Cooperation Between Dead Reckoning (Path Integration) and External Position Cues

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1. INTRODUCTION. *Dead reckoning* (also called path integration[1]) is the process by which a navigating organism derives its current position relative to an Earthbound reference point from its own locomotion. Dead reckoning requires the continuous *estimation of changes in direction and location* through self-generated signals and the *computation of position* on the basis of these signals.

(i) Hymenopterous insects measure rotations and translations mainly with the help of optical references such as the Sun and translational visual flow.[2] By contrast, mammals are able to estimate their position on the basis of purely 'internal' information; that is, signals generated in the vestibular system by inertial forces, somatosensory feedback, and efference copies (copies of central commands that control the performance of rotations and translations). Obviously, the assessment of the angular and linear components of locomotion is much more precise if it is assisted by external references than if this is not the case.[3]

(ii) Only man-made dead reckoning systems yield precise position information through the twofold integration over time of inertial signals deriving from angular and linear acceleration. On the biological level, all species tested so far seem to rely on a simplified form of path 'integration': in certain test situations, arthropods and mammals (including humans) commit similar systematic errors.[4] This suggests that species from unrelated taxa update position according to a similar algorithm.[5]

Stable external references are used by all sedentary species for recognising and pinpointing particular goals within the home range. Olfactory and tactile cues may guide the subject to the goal or confirm the arrival at the goal station. Visual landmarks play a privileged role in navigation, as they are best suited to control not only the execution, but also the planification of a specific path. In contrast to dead reckoning, the reliance on external position cues depends on elaborate learning processes that allow the subject to identify each particular cue and to associate it with a given location. Furthermore, landmark-place associations enable a subject to pilot only if they are related with each other to represent

https://doi.org/10.1017/S0373463397007583 Published online by Cambridge University Press

familiar space in the form of an integrated system, such as a map. Here again visual landmarks play a predominant role, although olfaction may for instance potentiate the learning process by which visual cues are integrated in spatial memory.[6]

Recent theories of navigation in animals and man emphasise the interplay between dead reckoning and external position cues on the level of behaviour,[7] of the corresponding neuronal substrate[8] and of neuromimetic (connectionist) models.[8,9,10,11] From a functional viewpoint, dead reckoning and landmark navigation are complementary and therefore ideally suited to cooperate with one another in order to optimise navigation.

Dead reckoning is a continuously and automatically ongoing process which helps the subject to remain informed on his position within the familiar home range.[12] In a totally new environment, dead reckoning permits the subject to return to the point of departure of its first excursion[5] and therefore to centre its exploratory activities on a fixed reference point, independently of any learning process. However, being based on an iterative (step by step) form of information processing, dead reckoning is affected by cumulative errors. Finally, route-based position information is stored in short-term memory and is therefore of an evanescent nature, unless it leads to the memorisation of fixed vectors that link particular places to each other on a long-term basis.

Contrary to dead reckoning, external position cues may be used discontinuously, through 'episodic fixes'.[7,13] Furthermore, landmark navigation or piloting requires complex forms of learning and of processing long-term landmark-place associations. The more spatial memory encodes the geometric relationships between different locations within an integrated map system, the safer the storage of its content.

How can dead reckoning and landmark navigation complement each other? First of all, dead reckoning may play a crucial role in assigning particular landmarks to particular places. During the first explorations of its environment, a young animal updates its position in relation to its point of departure at its home. From its own current position it may deduce the position of newly encountered landmarks and therefore label particular places with particular landmarks. Later on, when the animal knows its home range, dead reckoning may either confirm or correct landmark-place associations. Further, dead reckoning may enable the subject to use ambiguous landmarks that can only be identified through their position.

Conversely, episodic fixes on the known landmark panorama may either confirm or reset the state of the path integrator. It is on this condition only that dead reckoning that is not assisted by external references and is therefore affected by rapid drift can remain functional over longer distances. Landmarks are also necessary for confirming the zero state of the path integrator when the goal region has been reached and for specifying the final approach of the goal.

