Review article

On the origins of autobiographical memory

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Abstract

Tolving [27] argues that one form of explicit memory, autobiographical memory is uniquely human and has no nonhuman animal antecedents. We suggest that a form of memory used by humans and nonhuman animals, dead reckoning, shares a common limbic strucure, including the cingulate cortex and hippocampus, and involves similar processes in recognition of self-action. Thus, it may be homologous to, and an antecedent of, autobiographical memory in humans.
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1. Introduction

Schacter [22] describes the 1980s as the beginning of the modern memory revolution because of the realization during that decade that memory comes in different forms, two of which are explicit and implicit memory. Explicit memory is the conscious, intentional recollection of previous experiences. You can describe what you had for breakfast this morning, how you travelled to school, and to whom you spoke since you woke up. These are explicit memories. You can also describe events that have taken place in the past, and you know the identity of family, friends, local or world leaders, and many famous personalities. These are also explicit memories. Implicit memory is an unconscious, nonintentional form of memory. Your ability to use language or to perform motor skills such as riding a bicycle or playing a sport are examples of implicit memory.

The study of explicit memory in human vs. nonhuman animals poses some problems both in relation to the evolution of memory systems and their neural substrates. Explicit memory is assessed using language-based tests, making it difficult to present parallel tests to nonhuman animals that do not speak. Parsimony, nevertheless, suggests that from an evolutionary per-

spective the antecedents of human forms of memory will be found in animals [4]. In opposition to the idea that there is evolutionary continuity in memory systems across animal species, Tulving [27] argues that one form of explicit memory, autobiographical memory, is uniquely human and has no nonhuman animal antecedents. It is this claim that we will discuss.

We will suggest that autobiographical memory does have nonhuman animal antecedents both as a form of memory and in terms of neural structure. In the following sections we first describe autobiographical memory and the claim that it is unique to humans. We then describe a form of memory used by humans and nonhuman animals, dead reckoning, and we will suggest that dead reckoning is homologous to and an antecedent of autobiographical memory in humans. We will also argue that autobiographical memory and dead reckoning share a common neural substrate, and we will suggest ways in which dead reckoning may have become elaborated as autobiographical memory.

2. Autobiographical memory

Tulving [27] proposes that explicit memory comes in two forms: episodic memory and semantic memory. Episodic memory consists of singular events that a person recalls. This form of memory is also referred to as autobiographical memory, the term that we will use

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here. Knowledge about the world—all knowledge that is not autobiographical—is referred to by Tulving as semantic memory. Thus, semantic memory includes knowledge of historical events and of historical and literary figures. It includes the ability to recognize family, friends, and acquaintances. It also includes information that one has learned in school, such as specialized vocabularies, reading, writing, and mathematics. Tulving's patient K.C. illustrates the loss of autobiographical memory with preserved semantic memory:

K.C. was born in 1951. At the age of 30 he suffered a serious closed head injury in a motorcycle accident, with extensive brain lesions in multiple cortical and subcortical brain regions including medial temporal lobes, and consequent severe amnesia. Nevertheless, most of K.C.'s cognitive capabilities are intact and indistinguishable from those of many healthy adults. His intelligence and language are normal; he has no problems with reading or writing; his ability to concentrate and to maintain focused attention are normal; his thought processes are clear; he can play the organ, chess, and various card games; his ability to visualize things mentally is intact; and his performance on short-term memory tasks is normal. He knows many objective facts concerning his own life, such as his date of birth, the address of his home for the first 9 years of his life, the names of some of the schools he attended, the make and color of the car he once owned, and the fact that his parents owned and still own a summer cottage. He knows the location of the cottage and can easily find it on a map. He knows the distance from his home to the cottage and how long it takes to drive there in weekend traffic. He also knows that he has spent a lot of time there. His knowledge of mathematics, history, geography, and other 'school subjects,' as well as his general knowledge of the world, is not greatly different from that of others at his educational level.

