Thus, the hamsters took nearly the same average time (2.6 s and 2.7 s) to return from P2 to the arena periphery in baseline and in baseline-with-circling trials. By contrast, the mean return time to the nest was 9.5 s in baseline trials and 18.3 s in baseline-with-circling trials. For clockwise trials, this variable differed significantly between the two types of baseline trials ( $N=8$ ,  $T=1$ ,  $P<0.02$ , Wilcoxon matched-pairs signed-ranks test).

To summarise, when tested in continuous darkness, the hamsters return to the current nest position, where they have initiated their excursion, and therefore rely on PI. This is also testified by the fact that the greater the sinuosity of the outward journey, the greater the dispersion of the homing directions, since PI is necessarily affected by cumulative errors.

In fix conditions, all subjects show a completely different homing pattern. As confirmed on the second order level by Hotelling's confidence interval test, the mean orientation of the experimental group is now directed towards the standard nest location. Fix-with-translation trials differ from baseline-with-circling trials only through the short illumination of the experimental room, during which the animal walks along one more circle. However, the two test conditions yield systematically different orientation data in both clockwise and counterclockwise trials and in the beginning as well as at the end of the return trips ( $B=26.3$ ,  $P<0.01$ , Mardia-Watson-Wheeler test).

Positive results in the fix-without-translation condition confirm that our hamsters take up position (or head direction information; see below) during the fix interval, and follow the visually provided information to return home. And, more to the point, to return towards the standard nest location in fix-with-translation trials, the hamsters have (1) to reset their path

integrator to a new, visually induced position vector and (2) readjust this vector – by means of PI – during the progression from P1 to P2.

The question of whether the visual references reoriented homing more frequently and accurately in fix-with-translation than in fix-without-translation trials was given special importance (see Introduction). In our current data set, the previously observed difference between the results from the two types of fix trials subsists but is much reduced. In both fix conditions, all second order vectors are significantly (re)oriented in the general direction of the standard nest location. A difference exists, however, in the ratio of significant first order vectors: seven out of 16 first order vectors representing the subjects' orientation at the end of homing are non-significant in fix-without-translation trials; in fix-with-translation trials, this was the case for two out of 16 first order

vectors. A similar difference appears between the ratios of non-significant first order vectors pertaining to the animals' initial orientation in the two categories of fix trials. Furthermore, our subjects took a fix in 150 out of 190 (79%) fix-without-translation trials and in 161 out of 191 (84%) fix-with-translation trials. Thus, the results from the eight subjects confirm, but only to a very limited extent, the previously noticed difference between the data from the two fix trials.

The fact that a visual fix acts slightly more on the homing direction when it is followed by a final translation than when it is not remains puzzling, in particular if we compare the fix–return interval (i.e. the interval between the end of the fix and the start of the return trip) in the two fix conditions: In fix-without-translation trials, the mean fix–return interval (20.0 s) that was included in a mean outward plus pouching time of 34.5 s was shorter than in the fix-with-translation condition

