Building a cognitive map by assembling multiple path integration systems

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Abstract Path integration and cognitive mapping are two of the most important mechanisms for navigation. Path integration is a primitive navigation system which computes a homing vector based on an animal's self-motion estimation, while cognitive map is an advanced spatial representation containing richer spatial information about the environment that is persistent and can be used to guide flexible navigation to multiple locations. Most theories of navigation conceptualize them as two distinctive, independent mechanisms, although the path integration system may provide useful information for the integration of cognitive maps. This paper demonstrates a fundamentally different scenario, where a cognitive map is constructed in three simple steps by assembling multiple path integrators and extending their basic features. The fact that a collection of path integration systems can be turned into a cognitive map suggests the possibility that cognitive maps may have evolved directly from the path integration system.

Keywords Cognitive map · Path integration · Spatial updating · Evolution · Navigation

Introduction

Path integration is a navigation mechanism that allows an animal to return to its home location through a novel, direct path after an outbound journey by maintaining a homing vector. The basic idea of path integration is continuous updating

by vector summation.¹ Path integration is usually treated as a process that updates the navigator's location relative to home by adding the self-displacement vectors to the previous self-position vector. Alternatively, path integration can also be the calculation of the home location relative to the navigator. The home location is represented as a vector, and its length and bearing are changed by subtracting vectors of self-displacement from the homing vector of the previous instance (Fig. 1a). In both cases, this process is based on perception of self-motion.

The current paper reviews features of path integration and proposes a new theoretical model that creates a basic cognitive map by assembling multiple path integrators. The basic path integration system includes three components (Fig. 1b). The first component is the self-motion estimation system. Various types of perceptual information may be used to estimate the direction and distance of self-movements, including internal cues such as vestibular signal, proprioceptive information, energy expenditure, and motor command, and external information such as optical flow and auditory information (Berthoz, Israel, Francois, Grasso & Tsuzuku, 1995; Kirchner & Braun, 1994; Ronacher & Wehner, 1995; Srinivasan, Zhang, Altwein, & Tautz, 2000; Zhang, Zhang, & Wang, 2013). The second component is the spatial representation of the home location, usually referred to as the homing vector, which provides information about the distance and direction

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¹ Here “continuous” means “un-broken”, i.e., the displacement vectors have to be connected with no gap in between (Fig. 1a). The integration does not need to be “continuous” in the sense of moment-by-moment calculation; it can be a discrete step process. The exact computational mechanism for path integration is not well understood, and there are different hypotheses about how often the calculation is performed, whether the motion information is stored, and whether it is based on displacement vectors, velocity vectors, acceleration, or something else (Loomis et al., 1993; Müller & Wehner, 1988; Wan, Wang, & Crowell, 2013).

Fig. 1 An example of the path integration process (left panel). The navigator makes three movements **M1**, **M2**, and **M3**, and the homing vector is computed by vector subtraction as $H = -M1 - M2 - M3$. The right panel shows the three components of a path integration system

to the origin of the trip. This representation is a dynamic one and changes as the animal moves. The third component is the integrator, which combines the current homing vector with the self-motion estimation to generate a new homing vector through a vector summation/subtraction process. The new vector then replaces the old vector and is stored in the dynamic spatial representation.

There is ample evidence that path integration is a common process among navigating animals, including insects, crabs, fish, birds, rodents, and humans (Alyan & McNaughton, 1999; Collett & Collett, 2000; Collett, Collett, & Wehner, 1999; Gallistel, 1990; Hughes & Blight, 1999; Layne, Barnes, & Duncan, 2003; Loomis et al., 1993; Mittelstaedt & Mittelstaedt, 1980; Saint Paul, 1982; Wehner & Srinivasan, 1981). For example, Wehner and Srinivasan (1981) studied desert ants that left their nest to forage in a relatively featureless ground, traveled on random routes and might end up in any direction from the nest. Once they found food, they took a direct path back home. If the ants were passively moved by a certain distance right after they discovered the food and were ready to return to the nest, the ants would take off in the same direction and travel the same distance as if they had not been displaced, suggesting that their ability to take the shortcut path back home is not a result of recognizing familiar locations but a path integration process.

