Spatial inference without a cognitive map: the role of higher-order path integration

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ABSTRACT

The cognitive map has been taken as the standard model for how agents infer the most efficient route to a goal location. Alternatively, path integration – maintaining a homing vector during navigation – constitutes a primitive and presumably less-flexible strategy than cognitive mapping because path integration relies primarily on vestibular stimuli and pace counting. The historical debate as to whether complex spatial navigation is ruled by associative learning or cognitive map mechanisms has been challenged by experimental difficulties in successfully neutralizing path integration. To our knowledge, there are only three studies that have succeeded in resolving this issue, all showing clear evidence of novel route taking, a behaviour outside the scope of traditional associative learning accounts. Nevertheless, there is no mechanistic explanation as to how animals perform novel route taking. We propose here a new model of spatial learning that combines path integration with higher-order associative learning, and demonstrate how it can account for novel route taking without a cognitive map, thus resolving this long-standing debate. We show how our higher-order path integration (HOPI) model can explain spatial inferences, such as novel detours and shortcuts. Our analysis suggests that a phylogenetically ancient, vector-based navigational strategy utilizing associative processes is powerful enough to support complex spatial inferences.

Key words: cognitive map, path integration, inference, goal-directed behaviour, head-direction vectors, vector learning

CONTENTS

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I. INTRODUCTION

The route travelled from home to the place of work can be considered as a chain of multiple environments linked to each other by common areas. When a place is unexpectedly blocked, such as by a traffic accident or roadwork, a spatial inference, which is the flexible and spontaneous ability to travel a novel route, can enable the use of alternative routes to the destination. The ability to use novel shortcuts and detours is thought to reflect a cognitive mapping process. A cognitive map is a representation of a set of familiar environments stored in a mental representation as a configural whole, and enables flexible navigation (Tolman, 1948). The first report of an animal's ability to perform spatial inferences was obtained about a century ago in Hsiao's (1929) pioneering experiments. Rats were trained to navigate a maze composed of three pathways of increasing length (X < Y < Z), each leading to a goal box at the other end (Fig. 1).

During each training session, a block was placed at the entrance to one the three alleys, thereby preventing access. The rats learned successfully to take the shortest available pathway. After training, rats received a single test trial with the block now placed in a new position (B), thereby preventing the use of either alley X or Y to reach the goal box (Fig. 1). Rats first entered the shortest available route, X, and found themselves blocked at B. Subsequent to finding the block at B, rats backtracked through the maze and overwhelmingly chose alley Z, suggesting they understood that entering Y would also lead to the block at B. After replicating this phenomenon with a larger number of subjects (Tolman & Honzik, 1930), Tolman (1948) concluded that rats are able to form a mental map-like representation of a familiar environment, or 'cognitive map', through exploration by gradually encoding and integrating spatial relationships between elements composing the environment. The cognitive map is conceived as a comprehensive representation of one's familiar environment seen as a configural whole, and enables flexible decisions as opposed to the trial-and-error learning advocated by behaviourists such as Thorndike and Watson (Tolman, 1948). According to behaviourism, when an unpredicted change in the environment occurs that prevents the utilization of previous learning, finding the most efficient alternative route requires new learning. According to Tolman (1948), however, the first time the rat was faced with the block at a novel location B, it referred to its cognitive map to derive the proper spatial inference to reach the goal and chose route Z over Y. The single test of a novel situation,

by definition, cannot be solved by trial-and-error learning, and is thought to involve the use of a mental representation, specifically the cognitive map (Tolman, 1948).

(1) Place cells and the cognitive map

According to a series of seminal neurophysiological studies (e.g. O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978),
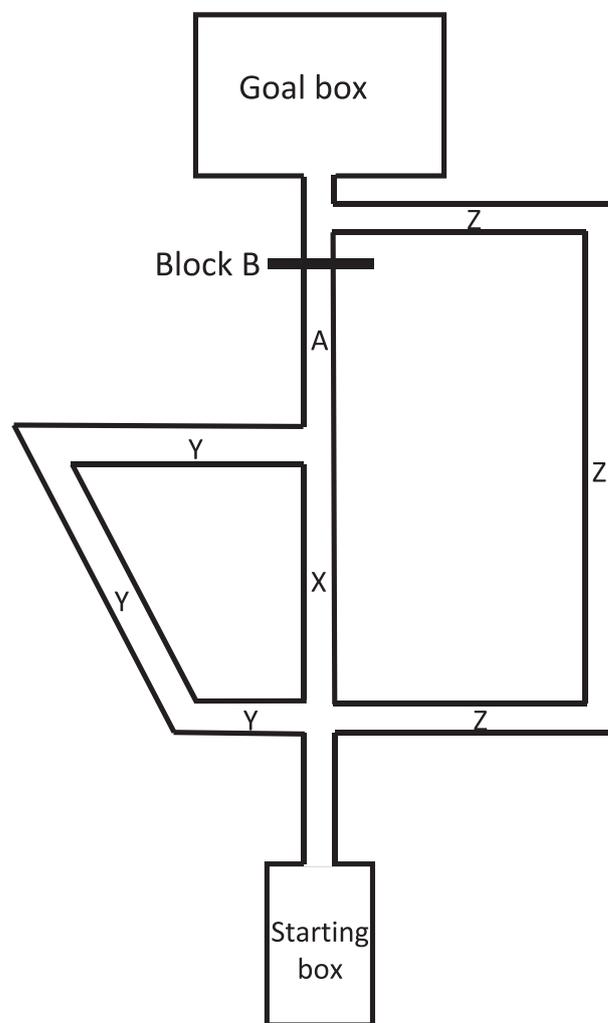

Fig 1. Schematic representation of the maze used by Hsiao (1929), where X, Y, and Z represent three pathways of increasing length that connect a starting box to a goal box, and A is a common segment shared by X and Y. The position of Block B is that of the test condition.

a cognitive map emerges from the activities of hippocampal place cells, each of which has a specific place field – a small area of the subject's current environment within which a given cell shows a maximal firing rate. Serial activation of place cells representing adjacent places should provide not only a system to determine one's current position but a prospective navigation strategy as well. Temporal sequences of place cell firing can be observed during navigation (Buzsáki & Moser, 2013), resting periods and sleep (replay), and have been proposed to play a role in memory consolidation [Maingret *et al.*, 2016; see Drieu & Zugaro, 2019 for a review]. The discovery of place cells had a major impact as it established a neurophysiological basis for the cognitive map. In addition to providing details of the properties of place cells, O'Keefe & Nadel (1978) also presented an updated version of Tolman's (1948) cognitive map theory. Their theory made a clear distinction between two navigational systems: the taxon and locale systems. The taxon system is based on egocentric information, where intra-maze and extra-maze cues are used to navigate, and follows associative-learning rules. Indeed, neural mechanisms of associative acquisition involving dopamine signalling systems have recently been shown to be involved in learning about spatial cues (A. Guru, C. Seo, R.J. Post, D.S. Kullakanda, J.A. Schaffer & M.R. Warden, in preparation). Taxon learning involves orientation and guidance learning, also known as response learning and beacon homing, respectively. Response learning consists of remembering the sequence of turns that leads to the goal place, and beacon homing refers to approaching an object, or beacon, that is always close to, and thereby marks the location of, the goal place. The locale system is map-based and utilizes allocentric information. It is in the locale system where hippocampal place cells contribute to the establishment of a mental representation of places in relation to landmarks in the environment. The locale system is considered flexible in that it connects places together and is able to activate representations of prospective routes through the sequential activation of place cells (O'Keefe & Nadel, 1978; Pfeiffer & Foster, 2013).

It is, however, unclear how place cells that code for places are involved in navigation using spatial inferences. A recent study points toward a role of place cells in encoding routes irrespective of their relationship/proximity to the reward (Duvelle *et al.*, 2019). Surprisingly, but not contradictory with the latter finding, place cells have also been shown to convey a success signal of the selected trajectory when a rat is at the goal place (Hok *et al.*, 2007), but do not code for destinations, and instead play a role in the discrimination of alternative routes (Grieves, Wood, & Dudchenko, 2016). As place cells specifically code for goal places, familiar places and trajectories, they are less likely to guide navigation through unfamiliar territory, which is the basis of many types of spatial inference. It is worth noting that place cells can also generate sequences of new combinations of relevant start and goal locations in familiar environments, suggesting that hippocampal sequence events can predict immediate future novel paths constituted of familiar places (Pfeiffer & Foster, 2013). There is, however, no evidence that this applies to novel paths constituted of novel places never experienced, even when the novel paths connect familiar places.

(2) Higher-order conditioning

Higher-order conditioning was discovered by Pavlov (1927) and involves the establishment of a conditioned response (CR) to a conditioned stimulus (CS) that itself had not been directly paired with the unconditioned stimulus (US). For example, a dog might learn that a bell CS signals a food US, such that the bell (S1) elicits salivation as a CR. Subsequently, a light CS is paired with the bell CS in the absence of food. When presented with the light, the dog salivates, despite the fact that the light itself had never been paired with food. The light therefore becomes a second-order CS (S2). Brogden (1939) reported a similar phenomenon that he termed sensory preconditioning. Sensory preconditioning is very similar to second-order conditioning except that the phases of training are reversed, such that the light is paired with the bell in Phase 1 of training, and then the bell is paired with food in Phase 2 of training. On a final test, the light elicits the CR.