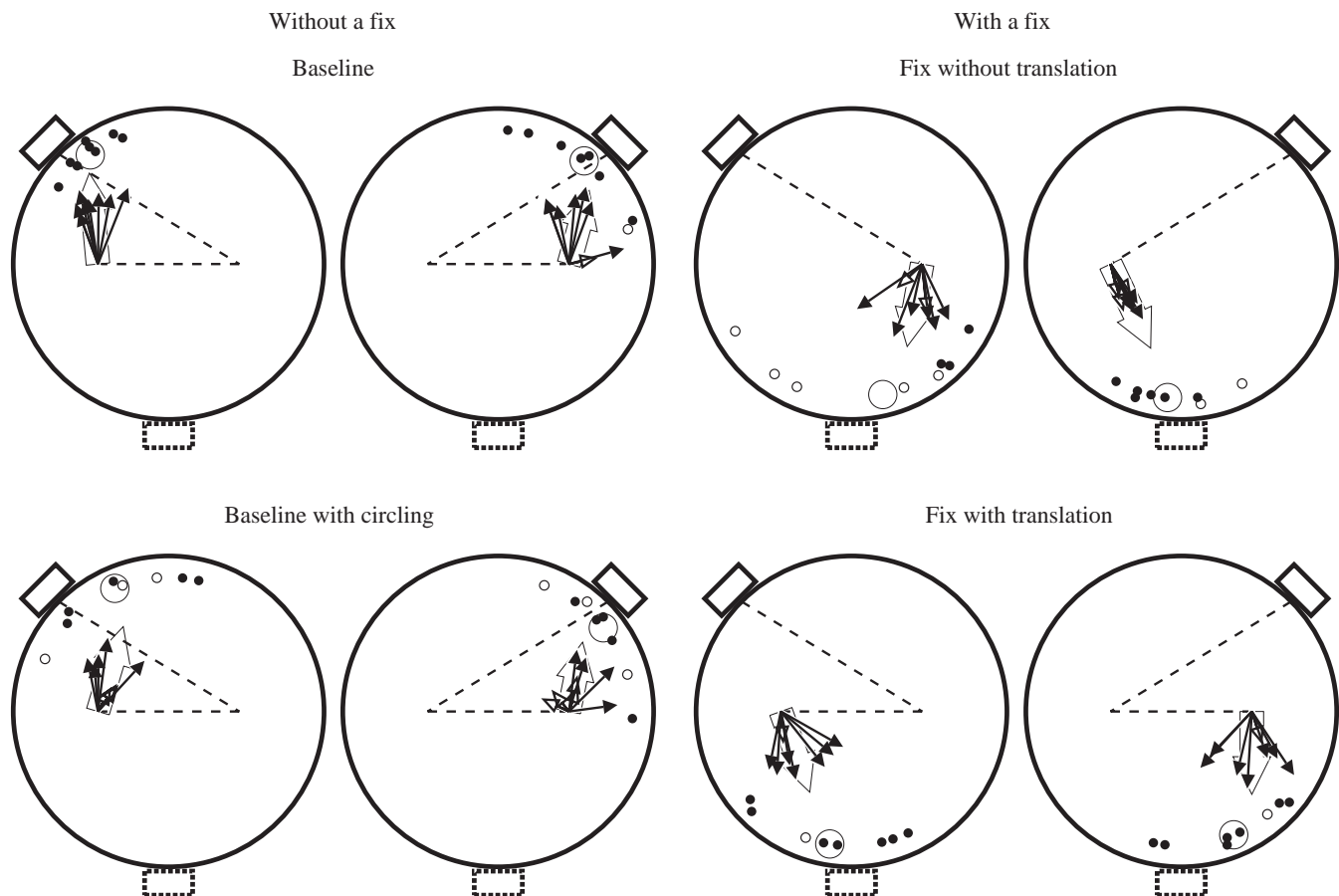


Fig. 5. Mean homing direction of repeatedly tested subjects in experiment I ( $N=8$ ). Each pair of large circles represents the arena in its clockwise (left) or counterclockwise (right) rotated position, and the two dashed lines inside are the two-leg outward journeys starting at the current position of the nest. The dashed rectangle beneath each circle represents the nest box in its standard  $0^\circ$  position, while the solid rectangle in the upper part of the diagram represents the rotated nest. The dots along the periphery of the arena circle indicate the mean orientation of each subject in 10–14 return trips, at the moment where the animal had reached the peripheral annular zone of the arena. The (larger) open circles on the same level represent the mean orientation of the whole experimental group. The arrows that are centred on the point of departure of the return journey represent the mean orientation of each subject at a distance of 35 cm from the starting point of the return. The mean orientation of the whole experimental group is represented by a large open arrow. For first order data, open symbols represent non-significant results and full symbols represent significant results ( $P<0.05$  or  $0.01$ ; test of Rayleigh). All second order data are significant at the  $0.01$  level (test of Moore).

(24.9 s included in 38.8 s). The difference between the two fix–return intervals is significant ( $N=8$ ,  $T=0$ ,  $P<0.01$ , Wilcoxon matched-pairs signed-ranks test). This means that the homing trip followed the presentation of visual cues significantly sooner in fix-without-translation than in fix-with-translation trials, a fact that should have enhanced the effect of the fix.

Finally, the mean return time to the arena periphery was 4.2 s in fix-without-translation trials and 3.3 s in fix-with-translation trials. These values are higher than in trials without a fix, most likely because the fix introduced a conflict situation. This may have been the case in fix-without-translation trials particularly, where homing occurred sooner after the conflict-inducing fix than in fix-with-translation trials.

In summary, the intermittent presentation of the familiar room environment reoriented the homing direction in all subjects in both types of fix trials. The fact that the animals returned to the standard nest location in fix-with-translation trials shows that they did not just take up visual position information but fed this information into an integrator and then updated their position (or direction) within a new reference frame throughout the end of the trial. In spite of the fact that this was not required in fix-without-translation trials, homing towards the standard nest location was slightly less precise in fix-without-translation than in fix-with-translation trials.

Let us finally emphasise that the subjects that were tested up to 14 times in each test condition showed no systematic changes in their behaviour during the test period. In particular, their results remained stable in the two categories of fix trials, with regard to the proportion as well as the accuracy of the reoriented homing trips.

### Experiment II

As already mentioned, due to the geometry of the outward journey in the arena with a peripheral nest, we could not answer an important question: did the animals reset their position, or only their sense of direction or internal compass, during the brief presentation of the room landmarks? In the first case, the animal establishes both its location and head direction, and in the second case only its head direction with respect to the standard nest location. In both cases, the new vector is modified by PI during further locomotion, both the linear and angular components of the (remaining) outward path being taken into account.

If the hamster resets only its internal compass during the fix, it will not notice that its location has changed after the fix but will feel its head direction in the room to be altered by  $135^\circ$ . The homing vector to the nest will, consequently, maintain the same length but will rotate by  $135^\circ$ . On the other hand, a full reset implies reprocessing location and orientation. In this case, subjective head direction will be modified by  $135^\circ$ , as before, but both the distance and direction to the nest will be recomputed on the basis of the corrected location. This new direction to the nest differs by  $\sim 98^\circ$  from its value before the fix.

Accordingly, if the hamsters had reset only their internal compass (or sense of direction) in the fix trials of experiment

I, they would have computed a return vector to a virtual nest location outside the arena. The homing directions from points P1 and P2 to this virtual nest would have been similar to, and therefore indistinguishable from, the homing directions towards the standard nest location (H. Mittelstaedt, personal communication; see also Mittelstaedt, 2000). We therefore carried out a second experiment in which the location of the nest box and the shape of the outward journey induced a clear difference between the homing directions that could be expected after a positional or a merely directional fix. Basically, the test procedures remained the same as before, with one essential difference: the nest box was located under the floor of the arena, at a distance of 50 cm from the arena border. Thus, the animals could no longer just proceed from the hoarding site to the arena periphery and then search for the nest entrance along the arena border. Instead, they had to aim at the nest entrance by taking into account both its bearing and distance with respect to the start of the return trip at the feeding place.