Along with all these normal abilities, K.C. has dense amnesia for personal experiences. Thus, he cannot recollect any personally experienced events, whether one-time happenings or repeating occurrences. This inability to remember any episodes or situations for which he was present covers his whole life, from birth to the present, although he does retain immediate experiences for a minute or two. K.C. has no particular difficulty understanding and discussing either himself or physical time. He knows many facts about himself, and he knows what most other people know about physical time, its units, its structure, and its measurement by clocks and calendars. Nevertheless, in Tulving's words, K.C. cannot 'time travel,' either to the past or future. He cannot say what he is going to be doing later today, tomorrow, or at any time in the rest of his life. He cannot imagine his future any more than he can remember his past.

Autobiographical memory has perhaps been overlooked as a special form of memory because persistent questioning is required in order to demonstrate the absence/presence of autobiographical memory. The following example described by Levine [10,11] illustrates a form of questioning used to investigate the presence of autobiographical memory. Were the questioner not persistent, G.O.'s impairment in episodic memory may well have been missed.

Do you have a memory of when you had to speak in public?

Well yes, I'm a call centre trainer with Modern Phone Systems so I did a lot of speaking because I did a lot, a lot of training all across Canada. I also went to parts of the States.

Do you remember one time that you were speaking? Can you tell us about one incident?

Oh yes! Well I trained thousands and thousands of clients on a wide variety of topics including customer service, inbound and outbound telemarketing. Handling difficult customers.

Do you remember one training session that you gave? Something that may have happened, a specific incident?

Well, for example I always recommended that people take customer-service first. And I always had people come up with four things about themselves, three that were true and one that was false. Not necessarily in that order.

But this was something ongoing, so every training session you would tell people this right?

Yes.

So what we're looking for is one incident or one time that you gave a training session or any other speeches that you want to tell us about? A specific incident.

Oh well I customized a lot of material for many, many companies. And I also did lots of training at the home office.

OK, so what we're asking is do you remember one time that you gave a talk?

Oh! Yes I do.

One specific time not over a series of times, one time, can you tell us about that?

Oh sure yes, it was at the home office and yes, many, many people were there.

One occasion. When did that take place?

When? Well I left Modern voluntarily in 1990.

But this one occasion when did it take place?

Ummm, well I started in the Modern home office.

I'm getting the impression that you have a really good memory for all the training that you've done but you don't seem to be able to come up with a specific talk that maybe stands out in your mind for any reason? Would you agree with that?

Oh yes well I always trained customer service.

So there was no talk that maybe something went wrong or something strange happened?

No, No I was a very good trainer [11].

As noted above, Tulving uses the metaphor of time travel in order to explain autobiographical memory. He states that everything in nature travels forward in time, but humans are unique amongst animals in that they can also travel backward in time. Tulving states that nonhuman animals are as capable as humans at producing their own kind, that they have minds and are conscious of their world, and that they rely on learning and memory to acquire life skills; however, he believes they do not have the ability to travel back in time in their own minds and revisit their past experiences. He also argues that episodic memory depends upon maturation in humans; therefore, it will not be found in babies and young children.

3. Dead reckoning

Most animals, and certainly most vertebrates, occupy territories that provide them with food, shelter, and safety. As these resources are unequally distributed, the animals must develop strategies of optimizing the use of their environment's resources while at the same time minimizing their own risk of injury or death. It seems unlikely that the brain regions that coordinate the optimal use of a territory's resources are a 'tabula rasa' upon which experience writes appropriate lessons for survival. Rather, it is likely that behaviors and brain regions that optimize the use of space have been preorganized by the lessons of the animal's evolutionary history.

Gallistel [7] proposes that animals have two strategies for navigating and thus coping with their spatial world. Piloting is a form of navigation in which an animal uses allothetic (external) cues for guidance. An animal may pilot to a visible cue or it may use the relational properties of a number of cues to reach a point in space. Such cues need only be sufficiently distanced so that they retain their locations relative to a moving animal [17].