2. EXPERIMENTS ON GOLDEN HAMSTERS. In our own work on spatial orientation of golden hamsters (*Mesocricetus auratus* W.) in the food hoarding situation, we started to analyse the interplay between dead reckoning and landmark-based navigation in *conflict situations*. This allowed us to analyse the

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relative weight hamsters attribute to each of the two systems. Depending on the experimental set-up, the hamsters' orientation was either unaffected by visual information,[12] or shifted between the dependence on locomotor and visual cues,[14] or else expressed a compromise between (adequate) visual references and dead reckoning. The last-mentioned alternative occurred in a large open arena, where the animal had access to distant room cues or to a single directional reference located at the arena periphery.[15,16,17] In these experimental conditions our subjects gave precedence to visual cues in a minor conflict opposing visual information and dead reckoning by 90°; by contrast, in an increased conflict between memorised visual references and dead reckoning, the hamsters relied on dead reckoning only or were completely disorientated.

Recordings of the activity of place cells in the hippocampus (that have a maximum firing rate when the rat is located in a specific place of the familiar test space) and/or head direction cells in the posterior subiculum and other brain areas (that respond to directional information only and therefore function like an 'internal compass') confirm these results on the neurophysiological level. Visual references tend to exert a greater control on these cells than internal signals induced by rotations, provided the conflict between the two categories of spatial information does not exceed certain limits[8,18] or is induced in a stepwise rather than in an abrupt manner.[19,20] From a functional viewpoint, these results suggest that rodents prefer to rely on the stable visual environment, but only as long as external position cues do not diverge too strongly or too suddenly from positional or compass information provided by motion.

Current experiments on hamsters test the *cooperation* between dead reckoning and external position cues in three different situations. We shall first describe our initial results on the hamsters' capacity to reset their path integrator through fixes on the distal landmark panorama (experiment 1), and then the use of non-visual (experiment 2) and visual (experiment 3) information to confirm vector information based on dead reckoning. In all our experiments, each subject, always a female, lives in her own, completely symmetrical arena with a peripheral nest, where she establishes her granary. The animal can commute freely between her nest and the arena by pushing a small circular door hinged at the top. Each subject is tested repeatedly in a particular test situation and filmed under infra-red light, olfactory and tactile cues being neutralised on the floor and along the peripheral wall of the arena. Experiment 1 involved in addition the continuous diffusion of pink noise by four loudspeakers.

2.1. *Resetting the path integrator through episodic fixes.* In the test trials of experiment 1 (Fig. 1), positional information which the subjects could gain through dead reckoning during the outward journey from the nest to a food source was jammed by rotating the subject during the food uptake on a platform.[21] Our question was whether the animals could retrieve their position vector (i.e. take a fix) with respect to the nest from the temporary presentation of familiar room cues and thus reset their path integrator. In the control trials (continuous darkness, no rotations and no visual fix) our five subjects showed well-orientated homing behaviour. In the experimental trials, if the animals were given no opportunity for a visual fix (continuous darkness, passive rotations),