### Procedures

The experiments took place in room B (town lab). The general organisation of the experiment, i.e. the categories, number and sequential order of trials, was identical to that of experiment I. Particular changes were made to adapt the test procedures to the new spatial conditions (Fig. 6) and to introduce slight simplifications.

Uncontrolled and controlled reference trials were performed as in experiment I. The homing directions were assessed with a mobile grid. A trial was considered as successful if, at a distance of 35 cm from the start of the return, the animal was located within a  $90^\circ$  sector that was centred on the nest hole.

In the experimental trials, the animals followed the outward paths that are described in Fig. 6. In trials with spoon-guided circles, the hamsters followed two full circles that passed through P1 in the dark. At the end of clockwise (counterclockwise) circles, the animal was automatically orientated away from (towards) the standard nest location. During the 10–12 s light-on interval, the animal followed the bait along one full circle in the opposite direction. In all trials, the hamster approached the food source by looking either away from or towards the standard nest location.

Special attention was given to eliminating (a) olfactory cues at the arena border and (b) the possibility of seeing the nest entrance in its current position in fix trials. (a) The lower part of the arena wall was covered with plastic sheets (height, 20 cm), which were permuted and/or turned upside down after each sequence of three experimental trials. (b) At the beginning of a fix trial, just after the animal had left the nest exit, the latter was covered by a cardboard sheet layered with glued sawdust. At the end of the trials, the sheet was removed.

In trials without a fix, the (rotated) nest hole was not covered. Thus, the animals may have been guided by nest odours during the final approach of the nest hole. The subjects' initial orientation, however, could not be influenced by (static) olfactory cues. As a general rule, we assumed throughout our

research that during locomotion controlled by PI, hamsters are not guided by olfactory gradients beyond a distance of 15–20 cm from the odour source (see also Durup, 1970).

Furthermore, we again took care to give the animals access to the nest in the region where they expected the nest to be. In trials without a fix, the arena was turned back into its standard orientation and the room lights turned on only after the animal had returned to the nest. In fix trials, the procedures were the same as in experiment I: if the subjects had taken a fix and returned towards the standard nest location, the lights were turned on and the arena was rotated to its standard position as soon as the animal had reached the arena border. At the same time, the sawdust sheet was quickly removed from the nest entrance.

The homing directions from points P1 and P2 were

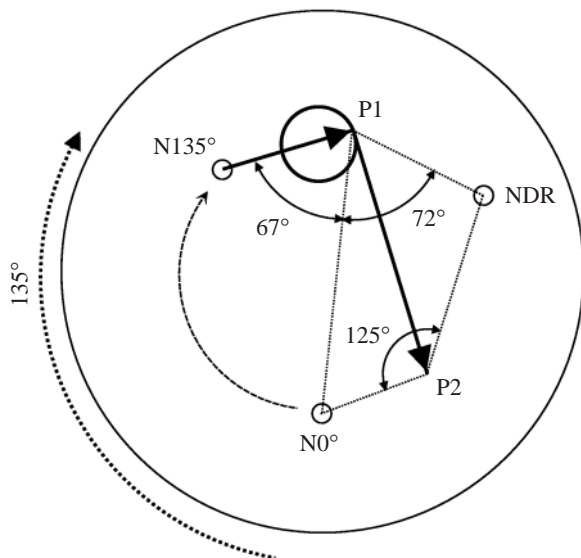


Fig. 6. Geometry of test space and outward journeys in experiment II. The nest box is located under the arena floor, the nest exit (diameter, 9 cm) being located at a distance of 50 cm from the arena wall. The hamster can easily climb from the underground nest into the arena. Before each test trial, the arena is rotated by 135°. The outward journey (continuous line with heavy arrows) leads from the (rotated) nest exit (N135°) over 60 cm to point P1, and, with the exception of fix-without-translation trials, over a further translation of 110 cm to point P2. In baseline trials, the animal proceeds to P1, where it takes up some food, and then to P2, where it fills its cheek pouches completely. Baseline-with-circling trials follow the same pattern except that the subject walks along two full circles near P1 (circle passing through P1) instead of taking up some food. In fix-without-translation trials, the animal walks to P1, follows two full circles in the dark, and then a further circle in the opposite direction under light. Fix-with-translation trials include an additional translation from point P1 to point P2 after the fix. During the fix at P1, the nest direction, as established by visual cues on the one hand and by PI on the other hand, diverge by ~67°. A full resetting would lead to the standard nest location N0°, and a partial (direction only) resetting to the virtual nest location NDR. The theoretical homing directions based on a full or a partial resetting differ by 72° at P1 and by 125° at P2.

measured with a mobile grid that was centred on the point of departure of the return, the 0° radius vector pointing to the standard nest location. The animals' angular position was measured at distances of 35 cm and 50 cm from the start of the return trip. The temporal parameters were measured as in experiment I and are mentioned separately for the two subjects.

#### First order statistics for experiment II

Out of a total number of eight hamsters that were selected as experimental subjects, only two cooperated throughout the test series and were well orientated in both types of reference trials. Clearly, asking hamsters to return to a centrally located nest after two-leg outward journeys with intermittent spoon-guided circling led the animals to the limits of their PI capabilities.