A different form of spatial behavior, and one that is less studied than piloting, is dead reckoning. Dead reckoning is a form of navigation that depends upon ideothetic cues (cues that are generated by the animal's own movement). The term dead reckoning derives from the contraction *ded*, from deduced reckoning. It refers to the ability of an animal to know how far it has travelled, to know where it is in relation to a starting point, to monitor the speed of its movement and travel time, and to add its directional changes. Dead reckoning was an early form of navigation used by sailors, and it is believed to be the form of navigation used by Columbus to travel between Europe and Central America. Sailors calculated speed by throwing a piece of wood overboard at a point on the bow. While the piece of wood floated

along the side of the boat, the sailors chanted until the wood passed a point on the stern. The chant was constructed such that the last word spoken corresponded to a specific speed; thereby, the chant served as a timing device. The sailors used a compass to monitor the direction of the course. Dead reckoning is still used today when fog limits the use of visual beacons; all a sailor needs is a speedometer, watch, and compass. Dead reckoning allowed sailors to know their current location and to return to the position from which their journey originated (Fig. 1).

First described by Darwin [3] as a possible form of navigation used by animals, dead reckoning has been demonstrated in a number of animal species in laboratory studies in which animals retrieve food or pups [6,24,16] or engage in spontaneous exploration [29,32]. Nonhuman animals do not have mechanical ways of measuring speed, time, and direction in order to dead reckon. Rather, they must use idiothetic cues. In principle, cues from a number of sensory systems, including proprioceptive and vestibular systems, can provide information concerning self-movement [29]. Sensory flow, including optic flow, gradients of sound and odors, and even wind resistance, can also provide information concerning self-movement [38]. An animal may also monitor its movements using the efferent copy of movement commands. Using these cues, if changes in velocity and direction are computed over time, an animal can know its location in relation to a starting point. In principle, the reciprocal of this computation allows an animal to return using the most direct route to its starting point.

Dead reckoning is adaptive in that it provides a way for an animal to navigate in circumstances that might otherwise be insurmountable. On an outward trip, an animal is not able to observe allothetic cues from the perspective that it will view them on its homeward trip;
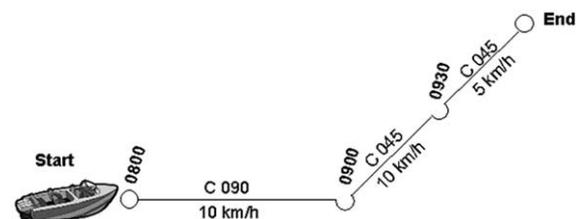

Fig. 1. A typical dead reckoning plot for a boat on the open sea. The closed circles represent points in which a fix from a known landmark was taken, thereby the location of the boat is known. The angled text above the circles and semicircles corresponds to the time the fix or a dead reckoning plot was taken, respectively. Numbers above the lines represent the course heading relative to north. The first leg of the trip is directly west corresponding to C090 (C270 would correspond to an eastern course direction). The speed travelled during a segment of the trip is listed below the lines on the plot. Semicircles represent dead reckoning points along the course. The captain of the boat needs a compass, speedometer, and a watch to successfully navigate to the fishing area in the absence of visual cues.

cues may change while it is travelling, such as occurs with darkness, or cues may be difficult to detect as might occur during nocturnal foraging. More importantly, it might be adaptive both for the purposes of safety and energy conservation to make a homeward trip that is faster and more direct than the outward trip [5,32]. For all of these reasons, a navigation strategy that depends upon allothetic cues may not be useful for making a return trip, whereas a strategy that relies upon computing a homeward course from cues generated on the outward trip will be useful.