Second-order conditioning and sensory preconditioning are both forms of higher-order conditioning. While several theories have been proposed to account for higher-order conditioning, one leading theory is that two associations, S2–S1 and S1–US, are linked together and stored as a representation of a S2–S1–US associative chain. This account is particularly applicable to sensory preconditioning (Honey, Iordanova, & Good, 2014). Associations that contain spatial, temporal, and causal information can therefore be linked together to produce rich mental representations from which novel spatial, temporal, and causal inferences can be derived (see Blaisdell, 2009 and Savastano & Miller, 1998 for detailed discussions). Accordingly, in the example of Fig. 1, when a rat finds itself blocked at location B, the spatial associations of the pathways of the maze lead the rat to infer that both the X and Y paths are blocked, and thus to take pathway Z. A wide range of organisms show evidence of higher-order conditioning, e.g. *Drosophila melanogaster* (Brembs & Heisenberg, 2001), honeybees *Apis mellifera* (Müller *et al.*, 2000), pigeons *Columba livia* (Sawa, Leising, & Blaisdell, 2005), rats (Chamizo, Rodrigo, & Mackintosh, 2006), and humans (Molet, Bugallo, & Gambet, 2011), which can serve as the basis of forming transitive relationships between events. Such a transitive process enlarges the scope of associative learning beyond simple trial-and-error learning or first-order associative learning.

(3) Path integration

Contrary to a reductionist conception of associative learning theories as blind stimulus–response associations (see Jensen, 2006), associative learning processes can generate new routes in the absence of direct past experience with the

route (Chamizo *et al.*, 2006). In addition to Pavlovian associative processes, another bottom-up mechanism – path integration – can be used for novel route taking. Path integration, also known as dead reckoning (first reported by Darwin, 1873), is a process that allows animals to keep track of their location using motion-related information, such as to navigate directly back to their home nest from the terminal point of an outward journey. This process involves continuously computing a vector between the animal's current location and their starting point (e.g. the home nest). This home vector maintains the distance and direction information necessary to return home successfully and is calculated from internal cues provided by vestibular and proprioceptive perception (Collett *et al.*, 1998; Schatz *et al.*, 1999; Etienne *et al.*, 2004). A characteristic and major limitation of path integration lies in the accumulation of errors during a journey that affect the estimation of position (Mittelstaedt & Mittelstaedt-Burger, 1973; Müller & Wehner, 1988; Wehner & Wehner, 1990). These errors can originate from noise in the sensorimotor system and during the process of vector arithmetic (Etienne *et al.*, 2004; Souman *et al.*, 2009). They affect the accuracy of a path integration strategy, especially for long journeys. Vectors can be anchored to external references (e.g. visual cues, geomagnetic fields, etc.), when available. This enables path integration to be reset when an agent takes a fix on familiar external references, thus correcting estimation errors of angular and linear components of locomotion (Etienne *et al.*, 2004). Path integration resetting has been shown in rodents and ants (Etienne *et al.*, 2004; Knaden & Wehner, 2006) and extends the range of use of path integration to long and complex journeys, subject to the constraint that external references are available.

The constant updating of distance and direction from the current position to the start location during a journey allows one to return directly to the start location simply by following the most recently computed homing vector. This can be achieved through vector arithmetic where a journey is decomposed into vectors (Etienne & Jeffery, 2004). The first vector starts at the beginning location, and any change of direction triggers the calculation of a new homing vector. Consider a simple journey between two places, A and C, where an animal changes direction only once at Place B, addition of the vectors A → B and B → C results in a new vector, A → C, while vector subtraction generates a vector of the same distance but opposite direction, that is C → A. Vector subtraction can thus be used to return directly to the starting point after a random journey. Furthermore, vector addition allows one to return to a previously discovered goal place by storing and retrieving the computed vector (Etienne *et al.*, 1998).

Vector arithmetic is a simple yet powerful mechanism that generates a direct bidirectional vector between a start place and a goal place. In the sunburst maze experiment (Tolman, Ritchie, & Kalish, 1946) for example, rats first had access to a sequence of three connected paths leading to a goal box (Fig. 2). After several trials navigating this configuration, the animals received a single test trial in which the former paths were blocked, and 18 new paths were made available, one of which led directly to the goal box. Most rats chose the paths heading toward the goal box, even though they had no prior experience travelling these paths. There are, however, two simpler alternative explanations as to how most of the rats made correct choices (Bennett, 1996). First, a light situated above and behind the feeder at the goal box was visible from anywhere within the room. As a result, this light could have served as a beacon, and taking the most direct shortcut could be accomplished merely by directly approaching the light that was associated with the reward. This explanation has recently been supported by a failure to replicate and extend the sunburst study of Tolman *et al.* (1946) to humans, in a test situation in which no light (or other) cue was located above the goal place (Wilson & Wilson, 2018). Interestingly, participants of a control group where the light cue was always present above the goal place were more likely to choose the correct path. A second explanation is that rats used path integration to determine the direction of the goal box from the circular platform (Fig. 2), stored this vector in long-term memory (Etienne & Jeffery, 2004), and retrieved it during the test. In line with this view, a recent study reported a successful use of shortcuts in a linear version of the sunburst maze with a deep reinforcement learning algorithm agent simulating the computational properties of grid cells (Banino *et al.*, 2018). A more recent grid-cell based vector navigation network model reported successful shortcut behaviour in an exact replication of Tolman *et al.*'s (1946) sunburst experiment (Edvardsen, Bicanski, & Burgess, 2020).

Importantly, to show evidence of cognitive mapping, path integration must not independently account for the results (Jacobs & Schenk, 2003; Singer, Abroms, & Zentall, 2006). In an attempt to overcome the challenges of neutralizing path integration as a solution to taking a novel path, and to test the existence of the cognitive map, Singer *et al.* (2006), in their second experiment, used a simple maze composed of three distinctive arms connecting one central platform to three separate goal boxes (Fig. 3).

In the training phase, rats were allowed to navigate from the central platform to any of the three goal boxes (Fig. 3A). The use of extra-maze cues was neutralized by rotating the maze within the room every day. A food reward was available in the central goal box and only one of the lateral boxes (reward and aversive sides counterbalanced across animals). Entries into the other lateral box were non-reinforced and the subject would have to wait there for 30 s before the trial ended. After reaching a learning criterion of 18 consecutive correct choices out of 20 (i.e. 90%), rats received 30 additional training trials to ensure that they had enough experience with the distinctive paths and their consequences. After completion of the 30 overtraining trials, rats received nine test sessions. The first, second, and fourth trial in each test session was a training trial identical to those received during the training phase. The third trial in each test session consisted of a test trial where the lateral arms were blocked at the central platform, and two new paths
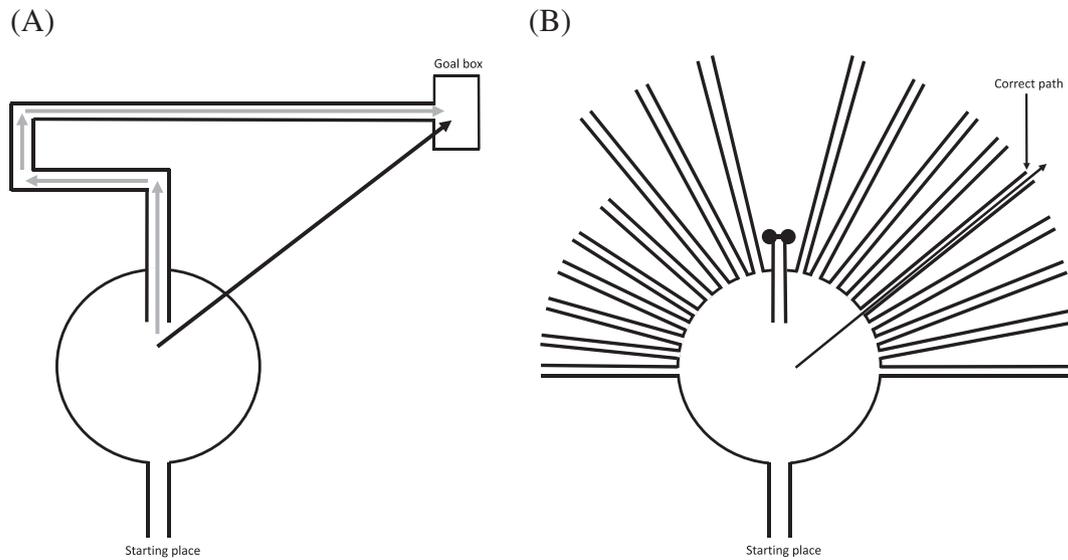
(A)   (B)