Although path integration is a prevalent navigation mechanism, it has at least three major intrinsic limitations. The first limitation is that it only represents the relationship between the animal and its home location, e.g., as a homing vector. This representation provides the animal with information on the direction and distance of its home from anywhere in the environment it is currently located, and therefore allows it to return to home through a shortcut along a straight line. However, the basic path integration process only contains one vector and therefore is limited in its usage.

The second limitation is error accumulation. Despite the multiple sources of information in self-motion perception, it is inevitable that some errors will occur in the distance and direction estimation. When such errors occur in one step, the

resulting homing vector will be erroneous. Because the computation of the homing vector for the next step is based on the homing vector of the previous step, the errors in one step will carry over to the homing vectors from that step on. In other words, errors will accumulate as the path integration process continues. As a result, the homing vector will become less and less accurate, and eventually become completely unreliable if the trip is long enough. Due to this error accumulation problem, path integration is generally useful for relatively short trips, and has to be used under its limit to provide reasonably accurate guidance for navigation.

The third limitation is that path integration requires uninterrupted processing and is vulnerable to disruptions. Because in each step of the path integration process, the homing vector is calculated from the homing vector of the previous step, any disruption will break the chain of this sequential process and cause the entire system to fail. For example, if the homing vector is lost in the middle of a trip, then the computation of the homing vector for the next step cannot be accomplished, therefore the path integration process has to stop and cannot be recovered until the animal somehow manages to return to its home and starts anew.

Because of these limitations, path integration has generally been considered a primitive form of navigation system. Humans and many other animals show navigation abilities that exceed these limitations. For example, humans can represent many locations, and go to any of them as they wish. Humans can also make long trips in familiar environments without suffering from forever-increasing errors in spatial localization due to error accumulation. Finally, humans are usually capable of recovering from disruption and disorientation in the middle of a trip based on knowledge of the environment.

It is generally believed that such navigation performance relies on a completely different type of mechanism, usually referred to as cognitive mapping (Gallistel, 1990; O'Keefe & Nadel, 1978; Tolman, 1948). Cognitive map is considered the most advanced form of navigation system, and not possessed by all species (Bennett, 1996; Wehner & Menzel, 1990). The exact nature of cognitive map is still under debate (Burgess, 2006; McNamara & Shelton, 2003; Wang, 2012; Wang & Spelke, 2000, 2002). Regardless of the nature and form of the representation, a basic cognitive map should meet several criteria that overcome the limitations of the path integration system. First, it should be relatively comprehensive, containing spatial information about multiple locations of the environment. Second, it should be able to support long and flexible trips within the environment that the map covers. Third, it should be persistent and can recover from disruptions in the middle of the trip. According to these criteria, humans clearly possess cognitive maps, and other species such as rats also possess this type of spatial representation (O'Keefe & Nadel, 1978; Wang & Spelke, 2002).

One important question that has been neglected in the literature is where the cognitive map comes from. Most theories of navigation emphasize the difference between cognitive map and path integration systems, and hypothesize a single, independent path integration system which may help with the integration of a cognitive map by feeding information to a separate cognitive map system. For example, walking between two environments or two separately learned routes may help “connect” them to form a larger, integrated mental representation (Montello & Pick, 1993; Richardson, Montello, & Hegarty, 1999). The following sections demonstrate a fundamentally different scenario, where a cognitive map is constructed from a collection of basic path integration systems in three simple steps, and discuss the possibility that cognitive maps may have evolved from path integration systems.

Building a cognitive map from path integrators

Step 1: Path integration to spatial updating

A basic path integrator represents the home location as a vector, and updates this representation by subtracting the self-motion vector from it. Although home is a very important place that an animal should care about, it is nonetheless just one location in space and there is nothing really special about it other than its meaningfulness to the specific animal. In other words, if a path integrator can represent the home location of an animal as a vector and update it as the animal moves, then in principle a path integrator should also be able to represent a different location, for example a food site, as a vector and update that vector in exactly the same manner a homing vector is updated. Therefore it should be a simple extension of the path integration system to include multiple path integrators, each representing a different location of interest to the animal as a vector, and updating this vector using the commonly shared self-motion vector produced by the self-motion estimation system. This collection of path integrators then becomes a new type of spatial representation, which is referred to as a spatial updating system (Klatzky et al., 1998; Waller, Montello, Richardson, & Hegarty, 2002; Wang, 2007a).