When, and if an animal does use dead reckoning, the process is less obvious than when it uses piloting. To demonstrate that an animal uses piloting requires the relatively simple control of allothetic cues, whereas to demonstrate that it uses dead reckoning requires the removal of all allothetic cues. For example, in one of our typical experiments, animals are first allowed to search for food on a large circular table under normal light conditions from a visible home base located on the perimeter of the table (Fig. 2, Panel B). Rats reliably carry large food pellets to the home base, and once they are comfortable doing so, two kinds of probe trials can be given [35]:

(1) To demonstrate piloting, rats are released from a 'hidden' home base located below the table, thereby eliminating the proximal home as a potential guide for piloting (Fig. 2, Panel C). Therefore, in the piloting probe, the rat can use the relational properties of room allothetic cues to reach the home base.

(2) To demonstrate dead reckoning, rats are released from a home base below the table with all the lights turned off. The dark probe removes all visual allothetic cues, and washing the table, and controlling room sounds, removes other allothetic cues with which an animal might navigate. This leaves only idiothetic cues available for navigation (Fig. 2, Panel D).

It is important to note that in the dead reckoning test, the animal is tested in an impoverished condition. Even though optic flow, auditory stimuli, and olfactory stimuli can contribute to dead reckoning, these cues are removed, and the animal is limited to using proprioceptive, vestibular, and efferent copy from movement commands. Despite this drawback, animals are excellent at dead reckoning in such a laboratory task.

4. Autobiographical memory and dead reckoning

As noted above, autobiographical memory is a form of memory in which a person time travels to a specific life event. Dead reckoning also allows an animal to time travel. It can revisit a past experience—its own record of the movements that it has just made. It can use that information adaptively, to locate its present position and to return to a location from which it initiated the
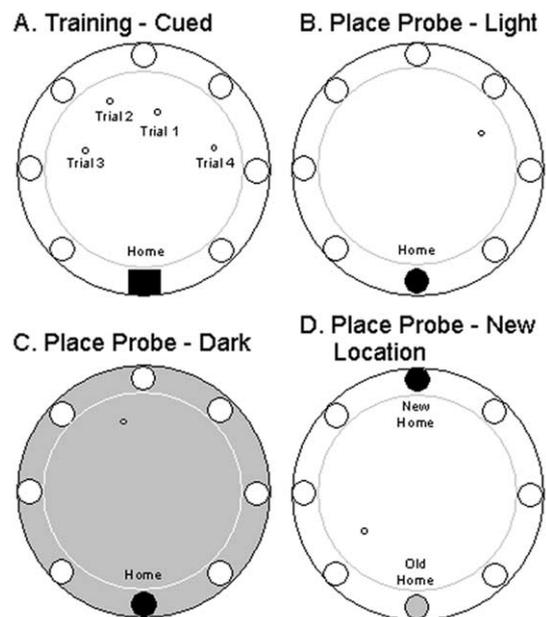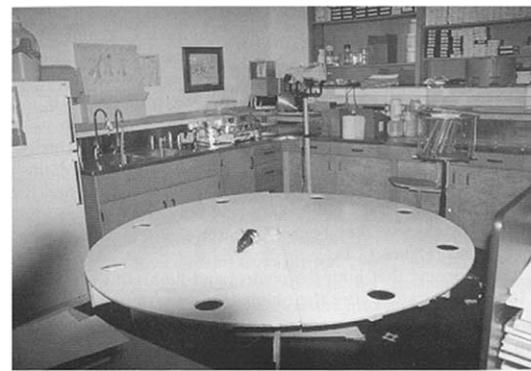

Fig. 2. The top panel is a photograph of the lightproof testing room used throughout the experiment. As one can see, many visual cues are available to the rat under light conditions. Under dark conditions, all visual cues are eliminated. The panel A is a schematic of the table and a possible sequence of food pellet placements for one day of training with the cued home base. Rats were required to find the food pellet prior to rebaiting the table. Panels B and C represent the conditions for the place and dark probes, respectively. Panel D corresponds to testing when the rat was released from a location different from that during cued training and probes.

trip. Thus, we suggest that this feature of dead reckoning is homologous to time travel in humans. The animal must have a home destination that it has in mind, it must choose to return to that location, and it must abstract from its previous behavior the necessary information/computation that will return it to that location.