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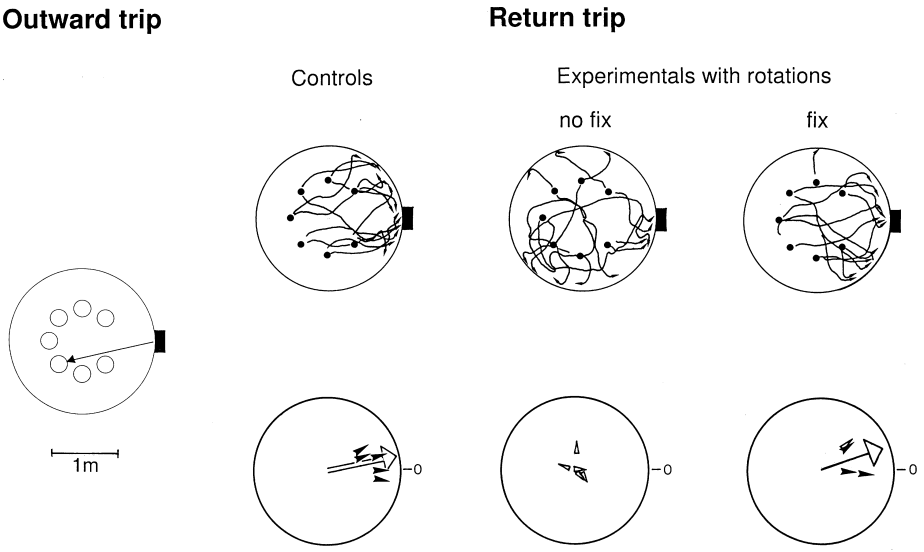


Fig. 1. The influence of the opportunity for an 'episodic fix' on the distant landmark panorama after path integration has been jammed. All trials occurred in continuous darkness (infra-red light), except for the experimental trials with a brief presentation of the landmark panorama (condition 'fix'). *Outward trip*: In all trials, the subject was led from its nest (small rectangle) to a platform (Ø = 25 cm) with a food source. The platform centre was always located at a radial distance of 50 cm from the arena centre; its angular location was shifted between trials, corresponding in each trial to one of seven different positions. *Return trip*: In the control trials, the subject filled its cheek pouches for about 30 sec on the stationary platform and then returned to the nest to empty its cheek pouches. In the experimental trials 'rotations and no fix', the subject was rotated on the platform (five full rotations in one direction, followed by five full rotations in the other direction, followed by a 90° rotation in the first direction) at the beginning of the food uptake, for about 10 sec. Then the subject continued to fill its pouches for about 20 sec and attempted to return home. In the experimental trials 'rotation and fix', the subject was rotated on the platform as in the above-mentioned experimental trials. However, after the end of the rotation, the ordinary room light was turned on for 10 sec to allow the animal to see the familiar room environment outside the arena. Thereafter the animal continued to collect food in darkness for 10 sec and then returned to the nest. The upper three diagrams to the right show the return journeys from the platform to the arena periphery of one subject in the three experimental situations. In each situation, the animal was tested twice with the platform in any given angular position. The lower three diagrams to the right represent the mean homing directions the subjects showed at a distance of 35 cm from the centre of the platform. In order to compute the mean direction, all return journeys were expressed in a coordinate system with the centre of the platform as origin and the platform-to-nest direction as the 0° reference direction. The small arrowheads indicate the mean homing direction for each subject (filled arrowheads: $P < 0{\cdot}05$ or $0{\cdot}01$; empty arrowheads: $P > 0{\cdot}05$; Rayleigh test). The large arrows indicate a significant mean homing direction (single line: $P < 0{\cdot}05$; double line: $P < 0{\cdot}01$, Moore's test) for the whole experimental group (unpubl. data, A. Griffin).

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they tended to be completely disorientated; by contrast, if they were briefly presented with the landmark panorama after the rotations, this opportunity for a fix (occurring well before the initiation of the return!) greatly improved the subject's homing direction, but did not completely restore the homing performance observed in the control trials. The detailed analysis of the return paths of individual subjects (upper diagram to the far right in Fig. 1) suggests that some hamsters may have taken up directional rather than positional information during the presentation of the familiar room environment.

In further experiments following the same rationale, the hamsters were led from their nest to a food source on a platform at the arena periphery, at an angular distance of 90° from the nest exit, were rotated and then presented with the visual environment for 10 sec, as in the above-mentioned experiment. However, at the end of the food uptake on the platform, they were led to a second food source at the arena centre, where they continued to collect food. Then they attempted to return home. In these conditions, the temporary sight of the distal visual environment at the first, peripheral food source did not allow the animals to home correctly from the second food source at the arena centre. However, our three subjects tended to return to the correct (nest-centred) half of the arena periphery. This preliminary result also points to the possibility that during the visual fix the hamsters may take up directional, but not positional information: the computation of the nest-related position during the passage from the first to the second food source could only have occurred if the hamsters knew their position at the moment they left the first food source.