Fig 2. Schematic representation of the sunburst maze experiment of Tolman *et al.* (1946) during (A) the learning phase, and (B) the test. The arrows represent the path integration mechanisms with grey arrows being vectors computed during exploration and the black arrow the vector resulting from the addition of those grey arrows. Black lines terminating with dots represent barriers.
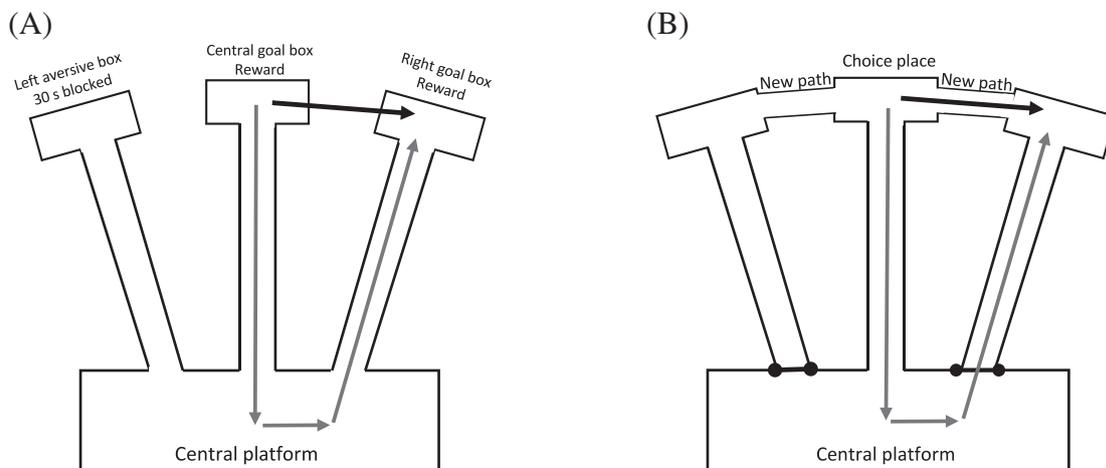
(A)   (B)

Fig 3. Schematic representation of the maze used by Singer *et al.* (2006) during the learning phase (A) and test phase (B). Grey arrows represent the paths animals experienced during the learning phase, and the black arrow represents the hypothetical vector resulting from path integration. Black lines terminating with dots represent barriers.

connecting the central goal box directly to the lateral goal boxes were opened (Fig. 3B). After receiving a reward in the central goal box, a majority of animals (15 out of 20) took the correct new path from the central goal box leading to the lateral goal box that had always been rewarded during training.

Unfortunately, rather than conclusive evidence of a cognitive mapping strategy, these results can simply be explained by response learning, where behavioural responses (e.g. turning left or right from the central platform to enter a lateral arm and reach the goal place) are reinforced or punished during the training phase. Specifically, during the training phase, turning to one side from the central platform (right for half of the animals and left for the other half) was reinforced by access to a food reward, while turning to the other side was punished by being restrained for 30 s. The reinforced turn from the central platform during the training phase also corresponded to the correct turn during the test from the choice place, suggesting that rats could simply have turned to the side that had been rewarded before the test run, and/or avoided turning to the side where they always received the time-out in the non-reinforced goal box. Simply said, the subjects may have learned the turn responses associated with a reward and punishment, respectively, during training, and generalized those responses to bias novel arm choice in the test phase.

The performance during the test run can alternatively be accounted for by path integration (Fig. 3). During the training phase, rats had opportunities to travel from the central goal box to the lateral goal box and *vice versa*. This would lead to the formation, by path integration, of a vector connecting the central goal box and the correct lateral goal box bilaterally. It is noteworthy that the authors conducted an experiment similar to that presented above in the same study, with no distinctive intra-maze cues and without any aversive consequence to incorrect choices (i.e. without restraining rats for 30 s). In this condition, rats did not perform above chance level when tested. The manipulation of two parameters between these two experiments, namely the presence of intra-maze cues and the punishment of incorrect choices, makes it difficult to interpret the results. The availability of intra-maze cues might have helped discriminating the alleys, as proposed by the authors. Alternatively, the absence of punishment might have decreased the cost of incorrect choices and could have biased rats in using a random-choice strategy. It appears, thus, that this study does not provide incontrovertible evidence in support of a cognitive map.

The ability of animals to keep track of their position and orientation based on proprioceptive information, vestibular activation, and optic flow suggests the existence of a neural network devoted to this particular navigational system. Neurons showing a high-rate of firing specifically when an animal is facing a particular direction, or head-direction cells (Ranck Jr., 1985; Taube, Müller, & Ranck, 1990), have been identified in 11 brain regions (see Dudchenko, Wood, & Smith, 2019 for a review), including the medial entorhinal cortex. The latter also has been shown to contain grid cells, which have the striking property of firing in discrete and regularly spaced places that fully cover explored environments (Hafting *et al.*, 2005). Interestingly, all the components of models for path integration have been found in the medial entorhinal cortex, making it a good candidate for investigating the neural mechanisms of path integration (McNaughton *et al.*, 2006).

II. SPATIAL INFERENCE WITHOUT PATH INTEGRATION

While response learning and reliance on extra-maze cues (especially a beacon) can easily be neutralized experimentally, dissociating path integration from cognitive mapping is challenging. There are, to our knowledge, only three studies that provide a clear demonstration of spatial inference when path integration is successfully neutralized.

(1) Spatial integration in pigeons

Two studies in pigeons support the role of cognitive maps, avoiding confounding factors such as path integration and beacon homing. Both studies involved pigeons learning to find hidden food using a cognitive map acquired in
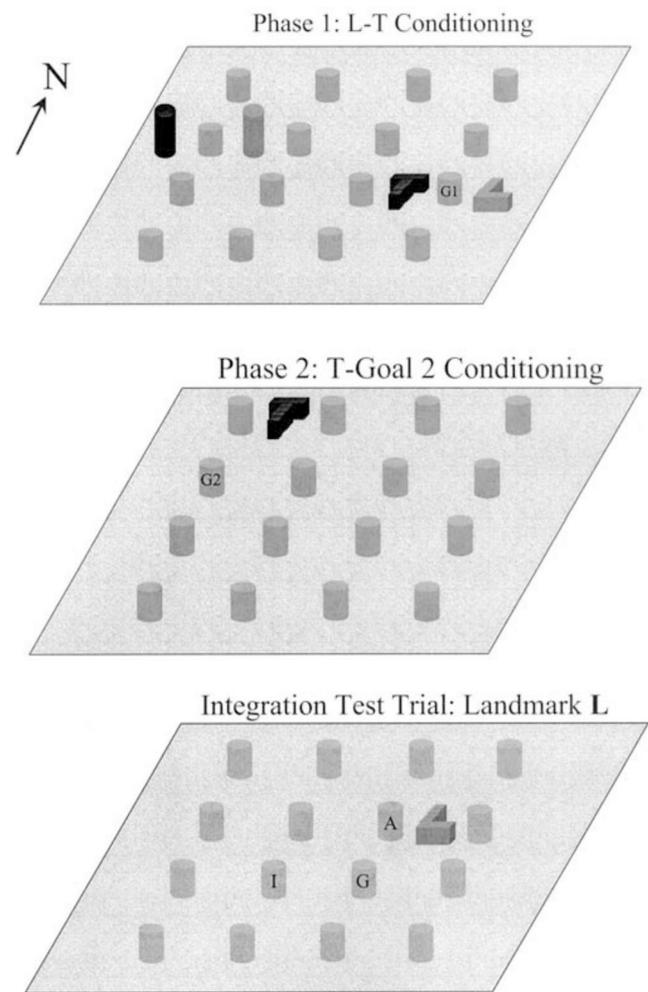

Fig 4. Diagram of the experimental arena used by Blaisdell & Cook (2005), showing the arrangement of the 4 × 4 grid of gravel-filled cups, the hidden food (G), and the landmarks (T, L, and two foils). The top panel shows the spatial arrangement of the consistent landmarks (T and L), goal 1 (G1), and inconsistent landmarks (cylindrical foils) during Phase 1. The middle panel shows the spatial arrangement of landmark T to goal 2 (G2) during Phase 2. The bottom panel shows the spatial arrangement of landmark L and the potential locations of search during the integration test. Letters on bottom panel: I = predicted cup for choices guided by the L → T → goal 2 hierarchical map, A = predicted cup for choices guided by the phase 1 L→goal 1 vector, and G = predicted cup for choices guided by a generalization to L of the T → goal 2 vector. Reprinted with permission of the authors.

piecemeal fashion using a spatial analog to the sensory preconditioning procedure. The experiment by Blaisdell & Cook (2005) involved pigeons navigating in an open arena (Fig. 4).

During the first phase of training, pigeons were presented with landmarks L and T with a consistent spatial relationship to each other and to a food goal located in between them

(G1). In Phase 2, pigeons learned to find food hidden in one of 16 food cups by using landmark T that had a consistent spatial relationship to the hidden food goal in a new location (G2). It is important to note that during each of these phases, the location of the landmarks and food goal within the arena changed stochastically across trials so that room cues and other features of the apparatus could not be used to locate the food. Rather, only the consistent spatial relationships between L, T, and G1 in Phase 1, and between T and G2 in Phase 2 could enable subjects to locate the food. Following Phase 2, pigeons were tested with trials on which they were presented with only landmark L to examine the potential integration of the spatial relationships acquired independently in phases 1 and 2. That is, if pigeons had encoded the L → T vector in Phase 1, and the T → G2 vector in Phase 2, then they could integrate these vectors because they contain the common element, T. The integrated L → T → G2 vector could then be used at test with landmark L to derive an L → G2 spatial inference. Evidence for this integrated set of relationships was shown in that pigeons searched for food most often at the location consistent with the inferred L → G2 vector. This result indicates that integration of binary spatial relationships acquired separately during Phases 1 and 2 allowed the pigeons to compute a never-before-experienced L → G2. This derived vector supported spatial inference. Sawa *et al.* (2005); see also Leising, Sawa, & Blaisdell, 2012) reported a replication of this finding using 2D digital displays on a touchscreen, and included additional controls to establish the necessity of a consistent spatial relationship between the landmark and the hidden goal in Phase 2 to enable the spatial inference at test.