Although it could be argued that dead reckoning is simply a reflexive response based upon just completed movements, there are a number of features of dead reckoning that suggest that it is more complex than this. First, whereas an animal may have made many hundreds of previous trips using dead reckoning, on each iteration it must select appropriate information con-

cerning its just completed excursion. That is dead reckoning would not work if there were interference from previous trips.

Second, there is evidence that an animal can access its previous movements even in a situation in which it had no expectation that dead reckoning might be required. Whishaw and Tomie [35] trained animals to forage from a hidden home base in the light for food that was placed in random locations on the circular table (Fig. 3). Because the home base was always in the same location, the animal was able to make its return trips by using the configuration of room cues that marked the location of its home base. After animals were completely familiar with this situation, their refuge was placed in a novel location on the table. As expected, the animals exited from the home base at its new location and located a food pellet. They then returned to the old starting location, which might be expected because this was the
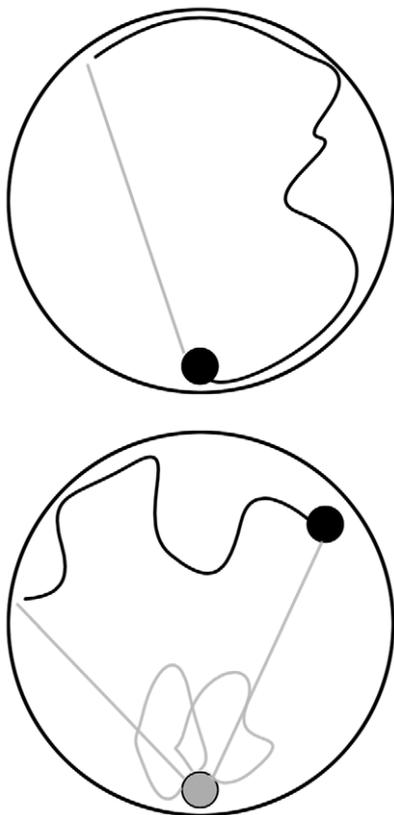

Fig. 3. Both panels are schematics of hoarding trips observed under normal conditions (top panel) and when the rats are released from a position 180 degrees different from that encountered during training (bottom panel). As can be seen in the top panel, the search pattern is circuitous (black line); after finding the food pellets, the rat heads directly to the home base along a non-circuitous path (gray line). When the rat is released from a novel location, the search pattern is circuitous (black line); upon finding the food pellet, the rat makes a direct path to the former location of the home base (gray line). The rat makes several short trips around the former location of the home base prior to returning to the new home base location.

target during the initial familiarization portion of the experiment. That the animals returned to the old starting location, indicated that they knew its location in relation to allothetic room cues. Upon finding that the refuge was not there, however, the animals then travelled accurately to the new starting location. They were able to display this 'zero trial learning' even though they had no expectation that they would have to return to that location and even though they had not received previous training on such a task. They also had not returned to this location using available allothetic room cues.

That the animals are able to return to the new location is remarkable when it is considered that the animals calculated their return trajectory using the portion of the outward trip in which they were searching for food and the portion of the trip on which they were piloting to the previous home base.

Definitive support for the idea that the animals used dead reckoning to return to the novel location was obtained by repeating the experiment in infrared light. Being deprived of distal visual cues, the animals then did not return to the previously correct starting location. Instead, they located the food and returned directly to the novel starting location with it.

Third, in the experiment just described, many animals, when tested in the light, upon finding that the home base was absent, made a number of brief excursions away from and back to the familiar home base, as if they were checking to see that the refuge cage was really not there, before returning to the new home base. Thus, in order to dead reckon to the new location, they had to ignore these movements in calculating their return trip. In other words, the animals time travelled to a particular portion of their outward trip in order to access information required for calculating their homeward trip.