Again, these results are backed up by single-cell recordings: in the absence of familiar visual references, the preferred direction of head direction cells started to drift, but was restored when the visual references were again presented.[22,23]

2.2. *The confirmation of self-generated vector information by external position cues.* Experiment 2 started from the question of whether hamsters could be trained to find a food source at a constant location without being helped by any external reference except non-visual cues at the nest exit, where they initiated path integration. To tackle this question, the animals were trained to reach from their nest a particular location where food was buried by following two different outward journeys (Fig. 2A). During the first part of these outward journeys, the subjects were led to a given point at the arena periphery; from there, they had to reach the goal by themselves, without any further guidance. In subsequent test trials, the animals had to proceed to the goal region after having followed a new guided path along the arena periphery. Figure 2B, C shows that the subjects orientated correctly from various points at the arena periphery to the goal location. This result suggests that the subjects were capable of computing the direction to the goal from their current peripheral position through the principle of vector addition. On the one hand, during the preliminary training phase they had memorised the goal region in form of a long-term nest-to-goal vector based on dead reckoning. On the other hand, throughout each outward journey, path integration was going on, so that the animals could constantly update their position-to-goal vector by subtracting the actually performed path from the current goal vector.

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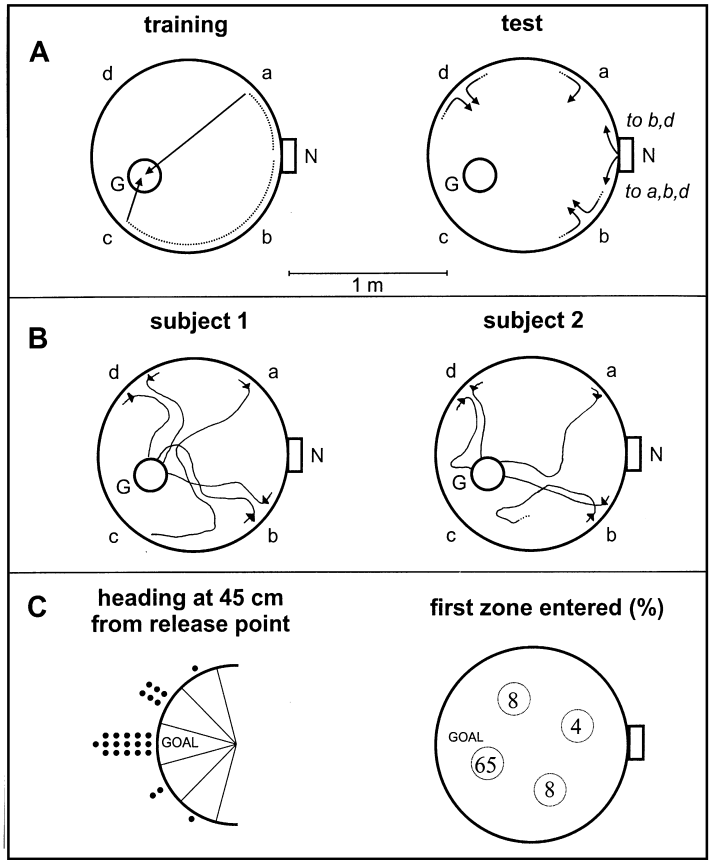