(2) Novel route taking in rats

In an experiment by Roberts, Cruz, & Tremblay (2007), rats were trained to navigate an enclosed 'plus' maze in which extra-maze cues were not available. Each of the four alleys ended in their respective end box containing distinctive intra-maze cues (Fig. 5).

In the first training phase, only three alleys and their end boxes (A, B, and D) were open. Rats were first fed in one of the end boxes, say D, with a small piece of cheese. They were then placed in one of the two other end boxes, A or B, that served as the start box. The animals were allowed to navigate the available sections of the maze, and were reinforced if they made a choice to return to D, which was re-baited with two new pieces of cheese. During Phase 1 training, each end box served equally often as the start box, goal box, and unbaited box. Rats mastered the task, thereby forming bidirectional mental connections between all end boxes. During the second phase of training, all rats were fed in C which had not been explored during Phase 1, and subsequently only rats from the experimental group were placed in B and allowed to return to C where they found two pieces of cheese. Finally, in the test phase, all rats were fed in C, and then placed in D. The four internal alleys of the maze were now unavailable, and the rats were forced to choose between two new peripheral alleys, only one of which led to goal box C. Even though the animals had no chance of connecting D to C during previous training, rats in the experimental group alone successfully chose the correct path leading from D to C by making a right turn. Reinforcement of a left turn in Phase 2 neutralizes a simple response-learning account. In this experiment, the investigators successfully overcame the challenging confound of path integration by preventing rats from travelling from D to C before the test, a prerequisite for a D → C vector to be generated by path integration.

How do the results of Roberts *et al.* (2007) fit with an account by cognitive map theory? Serial activation of place cells representing adjacent places provides not only a system to determine one's current position but a prospective navigation strategy as well. Nevertheless, this type of cognitive-map-based navigation mechanism cannot account for the results of Roberts *et al.* (2007). The rats in their study did not directly travel the route prior to testing, and thus should not have had
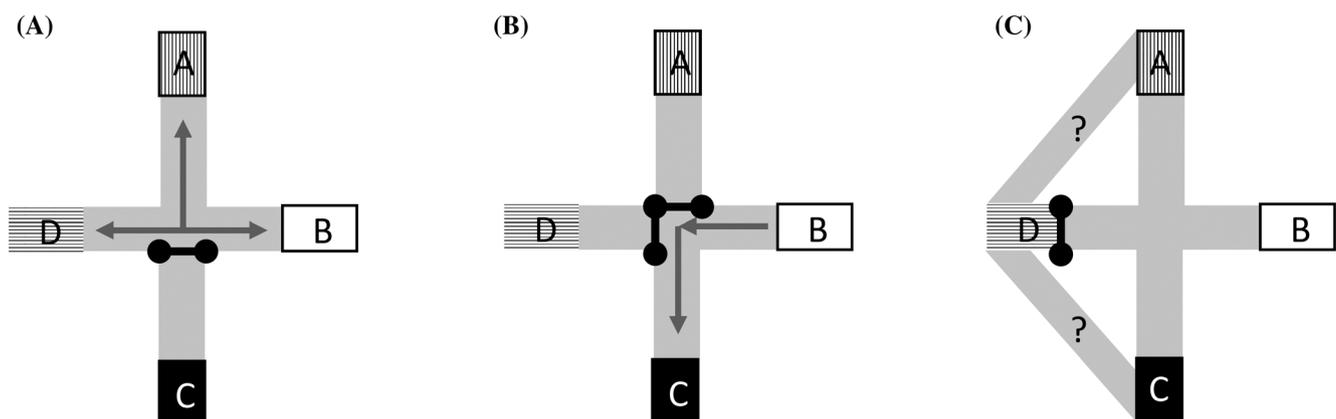

Fig 5. Schematic representation of the maze used by Roberts *et al.* (2007), seen from above during (A) the first phase, (B) the second phase, and the test (C). Arrows represent the paths animals took, and black lines terminating with dots represent barriers. "?" indicates the possible choices during the test. Each letter represents an end box.
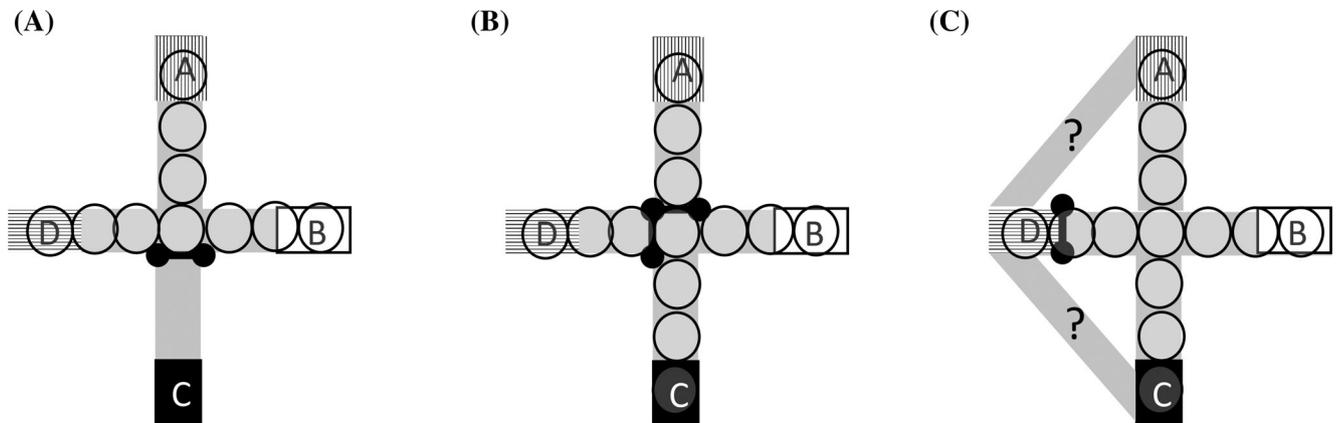
Fig 6. Schematic representation of the maze used by Roberts *et al.* (2007), seen from above during (A) the first phase, (B) the second phase, and the test (C). Black lines terminating with dots represent barriers. Circles represent place representations. Each letter represents an end box. "?" indicates the possible choices during the test.

any place-cell-based representation of the new peripheral alleys in the enclosed maze (Fig. 6). While the results of Roberts *et al.* (2007) confirm the ability of rats to make a spatial inference, a mechanistic account is yet to be offered for true novel route taking.

The unconfounded demonstrations of spatial inference described above are not explained by a place-cell-based cognitive map, higher-order conditioning (which could explain the results from the Blaisdell laboratory, but not those from the Roberts laboratory), or by path integration. We propose an extension of the theoretical framework developed by Blaisdell and colleagues (Blaisdell & Cook, 2005; Sawa *et al.*, 2005; Leising *et al.*, 2012) and further elaborated in Blaisdell (2009).

III. HIGHER-ORDER PATH INTEGRATION

(1) Presentation of the model

Our current extension is based on the vector arithmetic mechanism of path integration (Etienne *et al.*, 1998), and as a novel postulation, incorporates processes of higher-order associative learning to produce higher-order path integration (HOPI). We consider that direct vectors D → B and B → D are generated and stored when travelling from D to B and from B to D (Fig. 7A).

During subsequent explorations from B to C, the two new direct vectors constituting the route linking these two places are arithmetically integrated to compute a bidirectional first-order derived vector B⋆C (Fig. 7B). The direct vectors D → B and B → D can then be retrieved and integrated with the first-order derived B⋆C vector, resulting in the formation of a second-order derived vector D⋆C (Fig. 7C). Thus, HOPI uses vector arithmetic, but broadens its scope of application by including vectors stored in memory. The latter can be previously experienced direct vectors or previously derived vectors. This simple extension of Blaisdell's (2009) theory of

associative spatial integration enables the subject to determine the distance and direction between all familiar places, even between places that have never been directly connected during a journey, as long as vectors can be connected in piecemeal fashion through the linkage of common place elements. This can be achieved by retrieving a vector stored in memory, and connecting it to a new vector only if they share a common place (see Blaisdell, 2009, for further discussion of this process). It implies that vectors are anchored to external references, such as visual cues. Consistent with the resetting property of path integration, it enables vectors to be corrected during a journey whenever external references are used. The latter can be conceived as nodes connected together by vectors in an allocentric framework and makes HOPI suitable in extended complex environments, when external cues are sufficiently available.

For the sake of clarity, we distinguished direct vectors and first-order vectors in the presentation of our model. However, in reality, a direct vector is formed at each step and added to or subtracted from the vector formed at the previous step (Etienne *et al.*, 2004). Consequently, direct vectors as presented in our model should be considered as bidirectional first-order derived vectors.