Table 2 reports the subjects' orientation at a distance of 35 cm and 50 cm, and Fig. 7 at a distance of 50 cm from the start of the return. In baseline trials, both animals produced significant first order homing vectors. Three return vectors point more towards P1 than to the current nest position (Fig. 7). This bias may again be interpreted as a systematic inwards error (Müller and Wehner, 1988). In baseline-with-circling trials, the dispersion of the homing directions increases considerably (Fig. 7). Both subjects yield only one significant homing vector, which points again towards P1 rather than towards the current nest location. The absolute values of the time parameters varied between the two animals, subject 2 being slower and probably less confident than subject 1. The relationship between the same parameters in different trials was the same as in experiment I. To return to the nest in baseline and baseline-with-circling trials, subject 1 took a mean time of 11.0 s and 12.3 s, and subject 2 took 18.3 s and 23.4 s, respectively. In experiment I, the corresponding mean values to reach the nest entrance shown by the experimental group of eight subjects were 9.5 s and 18.3 s.

Fix-without-translation trials (Fig. 7) yield clear results: in clockwise and counterclockwise trials, both animals home significantly in the general direction of the standard nest location and therefore have taken a full positional fix. The results from fix-with-translation trials are much less homogeneous. The homing directions of subject 1 (continuous vectors) point precisely to the standard nest location (N0°) in clockwise trials. In counterclockwise trials, the animal deviates by 42° counterclockwise from this direction. Most likely, the animal took a positional fix but then did not sufficiently update its new position coordinates during the final translation to the food source. This interpretation is confirmed by the detailed presentation of the homing journeys (Fig. 8). The other animal (dashed vectors) yields one significant vector only, which points halfway between N135° and P1, suggesting that the animal planned a homing trip back to the rotated nest location and committed again an inward error. For both animals, the mean fix–return interval is again (non-significantly) shorter in fix-with-translation than in fix-without-translation trials.

In summary, in fix-without-translation trials, both subjects homed towards the standard nest location and therefore had

taken a position fix. However, in fix-with-translation trials, only one subject was able to take a fix and to update the new position vector during the second outward leg. Finally, and most importantly, none of the eight vectors that were obtained in fix trials pointed towards the virtual nest location (NDR in Fig. 7), which would result from a directional fix acting on the animal's azimuth only. We therefore conclude that, in hamsters, the resetting process concerns both the animals' position and sense of direction rather than the sense of direction only.

*Homing paths from one subject*

Fig. 8 represents the complete return paths of subject 1 in clockwise trials. In the majority of non-fix trials, the subject returns to the nest hole on the open arena floor along an indirect path. Even in baseline trials, only three of 11 return paths lead fairly directly from the food source to the rotated nest hole. In five trials, the homing path follows a detour that can be interpreted as backtracking the outward trip. In

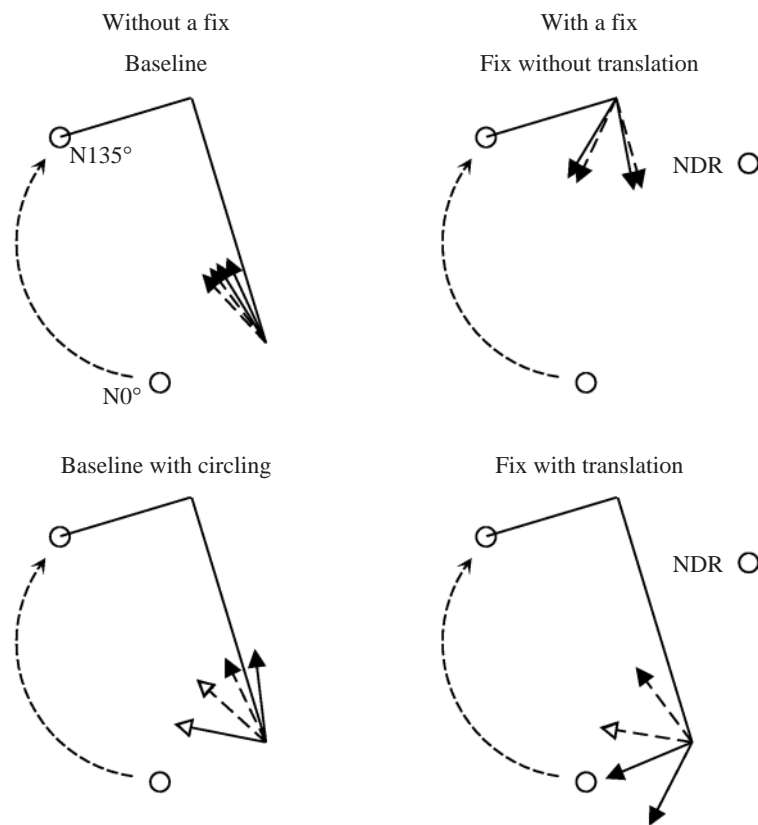


Fig. 7. Mean homing directions of two subjects in experiment II. The homing directions are measured at a distance of 50 cm from the point of departure of the return. The mean return vectors (arrows) are superimposed on the outward trip to the food site (solid lines; circling not shown). The four vectors in each graph represent the homing directions of subjects 1 (solid arrows) and 2 (dashed arrows) in clockwise and counterclockwise trials. Vectors from counterclockwise trials are presented mirror-reversed. (Solid arrowheads,  $P < 0.05$ ; open arrowheads,  $P > 0.05$ ; test of Rayleigh.) Circle NDR represents the location of a virtual nest that would result from a partial resetting acting on the subject's azimuth only.