An example of how such a spatial updating system operates is shown in Fig. 2. When the animal leaves home, a homing vector is created and maintained by a standard path integrator. When the animal makes a movement $M1$ and reaches the food location, the standard path integrator updates the homing vector using $H = -M1$. When the animal makes another movement $M2$ and reaches the water location, the standard path integrator again updates the homing vector using $H' = H - M2$. In addition, a new, food vector is created by a second path integrator and this path integrator for the food location similarly updates the food vector using $F = -M2$. When the animal

continues to move, a third path integrator creates and maintains a water vector W , and all three path integrators update their own vectors using the same self-movement information. As a result, wherever the animal goes, it always carries a set of vectors, each pointing to one of the locations it's interested in.

This collection of independent path integrators thus becomes a dynamic map of the environment. Although each of them is just a simple path integration system, and performs its own computation independent of the other ones, as a group they can serve as a comprehensive spatial representation to guide navigation to any of these destinations as the animal wishes. Because this mental map is dynamic, and changes as the animal moves, it is not itself a cognitive map in the traditional sense. However, it already contains the same type of spatial information required for a cognitive map.

More generally, an animal does not have to physically move to a location to create a vector of that location. If the animal can perceive a target some distance away from its current location, in principle it should be able to estimate its direction and distance and generate a vector for that target based on the perceptual information. This vector can then be maintained by a path integrator and updated as the animal moves. In addition to the location of a target, in principle an animal can also maintain and update the orientation of a target or a group of targets relative to its current heading (Amorim, Glasauer, Corpinot & Berthoz, 1997). In this case, the orientation of the target(s) relative to the animal's heading is represented as an angle. While the animal moves, the rotational component of self-motion (i.e., self-turning) is subtracted from the target's current orientation value, and the result replaces the old one as in a standard path integrator (Fig. 3).

Step 2: Long-term memory

To make a more stable and permanent map, a long-term memory system is required. There are at least two ways to build this long-term representation. First, since a functional vector representation is already available in the spatial updating system, it can simply be copied as is to the long-term memory without any modification or transformation. In other words, the long-term memory version can be just a “snapshot” of the dynamic map of the spatial updating system at a given moment, including all the vectors being maintained and updated by each of the path integrators, except that the long-term memory representation is static and does not change as the animal moves.

Second, a long-term memory representation can also be acquired from perception directly, under the special condition when multiple targets can be perceived from a given location. In this case, information about the distance and direction of each target from the observation point is available from perception directly, and such information can then be stored in long-term memory. Note that only the individual target's spatial location is needed, and no relational information among

Fig. 2 An example of the spatial updating process. The top left panel shows the environment with home, food and water locations, while the navigator is at home. The top right panel shows the navigator making a movement **M1** to the food location, and the standard path integrator updates the homing vector $H = -M1$. The lower left panel shows the navigator making another movement **M2** to the water location. The standard path integrator again updates the homing vector $H' = H - M2$, while a new path integrator creates and updates a food vector $F = -M2$.

The lower right panel shows the navigator making a third movement **M3**. The homing vector is updated as $H'' = H' - M3$, the food vector is updated as $F' = F - M3$, while a new water vector is created by a new path integrator and updated as $W = -M3$. As the navigator continues to move, the self-movement vector will be subtracted from each target vector to maintain a dynamic representation of where each of these places is from the navigator's current position

the targets is required. This representation can provide the same type of spatial information as the one copied from the dynamic map, and therefore can serve the same purposes.

In both cases, the static mental map contains comprehensive spatial information about multiple locations in the environment. Moreover, it is stable and permanent, and the spatial information in this representation can be retrieved later on to guide navigation whenever a disruption occurs; therefore it is a conventional type of cognitive map according to the three criteria. There is a caveat, however. The spatial information copied from the dynamic map or acquired from perception at a given observation point is only correct when the animal is at that same location. If the animal tries to use this recorded information when it is at a different location, as it generally happens, all the vectors will be pointing to the wrong places. In order to make proper use of this snapshot map, a recalibration

process is needed to adjust for the discrepancies after those vectors are re-loaded into the spatial updating system.