A simple mathematical formalization of HOPI is straightforward as it follows the modern system of vector algebra (Gibbs, 1881; Heaviside, 1971; see Chappell *et al.*, 2016 for a review). In this system, a vector is a line segment in a Euclidean space, that is defined by its direction and length. A bound vector $\overrightarrow{AB}$ is composed of an origin A, or tail, which corresponds to its starting point, and a head B, which corresponds to the point where it terminates. Vectors for which the origin is ignored are called free vectors, such that two free vectors $\overrightarrow{AB}$ and $\overrightarrow{CD}$ of the same direction and length are considered equal. In our model, only bound vectors are considered, and can be subjected to addition and subtraction with only one restriction to the modern system of algebra being required: two vectors can be added or subtracted only if the head of one corresponds to the origin of the other. That is,
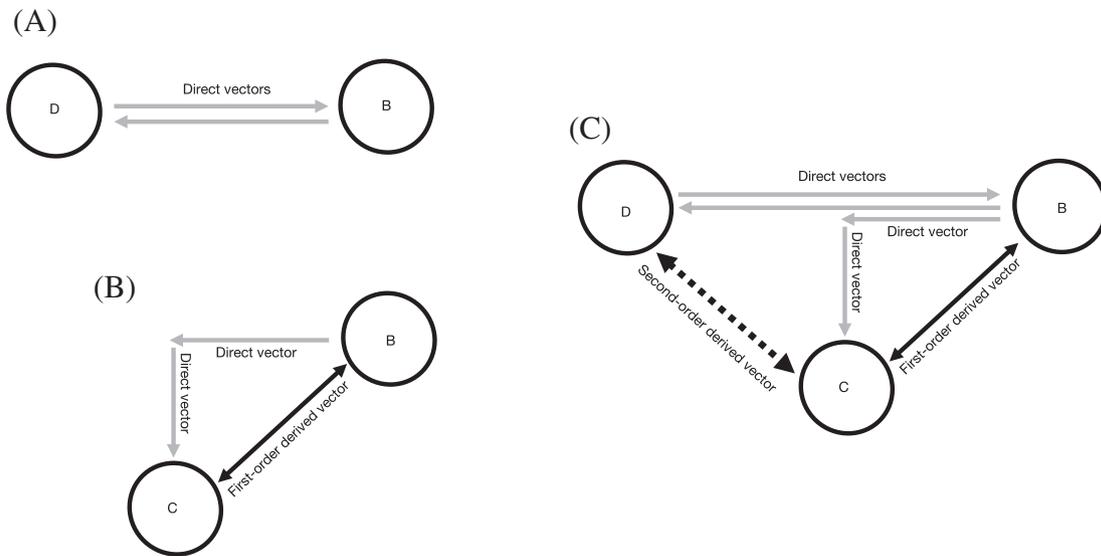
Fig 7. Schematic of the concept of higher-order path integration. The letters refer to different places. (A) and (B) represent two routes travelled independently and stored in memory. (C) represents the mental integration of these two memories into a unified whole. Continuous grey arrows represent direct vectors. Solid black arrow represents first-order derived vector computed by vector arithmetic between direct vectors. The dashed black arrow represents a second-order derived vector resulting from vector arithmetic between a direct vector and a first-order derived vector.

$\vec{AB}$ and $\vec{BC}$ can be added or subtracted, resulting in $\vec{AC}$ or $\overleftarrow{AC}$ respectively: $\vec{AB} + \vec{BC} = \vec{AC}$, and $\vec{AB} - \vec{BC} = \vec{CA}$. However, $\vec{AB}$ and $\vec{CD}$ cannot be added, nor subtracted. No distinction is made between vectors that have been generated in a current journey or retrieved from memory.

(2) Higher-order path integration in novel route taking

Let us consider how this revised spatial-integration hypothesis can explain the results of Roberts *et al.* (2007). In their Experiment 3, rats travelled between D and B during the first phase of training, resulting in the formation of a direct D → B vector (Fig. 8A). In the second phase, animals then navigated from B to C, generating a first-order derived B → C vector (as well as the direct B → Centre and Centre→C vectors; Fig. 8B). Vector arithmetic of D → B and B → C was then possible since they shared B as a common (linking) place. Vector arithmetic resulted in a new second-order derived vector D → C that indicated the distance and direction of C from D (Fig. 8C). In their experiment, place-cell-based cognitive mapping was neutralized, as during the test only two new alleys were available in which place cells had not yet started firing, making HOPI the only successful strategy.
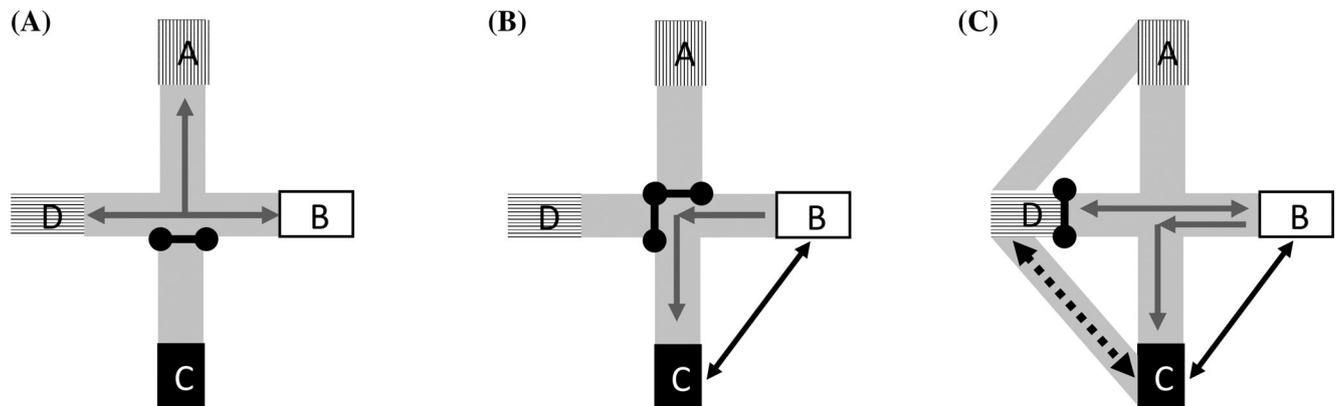

Fig 8. Schematic representation of the maze used by Roberts *et al.* (2007) during the two learning phases (A and B, respectively) and during the test phase (C). The underlying strategy based on higher-order path integration is represented as follows: solid grey arrows represent direct vectors; solid black arrow represents a first-order derived vector computed by vector arithmetic between direct vectors; dashed black arrow represents a second-order derived vector resulting from vector arithmetic between a direct vector and a first-order derived vector.

(3) New predictions derived from the model

We propose an experimental arrangement where sequential activation of place cells, as well as the use of direct vectors, are neutralized, and where cognitive mapping, the use of a first-order derived vector, and HOPI lead to different behavioural outcomes (Fig. 9). The first phase of learning is similar to that of Roberts *et al.* (2007), with the subjects allowed access to A, B and D, but here the position of A is central, and that of B has been changed such that the direction of first-order derived vector A → B is unique (Fig. 9A).

In phase 2, the subjects learn to reach a reward at the goal box C from place B (Fig. 9B). The goal box C is here positioned such that the second-order derived vector C → A is distinct from the first-order derived vector A → B and its direction is also different from the direction that would result from a cognitive mapping strategy or from the use of direct vectors (Fig. 9C). During the test phase (Fig. 9D), the animals start from A, and have to choose between three new pathways that connect A to B, C, and a new box E with the shortest possible distance. The path used during the learning phases is now blocked, neutralizing a cognitive mapping strategy, and the use of direct vectors. Intra-box cues, as in Roberts *et al.* (2007), are critical for the animals to retrieve correctly the vectors anchored to each place during the learning phases. The use of a first-order derived vector should mean that rats choose the path directly leading to B, suggesting that place B became a secondary reinforcer during Phase

2, or a good predictor of access to the reward. Alternatively, the use of HOPI should produce choices of the path directly leading to C. If the subjects solely rely on a place-cell-based cognitive mapping strategy or direct vectors, their responses should not be biased to any of the three choices available, and a performance at chance level should be expected.

IV. DISCUSSION

Whether or not animals build and use a cognitive map to navigate adaptively has been under active debate since Hsiao's (1929) pioneering experiment. Tolman was convinced that rats solved maze problems with responses that were more than merely reflexive responses to stimuli, and his accumulated evidence was inconsistent with a behaviourist associative learning framework, leading him to postulate a theory of cognitive mapping (Tolman, 1948). The neural basis for a cognitive map in vertebrates was illuminated with the discovery of place cells in the hippocampus, each of which fire in response to a specific familiar place (O'Keefe & Nadel, 1978). The ability to take novel shortcuts without trial-and-error learning when other routes to the goal place are blocked is a hallmark of the locale system (i.e. cognitive mapping) and is thought to be beyond the scope of taxon learning. Tests of novel route taking have thus
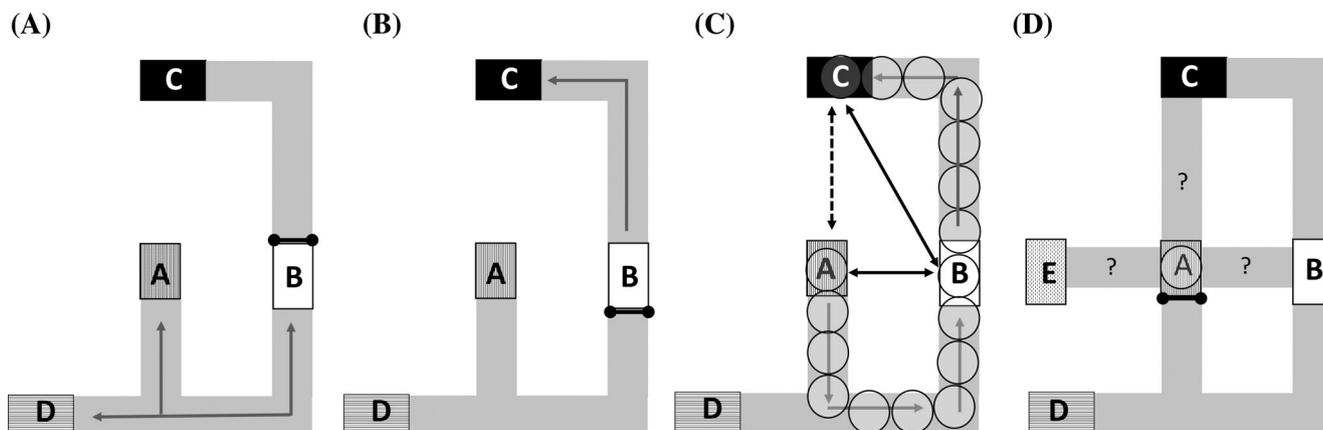