Fig. 2. Going to a food goal through long-term vector information, without the help of external position cues. All hoarding excursions occurred in continuous darkness. A: Training and test conditions. During a preliminary training period, the animal was led (hatched line) by a weakly illuminated bait from its nest (N) to a point a or c along the arena periphery. From a or c the subject had to learn to proceed by itself (continuous line) to a food source (G for goal) hidden in the thick sawdust layer on the arena floor, 30 cm from the arena wall. During the test trials, the subject was led from the nest along five new routes to three points (a, b or d) at the arena periphery. The arrows indicate the end of the guided outward journeys. The animal then proceeded by itself to the assumed goal region, where no food was buried. Before each test trial, olfactory cues within the arena were neutralised by stirring the thick sawdust substrate and by covering the walls with plastic bands. B: The test paths followed by two individuals. The continuous lines within each circle represent the path each subject followed from the peripheral end point of a guided outward journey. C: The goal direction chosen by the 8 subjects. The diagram to the left represents the position (dots) of the subjects at a distance of 45 cm from the end points of the guided outward journeys with respect to five 30° sectors, the midline of sector GOAL pointing from the peripheral end point of each outward journey to the centre of the goal region. Each subject underwent 2 to 5 test trials. The diagram to the right indicates the proportion of the 26 trials in which the zone of the goal and three symmetrically disposed control zones (Ø = 20 cm) were visited first. For each trial, the zone nearest to the peripheral end point was not taken into account (unpubl. data, J. Georgakopoulos and V. Derivaz).

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So far, we have only mentioned the choice of a given direction to the goal. An important point has to be added. With no food at the goal site, the animals did not stop there, but continued to walk without showing any sign that they had reached the goal region. By contrast, if food was buried at the usual location, as was the case in training and control trials, the hamsters remained on the spot and dug the food out. Thus, to stop and perform the expected instrumental response at the goal, the animals seemed to need specific, most likely olfactory cues[24] that confirmed their arrival at the goal, or, in other words, confirmed that they had covered the whole length of the vector planned through vector subtraction.

In experiment 3, hamsters were tested according to procedures similar to the former experiment, except that the food goal was hidden in one of four identical cylinders, symmetrically disposed on the arena floor (Fig. 3). Originally, this experiment was conceived to test whether hamsters could identify a goal beacon through its position, which they had to derive from their own position vector based on dead reckoning. By itself, the completely symmetrical landmark array could not inform the animals on the goal location. In the training and test trials of the first phase (*Light*) of the experiment, the arena was briefly illuminated when

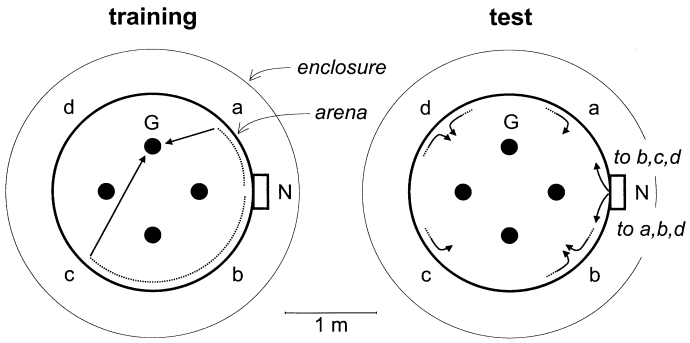


Fig. 3. Going to a food goal through long-term vector information, with the help of ambiguous landmark information. The subjects were trained and tested in an arena which was totally surrounded by a white optical enclosure consisting of cardboard panels and a cloth ceiling. Four identical, grey cylinders (diameter: 16 cm; height: 28 cm) formed a symmetrical landmark array at a distance of 50 cm around the arena centre, but only the hidden food cup of the cylinder at location G was baited in all trials. To reach the food, the subject had to enter the cylinder through one of four symmetrical openings at its bottom and climb up to the cup. During training, the animal was led from its nest N to point a (or c) in darkness. From a (or c) it had to learn to proceed by itself to the cylinder at location G. In test trials, the same subjects were led from the nest along six new routes to one of four different points (a to d) at the arena periphery (for clarity only the final parts of the guided outward journeys are indicated by arrows), from where they proceeded alone towards the goal. Training and testing occurred in two different light conditions. In condition *Light*, the symmetrical lighting above the optical enclosure was turned on briefly when the animal entered the arena from the nest, was turned out during the guided outward journey, and was turned on again just before the subject started to proceed from the arena periphery to the goal. In condition *Dark*, the trials occurred in darkness throughout. Before the test trials, intra-maze cues were neutralised as in exp. 2. Preliminary experiments had shown that hamsters do not smell out the food source hidden in the goal cylinder.