Step 3: From resetting to recalibration

It turns out that the basic path integration system, such as that in the desert ants, already has a resetting function that can serve as the basis to accomplish the recalibration process. For example, Wehner and Srinivasan (1981; Müller & Wehner, 1994) showed that desert ants reset their path integrator to correct for the errors accumulated during the foraging trip when they return to their nest. When these ants are ready to go home, they follow their homing vector and continue to perform the path integration process along their return journey until the homing vector reaches zero, indicating that they are close to the nest. Then the ants start a random search of the

Fig. 3 An example of how the orientation of a target or target set is updated based on estimation of self rotation. The orientation of the target S is 135° clockwise ($S = -135^\circ$) from the initial heading orientation of the navigator (lower position in dotted lines). When the navigator makes a movement with a body rotation of 45° clockwise ($R = -45^\circ$), the orientation of the target S relative to the navigator's new heading is updated by $S' = S - R = -90^\circ$

surrounding area. When they eventually find their nest, their path integrator would still show a non-zero vector pointing to a nearby location. This vector reflects the accumulated errors during the entire trip, including both the outbound and the return journeys. To correct for this error so that it does not carry over to the next trip, this error is subtracted from the path integrator and the homing vector is reset to zero.

This mechanism suggests that in a basic path integration system, accumulated errors can be removed when the animal reaches a known location where the correct vector value is known to be zero. When a path integration system is expanded into a spatial updating system with multiple integrators, each with its own vector representing a different target location, the same error-correction mechanism can be easily expanded to correct for the cumulative errors when the animal reaches any of the locations represented in the spatial updating system.² Figure 4 showed an example of how such correction works. When an animal carrying three vectors, i.e., home, food, and water, wanders around and performs spatial updating along the way, the same errors in its self-motion estimation will accumulate in all these vectors as a common error. When the animal reaches one of these destinations, e.g., the food location, it will find that its food vector still points to a nearby location, even though it should be zero had there been no errors in its calculations. Therefore this vector likely reflects the errors that have accumulated during its journey, which can

be removed from the spatial updating system by simply treating that error vector as an additional self-motion signal and subtracting it from each of the vectors in the spatial updating system. When this recalibration process is completed, the food vector will be zero, which is the correct value corresponding to the animal's current location verified by its perception, while the home and the water vectors are also corrected to point to the corresponding true locations.

In general, the animal does not have to be physically at one of these locations represented by its vectors to perform a recalibration. If the animal can perceive one of these locations from a distance, and make a reasonably accurate estimation of its direction and distance, then it can compare this perceptual vector with the one in its spatial updating system, and calculate an error vector based on their difference. This error vector can then be removed from the spatial updating system by subtracting it from all target vectors. This form of recalibration process requires an additional processor to compute the difference between the perceptual and updated vectors, and therefore is a little more complicated than the on-site recalibration process directly derived from the resetting mechanism in a basic path integration system.

It should be noted that this error correction mechanism only removes accumulated errors common to all target vectors, such as errors in self-motion estimation. These encoding errors are the main sources of errors in a path integration system (Fujita, Klatzky, Loomis, & Golledge, 1993; Klatzky et al., 1999; Wan, Wang & Crowell, 2013). Other errors that are specific to each individual path integrator, such as noise in the integrating process itself, cannot be corrected using this mechanism in general. This recalibration mechanism also cannot correct the errors introduced during the sequential learning process. For example, if the perceived self-motion vector **M1** in Fig. 2 has an error in it, then the homing vector will have an additional error that is not in the food and water vectors. Similarly, an error in the self-motion estimation **M2** will be incorporated in the homing and food vectors, but not in the water vector. These relative errors cannot be corrected using the recalibration process discussed above. They may be corrected through different mechanisms such as re-learning, when multiple targets can be detected perceptually at the same time and all target locations are re-coded.