Fig 9. Schematic representation of the maze seen from above, in an alternative procedure to that used by Roberts *et al.* (2007), designed to neutralize a place-cell-based cognitive mapping strategy and the use of direct vectors. (A) Phase 1 is similar to that of Roberts *et al.* (2007), where only end boxes A, B and D are explored. During Phase 1 training, each end box serves equally often as the start box, goal box, and unbaited box. (B) During Phase 2, all animals are only allowed to explore B → C. (C) Explanation of how the paths taken during phases 1 and 2 will produce different choice outcomes depending on the strategy (place representation, direct vectors, first-order derived vectors, or HOPI) used by the rats. The goal box C is here positioned such that the second-order derived vector C → A (dashed black arrow) is distinct from the first-order derived vector A → B (solid black arrow) and its direction is also different from the direction that would result from a cognitive mapping strategy (black circles) or from the use of direct vectors (solid grey arrows). (D) During the test phase, the animals start from A and can choose between three novel paths that connect A to B, C, and a new box E with which they have no previous experience. Black lines terminating with dots represent barriers. Circles represent place representations. Each letter represents an end box. Solid grey arrows represent direct vectors; solid black arrows represent a first-order derived vector computed by vector arithmetic between direct vectors; dashed black arrow represents second-order derived vectors resulting from vector arithmetic between a direct vector and a first-order derived vector. "?" indicates the possible choices during the test.

been the benchmark of cognitive map theory. Nevertheless, researchers have found it challenging to neutralize path integration in novel-route tests. Specifically, in most experiments investigating the cognitive map, it is still possible for the subject to navigate between two places using a direct connecting vector formed using path integration during exploration in the training phase of the experiment. This has been resolved only recently in a maze experiment using rats (Roberts *et al.*, 2007) and in studies of landmark use in pigeons (Blaisdell & Cook, 2005; Sawa *et al.*, 2005). Higher-order associative learning cannot be used to mentally 'fill in' place cell information for a route that has never been directly experienced, in order to connect the current place with a goal place. Path integration and higher-order spatial associations, however, result together in the formation of indirect vectors connecting two locations in known space, even if the route overlapping such a vector has never been directly experienced. This inferential process is limited to vectors computed during a journey for path integration or to directly observed landmark spatial relations for spatial integration.

Our model, HOPI, combines two taxon system mechanisms, namely higher-order conditioning and path integration, and is able to overcome the weaknesses of the locale and taxon systems as defined by O'Keefe & Nadel (1978). Higher-order conditioning enables two vectors that share a common place or landmark to be mentally connected. Applying a path-integration process in which currently computed vectors can be integrated with prior vectors stored in reference memory extends the scope of each process (i.e. path integration and higher-order conditioning) taken separately. This results in a vectorial representation that mentally connects any familiar place to any other familiar place, even when they have never been connected directly through experience. It is worth noting that goal-directed navigation ruled by path integration, or its higher-order version, constitutes a particular form of goal-directed behaviour as there is no spatial representation of the route leading to the goal. Thus, a cognitive map based on the HOPI mechanism is not like the 'field map' envisioned by Tolman (1948).

(1) Spatial inference without map-like representation

HOPI constitutes a new and powerful mechanism in spatial inference, consistent with spatial learning theories that have already emphasized the importance of vectorial information at the psychological level (Poucet, 1993; Blaisdell, 2009), and in line with the view that the taxon system is sufficient for complex spatial learning and navigation (Cheng, 2012), if its components can interact. In the non-spatial domain, higher-order conditioning enables animals to establish mental relationships between events never experienced together in the physical world. As such, we propose that it can be considered as a basis for creativity, where new behaviours arise from mental generation of associations not previously experienced. Higher-order conditioning has been shown to create unconscious biases in human decision making (Wimmer & Shohamy, 2012).

Consistent with this finding, humans are able to establish inferences in the spatial domain in sensory-preconditioning and second-order conditioning protocols (Bouchekioua *et al.*, 2013). Interestingly, when participants were asked how they resolved the spatial task, none were able to explain the strategy used, nor were they able to draw a topological representation of the environment explored in a piece-meal fashion, suggesting that a comprehensive spatial representation is not necessary for inferential spatial navigation. This finding suggests that a major distinction between place-based cognitive mapping and HOPI is that the latter provides a navigational system without needing a comprehensive topological representation of the environment, while the opposite is true for place-based cognitive mapping. This observation substantiates two recent findings in human virtual navigation tasks. In the first study, participants were able to use portions of a virtual maze for successful shortcuts and detours, even if they violated Euclidian rules. Yet the human participants were unaware of those portions, suggesting that they did not rely on a metric representation of the maze to make spatial inferences (Warren *et al.*, 2017). In a more recent study that failed to replicate the results of the Tolman *et al.* (1946) sunburst-maze shortcut behaviour when a light cue over the goal place was neutralized, Wilson & Wilson (2018) found no correlation between map-drawing accuracy and accuracy of pointing towards the goal during the test. Interpretation of the participants' sketch-map drawings should, however, be made cautiously, as this has been shown to be affected by inter-individual differences in drawing skills and interpreter bias (Friedman & Kohler, 2003). Interestingly, one recent study found that a significant decrease in the time spent by human participants exploring complex virtual mazes was associated with increased subsequent sketch-map quality (Gehrke *et al.*, 2018) – an analysis that neutralized inter-individual differences in drawing skills.

The successful demonstration of novel route taking by Roberts *et al.* (2007) and Blaisdell & Cook (2005) by no means invalidates the cognitive map hypothesis. Conversely, the ability to take novel routes or shortcuts is intuitively predicted by Tolman's (1948) cognitive map theory, and has stimulated a large number of studies employing new experimental designs that deepened our understanding of spatial learning and memory. Our HOPI model is consistent with other studies proposing simpler mechanistic analyses of flexible navigation that do not imply veridical place-cell-based cognitive processes (Mackintosh, 2002; Cruse & Wehner, 2011), as well as with a cognitive map process more in line with the functional account by Gallistel (1990) that any mechanistic process that accomplishes detours and novel shortcuts through unfamiliar locations to navigate to goals counts as a cognitive map.

(2) Limits of existing similar models

The model we propose here falls within an expanding body of literature that considers vector-based learning as a powerful navigational strategy in which a comprehensive topological representation of the environment is not necessary, even when facing new situations such as detours, shortcuts, and

novel route taking. A recent vector-based model grounded in insect neurophysiology and neuroanatomy data is consistent with the formation of higher-order vectors as defined herein (Le Moël *et al.*, 2019). However, their model could not be used to compute a higher-order vector from the start place in the test situation of Roberts *et al.* (2007) (see Fig. 6C), where rats have to make a decision between two new routes. To achieve vector arithmetic of vectors D → B and B → C in the Le Moël *et al.* (2019) model, the agents would have to travel physically to B to retrieve the B → C vector. Another study proposed a heading-vector model based on head-direction cell properties and a path integration process (Kubie & Fenton, 2009). It uses vector arithmetic to connect all places explored in a single journey. While this process can be used to estimate a direct path between each place explored, it is limited to a single exposure to a new environment and does not generate predictions in situations where barriers are introduced, such as in the test situation of Roberts *et al.* (2007) (see Fig. 6C), where a new barrier prevents the animals from travelling familiar paths. For these reasons, this vector-heading model is outside the scope of novel route taking described above, which involved acquisition and integration of separately explored pieces of an environment. The specificity and novelty of our approach is the combination of two basic and well-documented mechanisms that are phylogenetically ancient (found in both chordates and arthropods): higher-order conditioning and path integration.