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the subject entered the arena from its nest. Then the animal was led in darkness to one of the peripheral points (a to d). Now the lights were turned on again, so that the animal could see the cylinders until the end of its hoarding excursion. As shown by Table 1 (first row), the six subjects showed an unexpectedly high

Table 1. Percentage of trials performed and of the choice of the correct cylinder in experiment 3*

Final path in	% trials performed	% correct first choice
Light	97	89
Darkness	67	96

* The first column indicates the lighting conditions during the subjects' ($n = 6$) unguided path to the goal cylinder in training and test trials. The second column shows the percentage of test trials in which the subjects performed the trials; that is, proceeded from the arena periphery to the landmark array and climbed into a cylinder. The third column represents the percentage of test trials in which the animals' first choice was the cylinder at the goal location with respect to the number of trials performed.

rate of success in the test situation. They proceeded in almost all test trials to the landmark array and climbed into a cylinder, their first choice being the cylinder at the goal location in all six trials (3 subjects), in five trials (2 subjects) or in three trials (1 subject). The success rate was lowest (83 and 50 percent) in those trials where the guided outward journey was longest and led to the end points b and d, which were never used as starting-points during the training trials.

Figure 4 represents the paths followed by one subject in a control experiment in condition *Light*. To make sure that the subject used no position cues from outside the arena, the arena was rotated by 90° before the beginning of each experimental trial. In these conditions, the subject initiated the outward journeys at the nest from a non-standard location with respect to the optical enclosure around the arena and the experimental room. If the subject depended on dead reckoning, it should proceed to cylinder DR, the location of which was determined by the current location of the nest, independently of any reference from outside the arena. This was indeed what the subject did in all six experimental trials. In a further control experiment, the arena was rotated by 90° counterclockwise, and the nest by 90° clockwise with respect to their standard position. Thus, three different (unbaited) cylinders remained correlated, respectively, (i) with the usual position of the goal cylinder in room space, (ii) with the usual position of the goal cylinder in the arena space, and (iii) with the goal cylinder as defined by dead reckoning starting at the current nest location. One subject underwent the usual six trials in these conditions and chose in four trials ($P < 0{\cdot}05$; binomial test) the cylinder at the position which was determined by dead reckoning (unpublished results).

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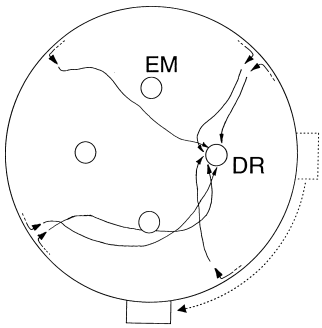


Fig. 4. Control experiment with a rotated arena. Before each experimental trial, the arena and nest (rectangle) were rotated clockwise by 90° (arrow). The subject therefore started the outward journeys from a non-standard location in room space. Extra-maze cues would lead the animal to cylinder EM, while dead reckoning would lead to cylinder DR. The continuous lines represent the subject's path from the arena periphery to the chosen (unbaited) cylinder, after six different guided outward journeys (the final parts of the guided journeys are indicated by arrows). The trials occurred in condition *Light*. For further explanations see legend of Fig. 3.