Also note that a discrepancy between the spatial updating system and the perceptual feedback does not necessarily lead to a recalibration. There are different ways an updated vector may differ from the one obtained from the perceptual information. The most common cause is the accumulated error during the integration process. However, discrepancy can also occur if the environmental feature itself has moved (e.g., unstable landmarks), or if the animal misidentifies a similar object/place as the original one (misidentifications). In principle a recalibration should be performed only when the discrepancy is due to updating errors. When the landmark itself has

² The resetting function requires an object recognition capability to identify a specific target, namely home, based on its perceptual features. Consequently, the extension to a recalibration process requires the extension of this object recognition capability from recognizing home to recognizing other targets using the same mechanism. The object recognition system is generally considered to be in the ventral pathway separate from the navigation systems such as path integration and cognitive maps.

Fig. 4 An example of the recalibration process. The left panel shows the navigator making a movement and reaches the food location. However, the self-motion estimator under-estimates the length of the displacement, with the perceived movement vector M being smaller than the actual movement. As a result, the updated vectors H , W , and F all correspond to where the misperceived self-movement ends, not where the navigator actually is. The right panel shows the results of the spatial updating

process H , W , and F (same as in the left panel) in dotted lines. An error is detected, since the non-zero food vector F contradicts the perceptual information. A recalibration process is carried out by subtracting this error vector ($Err = F$) from the three vectors. The resulting recalibrated vectors H' , W' , and F' all point to the correct locations, and the error in the self-motion estimation is thus removed from the system

moved, the animal should replace the vector for that landmark only with the perceived vector, but should not use this landmark information to recalibrate the other target vectors. When the discrepancy is due to mistaking a similar landmark at a different location, the animal should retain all the original vectors, and add a new vector to represent the perceptually similar, but different object.

That means an animal may use different strategies to resolve a discrepancy between the spatial updating system and the perceptual feedback based on its assessment of the likely cause of this conflicting information. For example, it has been shown that hamsters tend to reset their path integration system by landmarks when the discrepancy is small, but will ignore the landmark information when the discrepancy is large (Etienne, Teroni, Hurni, & Portenier, 1990). This is reasonable because a relatively small discrepancy is likely a result of the error accumulation in the integration process, while a huge discrepancy beyond the reasonable expectation of the updating errors (such as those in opposite directions) is more likely due to other causes (such as unstable landmarks moved to a different location). Moreover, the recalibration of the spatial updating system by perceived environmental features may be based on perception-only (i.e., using the perceived vector as the correct one to recalibrate the other vectors) or integrative (i.e., using a weighted average of the two vectors as the correct vector and do the recalibration accordingly), depending on the animal's assessment of the reliability of the two sources of information. For example, it has been shown that people may combine the path integration and landmark information when they are in conflict (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008), which is an example of integrative recalibration.

Although the recalibration mechanism is intended for the correction of the accumulated errors, it can readily be used for

the recalibration needed when a snapshot representation from the long-term memory is reloaded into the spatial updating system after a disruption, because the error that needs to be corrected is a global, common error, which is mathematically the same as the cumulative error incurred during the regular path integration process. To use the snapshot memory after disruption, the stored vector information needs to be reloaded into the spatial updating system, so that the animal has an initial estimation of each of the places in the environment. In addition, the animal needs to look around to gather perceptual information. If any of these targets can be identified, then it can obtain a perceptual vector for that target, and perform the recalibration in the same way as in the correction of the cumulative errors. If no known target can be found, the animal needs to move around until it finds one, and then perform the recalibration. During the search for a known target it may use the temporary map as a guide, and continue to update this map as it moves around.

The resulting cognitive map

With these three simple steps, a functional cognitive map system is constructed from multiple copies of basic path integrators. This system contains two spatial representations, a dynamic map made of multiple independent path integrators, each maintaining and updating a vector for one target location in the working memory, and a static map in long-term memory which is a snapshot copy of the dynamic map at a given moment or a snapshot of the targets perceived from a given location. In addition, a recalibration mechanism is adopted from the resetting function of the basic path integrators to correct for the accumulated errors in the spatial updating system at any of the known targets, and to recalibrate the vectors when the snapshot map is reloaded into the spatial updating system after a disruption. The targets being represented and

updated may have distinctive features (such as landmarks). They can also be any arbitrary position in space with no recognizable perceptual features (such as a location on the ground with uniform texture under which some food was hidden). An animal may return to both types of targets based on their corresponding updated vectors, although only the former can be used for recalibration.