Table 2. Homing directions: experiment II

Subject	Experimental conditions															
	Without a fix				With a fix											
	Baseline		Baseline with circling		Fix without translation		Fix with translation									
	+135°	-135°	+135°	-135°	+135°	-135°	+135°	-135°								
	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$	$\theta$	$r$				
I 1	+86	0.66**	-79	0.53	+108	0.54*	-40	0.21	+26	0.63**	+16	0.56*	-21	0.43	+52	0.68**
2	+59	0.20	-72	0.62*	+79	0.69**	-42	0.43	+18	0.80**	+37	0.72**	-10	0.12	-91	0.23
II 1	+86	0.67**	-79	0.57*	+104	0.67**	-32	0.43	+25	0.67**	+17	0.54*	-2	0.60**	+42	0.60*
2	+74	0.55*	-68	0.65*	+85	0.69**	-63	0.51	+19	0.87**	+22	0.72**	+30	0.41	-74	0.55*

Part I and II refer to the subjects' mean orientation at a distance of 35 cm and 50 cm, respectively, from the starting point of the return. The 0° reference direction points from the point of departure of the homing trip to the standard nest location. For each experimental condition, the mean orientation of each subject in 10–14 trials is indicated by first order vectors ( $\theta$  and  $r$  = angle and length of vectors, respectively). One or two asterisks indicate that  $r$  is significant at the 0.05 or 0.01 level, respectively (test of Rayleigh).  $N=2$ .

counterclockwise trials by the same subject (not shown here), backtracking was observed in four out of 10 trials. Note that this apparent backtracking behaviour never follows the precise shape of the outward trip and therefore cannot be controlled by olfactory or tactile outbound traces.

In baseline-with-circling trials, the homing paths show, as expected, an increased sinuosity (Fig. 8). The upper graph reproduces the five most direct return paths, in which the animal does not contact the arena wall. Only two returns are fairly direct. Three homing paths take again the form of backtracking, showing that the general shape of the outward journey has not been erased from short-term memory by the intervening spoon-guided circles. Note that, from a functional point of view, while this detour behaviour puts high demands on short-term

memory, it may increase the chances for the animal to come across cues encountered along the outward journey.

The lower graph represents the six return paths where the hamster contacted the arena wall. As the lower 20 cm of the wall were covered up with plastic bands, reaching and contacting the wall informed the animal only on its general location near the arena border. However, the combination between this information and the allocentric representation of head direction may have informed the animal on its position and therefore improved its orientation towards the nest hole. If we take into account clockwise and counterclockwise trials, the animal contacted in the arena wall in a total of 10 trials, and in six of these trials it proceeded thereafter straight to the nest entrance.

In spite of their tortuous shape, the animal's paths in trials without a fix cannot be explained by a trial-and-error strategy. The homing itineraries are clearly oriented towards the current nest location and are therefore planned ahead. To illustrate the difference between the convoluted, but nevertheless goal-directed, return journeys presented so far and a merely exploratory search path, the return journey of subject 2 in a clockwise baseline trial is represented in Fig. 8. Note that whatever the nature of the return path – oriented or following a trial-and-error procedure – the animal needs the assistance of external cues to reach the goal (Etienne, 2003). Thus, during the final approach to the nest hole, the subject generally follows a straight line, as if attracted by olfactory cues in the vicinity of the (open) nest hole.

Fix-without-translation trials convincingly show that the intermittent sight of the room landmarks reorients homing. In all but one of the 11 clockwise fix-without-translation trials, subject 1 starts by following a fairly straight path in the general direction of the standard nest location. Then it deviates from the initially chosen direction, always before contacting the arena wall. Compared with the beeline distance that the animal should cover