(3) A hypothetical neural basis of higher-order path integration

Consistent with HOPI, a recent study found that place cell firing represents the animal's route, not its goal, a characteristic that might help in spatial discrimination but not in determining the route leading to the goal place (Grieves *et al.*, 2016). This latter finding is in line with recent cognitive map theories that address how animals represent their current position but are restricted to familiar environments for navigation (O'Keefe & Burgess, 2005; Fuhs & Touretzky, 2006; Hasselmo & Brandon, 2008; Duvelle *et al.*, 2019). The physiological properties of hippocampal and para-hippocampal cells have been investigated extensively and show large heterogeneity of firing properties. Head direction (HD) cells, neurons that are activated preferentially in a particular direction (Ranck Jr., 1985; Taube *et al.*, 1990), constitute a potential neural basis of vector learning (Pearce, Roberts, & Good, 1998; Kosaki *et al.*, 2015). The medial entorhinal cortex, as well as pre- and parasubiculum (Boccara *et al.*, 2010) are of particular interest regarding path integration and vector learning. These two brain areas are composed of different types of neurons – grid cells, border cells, head direction cells, and object-vector cells, among others – that code metric information of familiar environments (see Rowland *et al.*, 2016 for a review). Recent identification of goal-direction cells in hippocampal CA1 neurons (Sarel *et al.*, 2017) make them a prime candidate for future investigation of the neural substrates of HOPI and may code for higher-order vectors that point directly towards goal places. Some reports suggest that neither the hippocampus nor the entorhinal cortex are necessary for path integration in rats (Alyan & McNaughton, 1999) or humans (Shrager, Kirwan, & Squire, 2008). By contrast, other studies found that lesions in the entorhinal cortex or hippocampus impaired path integration (Save, Guazzelli, & Poucet, 2001; Parron & Save, 2004; Van Cauter *et al.*, 2013; Allen *et al.*, 2014; Jacob *et al.*, 2017, 2019; Gil *et al.*, 2018), consistent with the hypothesis that path integration is processed in the entorhinal cortex, which would in turn transmit this information to the hippocampus through the perforant path (Parron, Poucet, & Save, 2006). The hippocampus has also been shown to be necessary for higher-order conditioning (Wikenheiser & Schoenbaum, 2016). It is thus plausible that direct vectors as well as first-order derived vectors are generated outside of the hippocampus, before converging to CA1 hippocampal goal-directed cells, where higher-order vectors could originate.

V. CONCLUSIONS

(1) Cognitive mapping predicts novel route taking, but experimental observations cannot be explained by simple (first-order) path integration. We found only three studies showing empirical evidence of novel route taking in which path integration was successfully neutralized. Specifically, subjects never had the opportunity to travel directly between the start place used at test and the goal place: they could only mentally connect these two places *via* an intermediate place.

(2) No mechanistic account of novel route taking was presented in these three studies, revealing limits of cognitive mapping and associative learning theories, as well as path integration.

(3) We propose a new model integrating higher-order conditioning and path integration, and demonstrate how HOPI can explain novel route taking without using a map-like representation of the environment. Independently acquired vectors are anchored to nodes (i.e. external cues), and can be generated *via* path integration and stored in memory with their associated nodes. Finally, they are mentally integrated using higher-order conditioning by mean of common elements these stored vectors share. Applying the path integration process to these stored vectors results in a higher-order vector that connects places not previously connected during direct experience, such as while navigating a maze.

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VII. REFERENCES

ALLEN, K., GIL, M., RESNIK, E., TOADER, O., SEEBURG, P. & MONYER, H. (2014). Impaired path integration and grid cell spatial periodicity in mice lacking GluA1-containing AMPA receptors. *Journal of Neuroscience* **34**, 6245–6259.

ALYAN, S. & MCNAUGHTON, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience* **113**, 19–31.

BANINO, A., BARRY, C., URIA, B., BLUNDELL, C., LILLICRAP, T., MIROWSKI, P., PRITZEL, A., CHADWICK, M. J., DEGRIS, T., MODAYIL, J., WAYNE, G., SOYER, H., VIOLA, F., ZHANG, B., GOROSHIN, R., RABINOWITZ, N., PASCANU, R., BEATTIE, C., PETERSEN, S., SADIK, A., GAFFNEY, S., KING, H., KAVUKCUOGLU, K., HASSABIS, D., HADSELL, R. & KUMARAN, D. (2018). Vector-based navigation using grid-like representations in artificial agents. *Nature* **557**, 429–433.

BENNETT, A. T. (1996). Do animals have cognitive maps? *Journal of Experimental Biology* **199**(1), 219–224.

BLAISDELL, A. P. (2009). The role of associative processes in spatial, temporal, and causal cognition. In *Rational Animals, Irrational Humans* (eds S. WATANABE, A. P. BLAISDELL, L. HUBER and A. YOUNG), pp. 153–172. Keio University, Tokyo.

BLAISDELL, A. P. & COOK, R. G. (2005). Integration of spatial maps in pigeons. *Animal Cognition* **8**, 7–16.

BOCCARA, C. N., SARGOLINI, F., THORESEN, V. H., SOLSTAD, T., WITTER, M. P., MOSER, E. I. & MOSER, M. B. (2010). Grid cells in pre-and parasubiculum. *Nature Neuroscience* **13**(8), 987–994.

BOUCHEKIOUA, Y., MILLER, H. C., CRADDOCK, P., BLAISDELL, A. P. & MOLET, M. (2013). Spatial integration of boundaries in a 3D virtual environment. *Acta Psychologica* **144**, 316–323.

BREMBS, B. & HEISENBERG, M. (2001). Conditioning with compound stimuli in *Drosophila melanogaster* in the flight simulator. *Journal of Experimental Biology* **204**, 2849–2859.

BROGDEN, W. J. (1939). Sensory pre-conditioning. *Journal of Experimental Psychology* **25**(4), 323–332.

BUZSÁKI, G. & MOSER, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nature Neuroscience* **16**(2), 130–138.

CHAMIZO, V. D., RODRIGO, T. & MACKINTOSH, N. J. (2006). Spatial integration with rats. *Learning & Behavior* **34**, 348–354.

CHAPPELL, J. M., IQBAL, A., HARTNETT, J. G. & ABBOTT, D. (2016). The vector algebra war: a historical perspective. *IEEE Access* **4**, 1997–2004.

CHENG, K. (2012). How to navigate without maps: the power of taxon-like navigation in ants. *Comparative Cognition & Behavior Reviews* **7**, 1–22.

COLLETT, M., COLLETT, T. S., BISCH, S. & WEHNER, R. (1998). Local and global vectors in desert ant navigation. *Nature* **394**, 269–272.

CRUSE, H. & WEHNER, R. (2011). No need for a cognitive map: decentralized memory for insect navigation. *PLoS Computational Biology* **7**(3), e1002009.

DARWIN, C. R. (1873). Origin of certain instincts. *Nature* **7**, 417–418.

DRIEU, C. & ZUGARO, M. (2019). Hippocampal sequences during exploration: mechanisms and functions. *Frontiers in Cellular Neuroscience* **13**, 232.

DUDCHENKO, P., WOOD, E. & SMITH, A. (2019). A new perspective on the head direction cell system and spatial behavior. *Neuroscience and Biobehavioral Reviews* **105**, 24–33.

DUVELLE, É., GRIEVES, R. M., HOK, V., POUCET, B., ARLEO, A., JEFFERY, K. J. & SAVE, E. (2019). Insensitivity of place cells to the value of spatial goals in a two-choice flexible navigation task. *Journal of Neuroscience* **39**, 2522–2541.

EDVARDSEN, V., BICANSKI, A. & BURGESS, N. (2020). Navigating with grid and place cells in cluttered environments. *Hippocampus* **30**(3), 220–232.

ETIENNE, A. S. & JEFFERY, K. J. (2004). Path integration in mammals. *Hippocampus* **14**, 180–192.

ETIENNE, A. S., MAURER, R., BERLIE, J., REVERDIN, B., ROWE, T., GEORGAKOPOULOS, J. & SÉGUINOT, V. (1998). Navigation through vector addition. *Nature* **396**, 161–164.

ETIENNE, A. S., MAURER, R., BOULENS, V., LEVY, A. & ROWE, T. (2004). Resetting the path integrator: a basic condition for route-based navigation. *Journal of Experimental Biology* **207**, 1491–1508.

FRIEDMAN, A. & KOHLER, B. (2003). Bidimensional regression: assessing the configural similarity and accuracy of cognitive maps and other two-dimensional data sets. *Psychological Methods* **8**(4), 468–491.

FUHS, M. C. & TOURETZKY, D. S. (2006). A spin glass model of path integration in rat medial entorhinal cortex. *Journal of Neuroscience* **26**, 4266–4276.

GALLISTEL, C. R. (1990). *Learning, Development, and Conceptual Change. The Organization of Learning.* Cambridge, MA: The MIT Press.

GEHRKE, L., IVERSEN, J. R., MAKEIG, S. & GRAMANN, K. (2018). The invisible maze task (IMT): interactive exploration of sparse virtual environments to investigate action-driven formation of spatial representations. In *German Conference on Spatial Cognition*, pp. 293–310. Springer, Cham.

GIBBS, J. W. (1881). *Elements of Vector Analysis*. Tuttle, Morehouse & Taylor, New Haven. https://doi.org/10.5479/sil.325602.39088000942730.

GIL, M., ANCAU, M., SCHLESIGER, M. I., NEITZ, A., ALLEN, K., DE MARCO, R. J. & MONYER, H. (2018). Impaired path integration in mice with disrupted grid cell firing. *Nature Neuroscience* **21**(1), 81–91.

GRIEVES, R. M., WOOD, E. R. & DUDCHENKO, P. A. (2016). Place cells on a maze encode routes rather than destinations. *eLife* **5**, 1–24.

HAFTING, T., FYHN, M., MOLDEN, S., MOSER, M. B. & MOSER, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature* **436**(7052), 801–806.

HASSELMO, M. E. & BRANDON, M. P. (2008). Linking cellular mechanisms to behavior: entorhinal persistent spiking and membrane potential oscillations may underlie path integration, grid cell firing, and episodic memory. *Neural Plasticity* **2008**, 658323.

HEAVISIDE, O. (1971). *Electromagnetic Theory; Including an Account of Heaviside's Unpublished Notes for a Fourth Volume*. Chelsea Publishing Co., New York.