To see whether and how the subjects depended on the sight of the cylinders in experiment 3 (phase *Light*), we repeated the same experiment in conditions where the hamsters could never see the landmark array (experiment 3, phase *Dark*). The six above-mentioned subjects were retrained and then retested as before, except that the entire hoarding excursions occurred in darkness. Now, the subjects showed an even higher success rate than in the initial phase (*Light*) of the experiment (Table 1, second row). However, the hamsters were much more reluctant to venture into the open arena space to reach the goal in darkness than in light. In 12 out of a total number of 36 trials the animals returned home along the arena border instead of proceeding towards the landmark array. The refusals were particularly frequent in those trials where the guided outward path led to points b and c, from where the subjects had to cross the longest distance to reach the goal site.

Taken together, these results again suggest that the animals performed their trajectory from the arena border to the goal through the principle of vector addition. However, in comparison to experiment 2, the execution of the autonomous path to the goal seemed to be assisted by the cylinder at the goal location. In the fully lit arena (*Light*), the sight of a cylinder at the goal location may have confirmed the current-position-to-goal vector based on vector subtraction while the animal was still at the arena border. Furthermore, while performing the autonomous goal-directed path, the animals could be guided continuously by the chosen cylinder. In darkness, the final goal vector could not be confirmed from a distance. This may explain the hamsters' frequent refusal to walk towards the goal. On the other hand, during the performance of the path to the cylinder, non-visual cues must have helped the hamsters to know they had covered the correct vector length.

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In summary, experiments 2 and 3 suggest that without any external position cues or a general directional reference from the environment, hamsters are capable of reaching a goal site outside their home either directly, or through detours, by processing self-generated vector information. With regard to our main question, namely the cooperation between self-generated and external position cues, our results suggest that even if route-dependent vector information plays a leading role, it has to be backed up by external cues at the goal site. While visual landmarks confirm both the final current-position-to-goal vector from a distance and the arrival at the goal, non-visual cues can only assure the animal that it has reached the goal.

3. CONCLUSIONS. Current technical navigation systems owe their precision to positional information derived both from the integration of inertial signals generated by motion and from site-dependent signals gained by means of satellites. We have seen that biological navigation systems too are controlled by route-based and site-dependent positional information; that is, vector information gained through inertial and other types of self-generated cues on the one hand, and location-based landmark information from the familiar environment on the other hand. Both types of information are ideally suited to complement each other. Their cooperation is all the more important on the biological level as receptor and central information processing systems always work with a certain degree of error.

The importance of dead reckoning in navigation by mammals has only been revealed by recent experiments in rodents and in man (for references see Reference 3), and further research has to show to what extent and how dead reckoning cooperates with landmark information in these species. A further question concerns self-generated vector information in itself. Do mammals use vectors stored in long-term memory only one by one, or do they interconnect vectors that lead from their home to various foraging sites, thus building a real vector map? So far, the existence of such a map has been proven on the human level only, through experiments on a blind child who was able to commute between different locations within the experimental room without the direct help of external references.[25]

Finally, the discovery of head direction cells in various brain structures of the rat (for recent reviews see References 26 and 27) points to the existence of an internal compass which works on the basis of visual references as well as internal signals generated by motion. The internal compass is updated by taking account of rotations only, ignoring translations. With regard to behavioural data, our initial results on homing behaviour in hamsters were compatible with compass orientation (that is, the choice of a constant homing direction, independently of the point of departure of the homing path[28]) and therefore induced us to search for an external compass. Negative results with respect to this question led us finally to the conclusion that in certain conditions the animals update only the representation of their head orientation and therefore possess an internal compass.[21,29] The existence of such a compass which, in natural conditions at least, remains always aligned with an inertial frame of reference, must play a crucial role in navigation by mammals.

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ACKNOWLEDGEMENTS

This research is supported by the Swiss NSF grant 31-39311.93. We thank T. Collett and R. Gallistel for invaluable commentaries on experiments 1 and 2.

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KEY WORDS

1. Animal navigation. 2. Mammals. 3. Dead reckoning. 4. Position cues.

https://doi.org/10.1017/S0373463397007583 Published online by Cambridge University Press