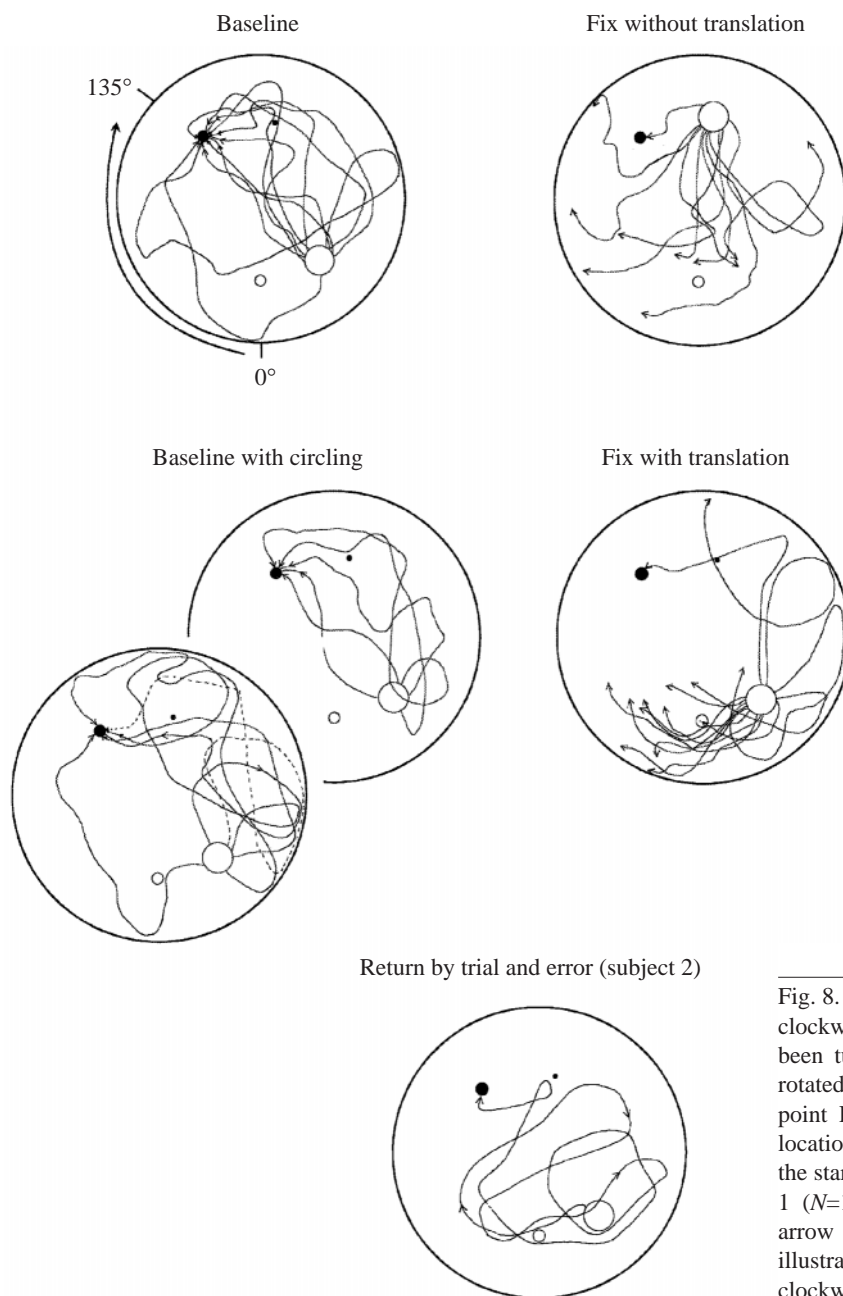


Fig. 8. Return paths of subject 1 in experiment II. Only clockwise data are presented. Before the trials, the arena has been turned 135° clockwise. The filled circle represents the rotated position of the nest hole, the small black dot represents point P1, and the small open circle represents the standard location of the nest hole. The large open circle encompasses the starting point of the return trips. The return paths of subject 1 ( $N=11-14$ ) are represented by a continuous line with an arrow and occasionally by a dashed line. The bottom graph illustrates a return path through trial-and-error exploration in a clockwise baseline trial by subject 2.

to match the real distance between P1 and the standard nest location (125 cm), the point of inflexion of the return trip occurred in seven trials after a shorter homing distance and in three trials after a nearly correct homing distance. It seems therefore that the animals tended to underestimate the relatively long homing distance. No circular search movements (Séguinot et al., 1993) were observed after the point of inflexion of the return trajectories.

The homing paths in 14 fix-with-translation trials (Fig. 8) gives a clearer picture of the animal's homing pattern than the previously described homing vectors (Fig. 7). In all but four out of 14 trials, the animal walks in the direction of the standard nest location and overshoots the 50 cm-long real homing distance. Inflexions in the initial homing direction occur beyond the virtual nest location, the animal turning predominantly away from the arena border, without contacting it.

These results show that in both fix conditions, subject 1 directs homing towards the standard 0° nest location. The point of inflexion of the homing direction is proportional to the real homing distance. However, the animal undershoots the long return distance in fix-without-translation trials and overshoots the short homing distance in fix-with-translation trials. This suggests that subjects that live throughout the test period in the experimental apparatus know by experience the general dimensions of the arena. To come back to the basic question that underlies experiment II, let us emphasise that homing occurred always towards the standard nest location and never to the virtual nest location, which would derive from a partial resetting process.

### Discussion

We examined whether golden hamsters, when tested in darkness and without the availability of non-visual external references, can reset their path integrator by taking a fix on briefly presented visual room cues (Fig. 1). The main data set was obtained in experiment I, in a large arena with a peripheral nest, our usual experimental set-up. After a guided two-leg outward journey from the nest to a food source (Fig. 2), the animals chose a particular direction to return to the arena border. There, they changed over to exploratory movements along the enclosure until they found the nest entrance through olfactory and tactile cues. Thus, the structure of the test space greatly facilitated homing by stopping the animals' initial progression at the periphery and guiding them along the arena wall until they found the nest entrance. We assume that the subjects, which lived in the experimental arena, developed this homing strategy during the habituation phase of the experiment (Siegrist et al., 2003).

In baseline trials, the first order homing vectors from the whole experimental group (Table 1; Fig. 5) and the homing paths from one subject (Fig. 4) show that, in continuous darkness, homing is oriented towards the current, rotated nest position, where the animals initiated a hoarding excursion and therefore also PI. Further, an increase in the sinuosity of the

outward journey strongly increases the dispersion of the homing directions (Etienne et al., 1988; Benhamou et al., 1990). Thus, after a two-leg outward journey comprising three to four full rotations and a time interval of ~40 s between the start of the outward journey and the start of the homing trip, 40% of the first order homing vectors are no longer significant (Fig. 5). Taken together, these results testify that the animals homed through idiothetic path integration only and that without the interaction with landmarks their homing performance deteriorated very rapidly when the sinuosity and duration of the outward journey to the food location were increased.