Fourth, there is evidence that animals may use dead reckoning as a step in solving piloting problems. When the home base is moved for a foraging rat, it learns to return directly to the new location, ignoring the previously correct location, in only a few trials. Presumably by viewing allothetic cues on its first dead reckoning return, it learns the new location in relation to these allothetic cues [35].

Navigating animals may use dead reckoning for still more complex forms of navigation. For example, an animal may learn that its home base is at a certain distance and direction from a particular allothetic cue or cue configuration. Thus, using such a cue, the animal may make a fix or running fix to initiate its homeward trip [7]. In principle, the use of an allothetic cue as a fix for a homeward trip may allow an animal to separate initial learning from subsequent recall by a substantial period of time.

5. The hippocampus and autobiographical memory

Tulving [28] proposes that autobiographical memory depends upon the ventral frontal lobe, medial temporal lobe, and uncinate connections between these brain regions in the right hemisphere. He proposes that similar regions of the left hemisphere are important for semantic memory. Corkin et al. [1,2,15,23] tested the medial temporal lobe patient H.M. for autobiographical memory and reports that, although this retrograde memory for semantic information is not complete, his retrograde amnesia for autobiographical memory is complete. He has no autobiographical memory of even his earliest childhood. Whereas Tulving has speculated that both the right frontal and medial temporal cortex are involved in autobiographical memory, Corkin's finding that H.M. has no autobiographical memory shows that damage restricted to the medial temporal lobes is sufficient to produce a loss of autobiographical memory. If dead reckoning is a behavior that is antecedent to autobiographical memory, it might be expected that it depends upon the same neural substrate.

There is evidence to indicate that damage to the hippocampus severely impairs dead reckoning in the rat. Rats with lesions to the fimbria-fornix [33], a major pathway of the hippocampal formation, or lesions to the cells of the hippocampus proper [12] can learn the allothetic version of the foraging task. They can leave the refuge, find food, and return directly to the refuge. If these animals are given the test in which the refuge is moved to a new location, they retrieve food to the old location, and make repetitive trips away and back to that location, but they only reach the new location by chance. When tested in the dark, they again fail to return directly to the new location and again only reach it by chance [12]. Furthermore, when allowed to explore an open arena, control rats make many direct homeward trips in both the light and dark, whereas rats with hippocampal damage do not. When given tests in which the route to the food target is more explicit (e.g. they follow a circuitous string marked with a distinctive odor) both control and hippocampal rats follow the string to food, but only the control rats take a short cut back to the refuge. Rats with hippocampal formation damage take the longer route of following the string back to the refuge. In addition, when given a circular trail to follow, control rats abort their search for food after completing one circle indicating that they are aware of the distance they have travelled. Rats with hippocampal formation damage persist completing one circle after another seemingly insensitive to the distance that they have travelled [31].

Several computational modeling studies suggest explanations for how the hippocampus might mediate dead reckoning-based navigation [37,21]. There are also electrophysiological studies suggesting that cells in the hippocampus respond to idiothetic cues used during dead reckoning, including vestibular signals, optic flow and whole body motion [18,25,26,36,20,8].

It is interesting that in reviewing the many hormones that target the hippocampus (corticosterone, angiotensin, insulin, etc.) Lathe [9] has suggested the hippocampal system may have a common evolutionary origin with the olfactory system. He proposes that the hippocampal system may have had an early role in sensing internal molecules, while the olfactory system sensed external molecules. Extrapolating from this idea, we suggest that the hippocampal formation may have evolved into an organ that came to sense other signals related to the 'self', including self-movement signals, and finally evolved as the substrate for episodic memory. In turn the olfactory system may also have taken on the more complex function of representing the objects that emitted chemical signals and so evolved as the substrate of semantic memory.