HOK, V., LENCK-SANTINI, P. P., ROUX, S., SAVE, E., MÜLLER, R. U. & POUCET, B. (2007). Goal-related activity in hippocampal place cells. *Journal of Neuroscience* **27**(3), 472–482.

HONEY, R. C., IORDANOVA, M. D. & GOOD, M. (2014). Associative structures in animal learning: dissociating elemental and configural processes. *Neurobiology of Learning and Memory* **108**, 96–103.

HSIAO, H. H. (1929). An experimental study of the rat's "insight" within a spatial complex. *University of California Publications in Psychology* **4**(4), 57–70.

JACOB, P. Y., CAPITANO, F., POUCET, B., SAVE, E. & SARGOLINI, F. (2019). Path integration maintains spatial periodicity of grid cell firing in a 1D circular track. *Nature Communications* **10**, 1–13.

JACOB, P. Y., GORDILLO-SALAS, M., FACCHINI, J., POUCET, B., SAVE, E. & SARGOLINI, F. (2017). Medial entorhinal cortex and medial septum contribute to self-motion-based linear distance estimation. *Brain Structure and Function* **222**(6), 2727–2742.

JACOBS, L. F. & SCHENK, F. (2003). Unpacking the cognitive map: the parallel map theory of hippocam-pal function. *Psychological Review* **110**, 285–315.

JENSEN, R. (2006). Behaviorism, latent learning, and cognitive maps: needed revisions in introductory psychology textbooks. *The Behavior Analyst* **29**, 187–209.

KNADEN, M. & WEHNER, R. (2006). Ant navigation: resetting the path integrator. *Journal of Experimental Biology* **209**(1), 26–31.

KOSAKI, Y., POULTER, S. L., AUSTEN, J. M. & MCGREGOR, A. (2015). Dorsolateral striatal lesions impair navigation based on landmark-goal vectors but facilitate spatial learning based on a "cognitive map". *Learning & Memory* **22**, 179–191.

KUBIE, J. L. & FENTON, A. A. (2009). Heading-vector navigation based on head-direction cells and path integration. *Hippocampus* **19**, 456–479.

LE MOËL, F., STONE, T. J., LIHOREAU, M., WYSTRACH, A. & WEBB, B. (2019). The central complex as a potential substrate for vector based navigation. *Frontiers in Psychology* **10**, 690.

LEISING, K. J., SAWA, K. & BLAISDELL, A. P. (2012). Factors that influence negative summation in a spatial-search task with pigeons. *Behavioural Processes* **90**, 357–363 PMID: 22503862.

MACKINTOSH, N. J. (2002). Do not ask whether they have a cognitive map, but how they find their way about. *Psicológica* **23**, 1.

MAINGRET, N., GIRARDEAU, G., TODOROVA, R., GOUTIERRE, M. & ZUGARO, M. (2016). Hippocampo-cortical coupling mediates memory consolidation during sleep. *Nature Neuroscience* **19**(7), 959–964.

MCNAUGHTON, B. L., BATTAGLIA, F. P., JENSEN, O., MOSER, E. I. & MOSER, M. B. (2006). Path integration and the neural basis of the 'cognitive map'. *Nature Reviews Neuroscience* **7**(8), 663–678.

MITTELSTAEDT, H. & MITTELSTAEDT-BURGER, M. L. (1973). Mechanismen der Orientierung ohne richtende Außenreize. *Fortschritte Zoologie* **21**, 46–58.

MOLET, M., BUGALLO, M. & GAMBET, B. (2011). Spatial integration using a 3D virtual environment with humans. *Behavioural Processes* **88**, 198–201.

MÜLLER, D., GERBER, B., HELLSTERN, F., HAMMER, M. & MENZEL, R. (2000). Sensory preconditioning in honeybees. *Journal of Experimental Biology* **203**, 1351–1364.

MÜLLER, M. & WEHNER, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences* **85**(14), 5287–5290.

O'KEEFE, J. & BURGESS, N. (2005). Dual phase and rate coding in hippocampal place cells: theoretical significance and relationship to entorhinal grid cells. *Hippocampus* **15**, 853–866.

O'KEEFE, J. & DOSTROVSKY, J. (1971). The hippocampus as a spatial map: preliminary evidence from unit activity in the freely-moving rat. *Brain Research* **34**, 171–175.

O'KEEFE, J. & NADEL, L. (1978). *The Hippocampus as a Cognitive Map*. Clarendon Press, Oxford.

PARRON, C., POUCET, B. & SAVE, E. (2006). Cooperation between the hippocampus and the entorhinal cortex in spatial memory: a disconnection study. *Behavioural Brain Research* **170**(1), 99–109.

PARRON, C. & SAVE, E. (2004). Evidence for entorhinal and parietal cortices involvement in path integration in the rat. *Experimental Brain Research* **159**(3), 349–359.

PAVLOV, I. P. (1927). *Conditioned Reflexes*. Oxford University Press, London.

PEARCE, J. M., ROBERTS, A. D. & GOOD, M. (1998). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature* **396**, 75–75, 77.

PFEIFFER, B. E. & FOSTER, D. J. (2013). Hippocampal place-cell sequences depict future paths to remembered goals. *Nature* **497**(7447), 74–79.

POUCET, B. (1993). Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. *Psychological Review* **100**(2), 163–182.

RANCK, J. B. JR. (1985). Head direction cells in the deep cell layer of dorsal presubiculum in freely moving rats. In *Electrical Activity of the Archicortex* (ed. C. H. BUZSAKI), pp. 217–220. Akademiai Kiadeo, Budapest.

ROBERTS, W. A., CRUZ, C. & TREMBLAY, J. (2007). Rats take correct novel routes and shortcuts in an enclosed maze. *Journal of Experimental Psychology Animal Behavior Processes* **33**, 79–91.

ROWLAND, D. C., ROUDI, Y., MOSER, M. B. & MOSER, E. I. (2016). Ten years of grid cells. *Annual Review of Neuroscience* **39**, 19–40.

SAREL, A., FINKELSTEIN, A., LAS, L. & ULANOVSKY, N. (2017). Vectorial representation of spatial goals in the hippocampus of bats. *Science* **355**, 176–180.

SAVASTANO, H. I. & MILLER, R. R. (1998). Time as content in Pavlovian conditioning. *Behavioural Processes* **44**(2), 147–162.

SAVE, E., GUAZZELLI, A. & POUCET, B. (2001). Dissociation of the effects of bilateral lesions of the dorsal hippocampus and parietal cortex on path integration in the rat. *Behavioral Neuroscience* **115**(6), 1212–1223.

SAWA, K., LEISING, K. J. & BLAISDELL, A. P. (2005). Sensory preconditioning in spatial learning using a touch screen task in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* **31**, 368–375.

SCHATZ, B., CHAMERON, S., BEUGNON, G. & COLLETT, T. S. (1999). The use of path integration to guide route learning in ants. *Nature* **399**, 769–772.

SHRAGER, Y., KIRWAN, C. B. & SQUIRE, L. R. (2008). Neural basis of the cognitive map: path integration does not require hippocampus or entorhinal cortex. *Proceedings of the National Academy of Sciences* **105**, 12034–12038.

SINGER, R. A., ABROMS, B. D. & ZENTALL, T. R. (2006). Formation of a simple cognitive map by rats. *International Journal of Comparative Psychology* **19**, 417–425.

SOUMAN, J. L., FRISSEN, I., SREENIVASA, M. N. & ERNST, M. O. (2009). Walking straight into circles. *Current Biology* **19**(18), 1538–1542.

TAUBE, J. S., MÜLLER, R. U. & RANCK, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience* **10**, 420–435.

TOLMAN, E. C. (1948). Cognitive maps in rats and men. *Psychological Review* **55**, 189–208.

TOLMAN, E. C. & HONZIK, C. H. (1930). "Insight" in rats. *University of California, Publications in Psychology* **4**, 215–232.

TOLMAN, E. C., RITCHIE, B. F. & KALISH, D. (1946). Studies in spatial learning I: orientation and the short-cut. *Journal of Experimental Psychology* **36**, 13–24.

VAN CAUTER, T., CAMON, J., ALVERNHE, A., ELDUAYEN, C., SARGOLINI, F. & SAVE, E. (2013). Distinct roles of medial and lateral entorhinal cortex in spatial cognition. *Cerebral Cortex* **23**, 451–459.

WARREN, W. H., ROTHMAN, D. B., SCHNAPP, B. H. & ERICSON, J. D. (2017). Wormholes in virtual space: from cognitive maps to cognitive graphs. *Cognition* **166**, 152–163.

WEHNER, R. & WEHNER, S. (1990). Insect navigation: use of maps or Ariadne's thread? *Ethology Ecology & Evolution* **2**(1), 27–48.

WIKENHEISER, A. M. & SCHOENBAUM, G. (2016). Over the river, through the woods: cognitive maps in the hippocampus and orbitofrontal cortex. *Nature Reviews Neuroscience* **17**(8), 513–523.

WILSON, S. P. & WILSON, P. N. (2018). Failure to demonstrate short-cutting in a replication and extension of Tolman et al.'s spatial learning experiment with humans. *PLoS One* **13**(12), e0208794.

WIMMER, G. E. & SHOHAMY, D. (2012). Preference by association: how memory mechanisms in the hippocampus bias decisions. *Science* **338**(6104), 270–273.