In trials with a fix, the brief presentation of the richly patterned visual room environment reorients homing towards the standard nest location in ~80% of the trials. In fix-with-translation trials, where the light-on interval occurred before the second leg of the outward journey, the animals not only took a fix but also updated their position (or head direction only; see below) with respect to the standard nest location while completing the outward trip to the feeding site. This means that the path integrator had been reset, i.e. that the visually estimated self-position vector with respect to the standard nest location replaced the previous PI vector that was anchored to the rotated nest. The resetting process may have been facilitated by the fact that PI started to drift before the presentation of the room cues, as shown by the dispersion of the homing direction in base-line with circling trials.

It should be emphasised that PI provides a navigator with vector information and therefore does not constrain the shape of the actually performed path. As shown by Fig. 4, particular homing trips follow a fairly direct, but not necessarily straight, path to the arena periphery. We observed this throughout our study on path integration in hamsters, in conditions where homing occurred in the dark, i.e. without a directional reference. Occasional loops at the beginning of the return trip are due to the initial orientation of the animal at the food site. On the other hand, in fix trials, changes in direction depend also on the fact that the animals were exposed to diverging self-generated and visual position information. These detours in the homing path do not take the form of circular, exploratory movements in search of substrate cues (Séguinot et al., 1993).

Experiment I left the basic question open of whether the subjects gained positional or only directional information from the brief sight of the landmark panorama and whether they therefore reset their path integrator or only their internal compass. This led us to experiment II, where we conceived the nest location and outward trips in such a manner that a position fix on the one hand, and a directional fix on the other hand, determined two virtual nest locations that implied clearly distinguishable homing directions (Fig. 6). As expected, the change from a peripheral to a more central nest location made homing much more difficult. The animals now had to return to a particular point on an open surface without the help of any external cue. This means they had to rely on self-generated direction *and* distance information.

Only two out of eight hamsters passed the reference trials of

experiment II and were submitted to the complete set of experimental trials (Table 2; Fig. 7). In trials without a fix, both animals returned to the general region of the rotated nest location, additional circling during the outward journey leading to a strong increase in the dispersion of the homing directions. All significant first order vectors from the two categories of baseline trials were affected by a considerable inward error, which may be related to the algorithm of PI (see Introduction).

As expected on the basis of former experiments where hamsters had to return to a goal on the arena floor through path integration only (Etienne et al., 1998), the return itineraries from both subjects were much less direct and uniform than the homing paths we observed in experiment I. Subject 1 showed two systematic forms of detour homing, which we suppose may increase the chance of finding the nest entrance: backtracking the outward journey, a route-based strategy, and taking up position information by combining the route-based representation of head direction with the tactually perceived orientation of the arena wall (see Fig. 8). That hamsters alternate or compromise between different types of homing behaviours, and therefore process route-based and/or location-based information in different ways, has been observed throughout our research (Teroni et al., 1987; Etienne et al., 1990a,b; Georgakopoulos and Etienne, 1994, 1997).

In fix-without-translation trials, where the animals could take a fix at the end of the outward journey, both animals homed significantly towards the standard nest location. The uniform homing pattern in this condition was obviously controlled by a position fix (Fig. 7). By contrast, in fix-with-translation trials, only subject 1 homed towards the standard nest location. Subject 2 yielded a significant return vector in counterclockwise trials only, which pointed towards the region of the rotated nest location, with the usual inward bias. The animal therefore gave priority to the position vector that was anchored to the point of departure at the rotated nest, assessed its position with respect to its point of departure throughout its excursions, and did not take into account the presentation of the room cues, as in the fix-without-translation trials.

As shown by Fig. 8, in both fix conditions subject 1 orientates its homing trips not only towards the standard nest location but also uses distance information. The majority of trajectories show an inflexion at a beeline distance from the start of the return that approximates the correct distance to the goal location (see also Séguinot et al., 1993). Furthermore, according to this criterion, the subject underestimates visually the distance to the goal in fix trials where the expected distance is relatively long (fix-without-translation trials) and overestimates the return distance in trials with a relatively short homing distance (fix-with-translation trials). Conversely, the hamster may have overestimated the distance it actually covered to reach a relatively distant goal (fix-without-translation trials) and underestimated the distance it walked to proceed to a relatively near goal (fix-with-translation trials). It is generally assumed that estimating and covering the approximately correct homing distance without the assistance of external cues depends on PI mechanisms that allow the

animal to plan, and also to execute, the correct length of the return path. Walking over the approximately right distance may, however, also depend on other factors, such as the animal's knowledge of the maximal dimension of the space it lives in (Bovet, 1992; Séguinot et al., 1993; Maurer, 1998).

Summing up, experiment II shows that our subjects took a position fix and reset their path integrator rather than only their internal compass: to wit, in fix trials the two animals returned predominantly to the (virtual) standard nest location, more seldom to the rotated nest and never towards the virtual nest location, which would result from a partial, merely directional, resetting process (Fig. 7). Furthermore, subject 1 knew the distance as well as the direction to the standard nest location (Fig. 8).