Thus, we propose that dead reckoning has been elaborated from a relatively simple system of monitoring self-movement to a much more complex system incorporating language to represent self-actions. A possible step in this evolution may have involved an association between allothetic cues and idiothetic cues in which allothetic cues served as signals for initiating dead reckoning responses. At first allothetic cues may have served as fixes for locating a present position and directing a trajectory while later in evolution they may have served as signals for the recall of previously experienced events. A step from having a salient allothetic cue calling forth a specific previously used motoric response could be a homologue of a salient verbal cue eliciting a previous personal experience.

6. Conclusions

According to Tulving, autobiographical memory requires three elements: (1) a sense of subjective time; (2) autonoetic awareness, the ability to be aware of subjective time; and (3) a 'self' that can travel in subjective time. There is evidence that rats use temporal information to guide responding. Studies examining a rat's ability to time events range from highly controlled operant procedures (for a review of procedures see [13,14,19]) to food handling studies [34]. For example, animals use time for estimating how long it will take to eat a piece of food as well as how long it will take to make a return trip to a home base [34,30]. We can only speculate upon whether rats have a sense of subjective time, or the ability to be aware of subjective time, but the fact that they can dead reckon suggests that time plays an important role in their behavior. In order to calculate a homeward trip, an animal must also know how long it has travelled, in addition to knowing its speed and direction of travel. Certainly the evidence that

we describe above does suggest the rat has a 'self' that can time travel because it can access remote idiothetic information in order to calculate homeward trips. Importantly, it is likely that self-movement information provides an animal with information about what it itself did at a particular time and place just as autobiographical memory allows humans to know what they did at a particular time and place. Thus, with respect to both function and neural substrate, dead reckoning may be an antecedent of autobiographical memory.

Acknowledgements

References

[1] Corkin S. What's new with the amnesic patient H.M.? Nat Rev Neurosci 2002;3:153–60.

[2] Corkin C, Amaral DG, Gonzalez AG, Johnson KA, Hyman BT. H.M.'s medial temporal lobe lesion: findings from magnetic resonance imaging. J Neurosci 1997;17:3964–79.

[3] Darwin C. Origin of certain instincts. Nature (Lond) 1873;7:417–8.

[4] Davis H. Understanding the rat's intelligence. Cognit Brain Res 1996;3:291–8.

[5] Drai D, Benjamini Y, Golani I. Statistical discrimination of natural modes of motion in rat exploratory behaviour. J Neurosci Methods 2000;96:119–31.

[6] Etienne AS, Maurer R, Saucy F, Teroni E. Short-distance homing in the golden hamster after a passive outward journey. Anim Behav 1986;34:696–715.

[7] Gallistel CR. The organisation of learning. Cambridge, MA: The MIT Press, 1990.

[8] Gothard KM, Hoffman KL, Battaglia FP, McNaughton BL. Dentate gyrus and ca1 ensemble activity during spatial reference frame shifts in the presence and absence of visual input. J Neurosci 2001;21:7284–92.

[9] Lathe R. Hormones and the hippocampus. J Endocrinol 2001;169:205–31.

[10] Levine B. Autonoetic consciousness and self-regulation in patients with brain injury. Int J Psychol 2002;35:223.

[11] Levine B, Black SE, Cabeza R, Sinden M, Mcintosh AR, Toth JP, Tulving E. Episodic memory and the self in a case of isolated retrograde amnesia. Brain 1998;121:1951–73.

[12] Maaswinkel H, Jarrard LE, Whishaw IQ. Hippocampectomized rats are impaired in homing by path integration. Hippocampus 1999;9:553–61.

[13] Meck WH. Selective adjustment of the speed of internal clock and memory processes. J Exp Psychol: Anim Behav Proc 1983;9:171–201.

[14] Meck WH, Church RM. A mode control model of counting and timing processes. J Exp Psychol: Anim Behav Proc 1983;9:320–34.

[15] Milner B, Corkin C, Teuber HL. Further analysis of the hippocampal amnesic syndrome: 14-year follow up study of H.M. Neuropsychologia 1968;6:215–34.

[16] Mittelsteadt ML, Mittelsteadt H. Homing by path integration in a mammal. Naturwissenschafen 1980;67:566–7.