Taking a position fix requires complex perceptual and central information processing (Gallistel, 1990; Gallistel and Cramer, 1996). In this research, we noticed that the probability of taking a fix was greatly enhanced if the hamsters walked in circles during the light-on phase. Apparently, the animals needed to explore the full landmark panorama to process position information. During their circular walk, different sectors of the visual environment were projected on the central zone (area centralis) of the hamsters' retina, which has a higher resolution (Tiao and Blakemore, 1976) than other regions of the animals' almost panoramic (Finlay and Berian, 1985) visual field. Furthermore, seeing the visual environment while moving added motion parallax cues to the input variables that are necessary for calculating position. Similar findings have been obtained on the neurophysiological level regarding the (re)setting process of the neural ensemble code for direction (Mizumori and Williams, 1993).

With respect to static position cues, the room environment provided the animals with an optimal constellation of references to identify their orientation and distance from the goal during the lights-on interval (Etienne et al., 1995a,b; Levy, 1999). The animals may have deduced directional information from the rectangular shape of the room (Cheng, 1986; Gallistel, 1990) and the differential patterning of the room walls and landmark objects. Distance information, which was used explicitly in experiment II only, might have been provided by the apparent size of the pattern on the room wall nearest to the nest and by the simultaneous view of the elevation of the arena border. Rats trying to locate the submerged platform in a Morris water maze (a place navigation task formally quite similar to our hamsters relocating the nest during the fix) rely on information about the geometry of individual landmarks outside the pool and about the geometry of the configuration of landmarks, but they also use the distance to the pool wall as a cue (Maurer and Derivaz, 2000). On the whole, we assume that in rodents, deriving position information from visual landmarks is a complex process that depends on many visual parameters.

In experiment I, special importance was given to the ratio of fixes that the animals took in fix trials without or with a (second outward) translation. According to our current, complete set of data, the proportion of trials where the subjects took a fix is



only slightly higher in fix-with-translation (84%) than in fix-without-translation (79%) trials (Table 1; Fig. 5). However, the data still remain counterintuitive. Fix-without-translation conditions require only the capacity for place navigation, while fix-with-translation trials demand, in addition, the transfer of visually gained position information into the path integrator and a further updating process with respect to the standard nest location. Furthermore, the time interval between the end of the fix and the beginning of the return trips was significantly higher in fix-with-translation than in fix-without-translation trials. This difference too should have facilitated the orientation towards the standard nest location in fix-without-translation trials, as argued previously.

On the other hand, in experiment II, which put much higher demands on the hamsters, the effect of the fix was more pronounced in fix-without than in fix-with-translation trials. At the same time, the detailed analysis of the performance of one subject showed that the animal was able to change the reference frame for returning to the standard nest location in fix-with-translation trials. The main result of this study is therefore that hamsters are capable of resetting their path integrator through a position fix and of subsequently updating their position within the changed reference frame.

To conclude, let us emphasise the functional importance of resetting idiothetic PI through external position cues. The basic mechanisms of PI are hardwired and therefore work independently of the navigator's experience with its current surroundings (Siegrist et al., 2003). In a new environment, PI may therefore be self-sustained, but only as long as the navigator returns at regular intervals to his (identifiable) point of departure (Golani et al., 1993; Eilam et al., 2003; Arleo and Gerstner, 2000) and combines, if necessary, PI with systematic search movements. At the nest, the path integrator is automatically reset to its zero state. However, for PI to become a general and essential component of navigation, it has to remain functional throughout an excursion, independently of the sinuosity, length and duration of the path. This means that the integrator has to be reset away from home as well.

From a comparative view point, the question arises of how subterranean rodents, and in particular blind species, navigate without the assistance of visual landmarks for identifying locations or for resetting PI. Congenitally blind rats reset their path integrator with the help of proximal, non-visual cues (Save et al., 1998), a strategy that may work in a restricted experimental space but hardly in the animals' home range. On the other hand, the hypothesis that rodents may use the earth's magnetic field not only for compass orientation (Mather and Baker, 1981; Kimchi and Terkel, 2000) but also as a directional reference for path integration has now been confirmed for the blind mole rat *Spalax ehrenbergi* (Kimchi et al., 2004). At the beginning of an excursion, the mole rat relies on idiothetic path integration. With increasing sinuosity and length of the path, the mole rat then switches over to the use of allothetic PI, with the earth's magnetic field as a general directional reference for assessing (changes in) head direction. It seems therefore that allothetic PI takes place from the beginning of a trip but gains

control over the animal's overt behaviour after a certain timespan only.

The fact that a mammal performs PI with a general directional reference, as is the case for hymenopterans that use the sun azimuth for measuring rotations and coding direction, opens up many questions. In particular, insects navigate over long distances with an astonishing accuracy by relying on PI alone, route-based and location-based information interacting much less in these insects than in rodents and other mammals (Wehner et al., 1996). Thus, desert ants do not reset their (global) PI system through familiar landmarks they encounter away from the nest (Collett et al., 2003). It would be of great interest to investigate how location-based and route-based references interact in a mammal that has evolved a precise PI system.

In contrast to the subterranean blind mole rats, hamsters and other rodents that forage above ground depend primarily on low-frequency visual references for spatial orientation. And, unlike hymenopteran insects, these species have evolved a navigation system in which PI and visual references interact continuously (Etienne and Jeffery, in press; Etienne et al., 1996). Thus, while desert ants reset their path integrator only when they arrive back at home, hamsters may take position fixes wherever they are in a familiar environment. In these rodents and other mammals, idiothetic PI can therefore be considered as an essential component of navigation, which updates the navigator's position in a continuous manner in continuous space and remains functional throughout the animal's home range.

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