[17] O'Keefe J, Nadel L. The hippocampus as a cognitive map. Oxford: Oxford University Press, 1978.

[18] O'Mara S, Rolls ET, Bertholz A, Kesner RP. Neurons respond to whole body motion in the primate hippocampus. J Neurosci 1994;14:6511–23.

[19] Roberts S. Isolation of an internal clock. J Exp Psychol: Anim Behav Proc 1981;7:242–68.

[20] Russell NA, Horii A, Liu P, Smith PF, Darlington CL, Bilkey DK. Hippocampal place fields have decreased stability in rats with bilateral vestibular labyrinthectomies. Soc Neurosci Abstr 2000;26:843–8.

[21] Samsonovich A, McNaughton BL. Path integration and cognitive mapping in a continuous attractor neural network model. J Neurosci 1997;17:5900–20.

[22] Schacter DL. Implicit knowledge: new perspectives on unconscious processes. Proc Natl Acad Sci USA 1992;89:11113–7.

[23] Scoville WB, Milner B. Loss of recent memory after bilateral hippocampal lesions. J Neurol Neurosurg Psychiatr 1957;20:11–21.

[24] Séquinot V, Mauer R, Etienne AS. Dead reckoning in a small mammal: the evaluation of distance. J Comp Physiol 1993;173:103–13.

[25] Sharp PE, Blair HT, Etkin D, Tzanetos DB. Influences of vestibular and visual motion information on the spatial firing patterns of hippocampal place cells. J Neurosci 1995;15:173–89.

[26] Taube JS, Burton HL. Head direction cell activity monitored in a novel environment and during a cue conflict situation. J Neurophysiol 1995;74:1953–71.

[27] Tulving E. Episodic memory: from mind to brain. Annu Rev Psychol 2002;53:1–25.

[28] Tulving E, Kapur S, Craik FIM, Moscovitch M, Houle S. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography finding. Proc Natl Acad Sci USA 1994;91:2016–20.

[29] Wallace DG, Hines DJ, Whishaw IQ. Quantification of a single exploratory trip reveals hippocampal formation mediated dead reckoning. J Neurosci Methods 2002;113:131–45.

[30] Whishaw IQ, Dringenberg HC. How does the rat (*Rattus Norvegicus*) adjust food-carrying responses to the influences of distance, effort, predatory odor, food size, and food availability. Psychobiology 1991;19:251–61.

[31] Whishaw IQ, Gorny B. Path integration absent in scent-tracking fimbria-fornix rats: evidence for hippocampal involvement in 'sense of direction' and 'sense of distance' using self-movement cues. J Neurosci 1999;11:4662–73.

[32] Whishaw IQ, Hines DJ, Wallace DG. Dead reckoning (path integration) requires the hippocampal formation: evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) tests. Behav Brain Res 2001;127:49–69.

[33] Whishaw IQ, Maaswinkel H. Rats with fimbria-fornix lesions are impaired in path integration: a role for the hippocampus in 'sense of direction'. J Neurosci 1998;18:3050–8.

[34] Whishaw IQ, Oddie SD, McNamara RK, Harris TL, Perry BS. Psychophysical methods for study of sensory-motor behavior using a food-carrying (hoarding) task in rodents. J Neurosci Methods 1990;32:123–33.

[35] Whishaw IQ, Tomie J. Piloting and dead reckoning dissociated by fimbria-fornix lesions in a rat food carrying task. Behav Brain Res 1997;89:87–97.

[36] Wiener SI. Spatial behavioral and sensory correlates of hippocampal CA1 complex spike cell activity: implications for information processing functions. Prog Neurobiol 1996;49:335–61.

[37] Worden R. Navigation by fragment fitting: a theory of hippocampal function. Hippocampus 1992;2:165–87.

[38] Wylie DR, Glover RG, Aitchison JD. Optic flow input to the hippocampal formation from the accessory optic system. J Neurosci 1999;19:5514–27.