This system meets all three criteria of a basic cognitive map. First, it is comprehensive and can guide navigation to any of the target locations from anywhere in the environment the animal happens to be located. Second, it can guide the animal to navigate within the environment covered by the map without suffering from forever-increasing cumulative errors, because with the representation of multiple target locations and the ability to remove the cumulative errors whenever the animal encounters one of them, the animal can generally keep the errors within a certain limit. Third, the long-term memory and the recalibration process allow the animal to recover from any disruption. Therefore a complete, basic cognitive map system is constructed from an ensemble of path integrators in three steps.

Some experimental evidence

The dynamic representation of multiple locations

It has been well known that humans can represent and keep track of their relationship with multiple targets when they change locations. For example, Rieser (1989; Wang, 2004a, 2007b; Wang & Brockmole, 2003a) asked people to learn an array of objects around them and then point to these objects after turning without vision to face a new direction. Their reaction time and accuracy in the novel facing direction were comparable to those in the learned direction, suggesting they were able to update their relationship to these targets during their body movement. This type of spatial updating can be performed when changing both positions and orientations (Klatzky, Lippa, Loomis, & Golledge, 2003; Rieser, Garing & Young, 1994; Simons & Wang, 1998; Waller et al., 2002; Wang et al., 2006; Wang & Simons, 1999).

Recent research examined the mechanism of such updating process and suggested that humans represent multiple target locations individually, and update them based on self-motion estimation. For example, Wang and Spelke (2000; Sargent, Dopkins, Philbeck, & Chichka, 2010; Waller & Hodgson, 2006; Xiao, Mou & McNamara, 2009) asked people to learn multiple target objects in a room. They then pointed to these targets before and after disorientation. People showed impairment in the internal consistency among their pointing responses to multiple targets when they were disoriented. The internal consistency among pointing responses to multiple targets can also deteriorate after extended movements (Waller &

Hodgson, 2006). These findings suggest that people represent multiple targets separately and update their locations individually, which leads to errors specific to each target during the updating process, resulting in changes in the configuration of multiple target representations after extended movements and perturbation in the spatial updating process. These findings are consistent with the dynamic vector representation updated using self-motion information. However, this experimental paradigm has only been applied to humans so far.

The snapshot

The traditional concept of long-term snapshot memory refers to visual memory of a scene, usually near a target location with environmental features (e.g., Collett & Cartwright, 1983). For example, Collett and Rees (1997) set up feeders marked by one or two nearby landmarks for wasps and honeybees. They recorded the routes the insects took and their posture as they approached the landmark or the feeder. They found that wasps and honeybees tend to approach the feeder from a constant direction, and their body orientation tends to align in roughly the same horizontal direction. As a result, the image in their retina will be roughly the same each time for an individual insect. Collett and Lehrer (1993) analyzed the motion patterns of the wasps during their first departure from a newly discovered feeder. The wasps fly in arcs roughly centered on the feeder and they turn to face the feeder towards the end of each arc (inspection point). These inspection points are precisely arranged along lines extending out from the feeder. These findings suggest that insects may take “snapshots” of relevant locations and recognize them by image matching.

There has been ample evidence that humans have spatial memory that corresponds to specific viewpoints, typically from the learning perspectives. For example, Diwadkar and McNamara (1997; Shelton & McNamara, 2001; Wang, 2004b, 2005) showed participants photos of several objects on a table, then tested their accuracy and reaction time in detecting a change of object position from a different perspective. People were best when tested in the studied perspectives, while errors and reaction time increased as a function of the angular deviation of the testing orientation from the studied orientation. Similar type of view-dependent behavior has also been shown in other animals (Georgakopoulos & Etienne, 1997; Griffin & Etienne, 1998; Sutherland, Chew, Baker, & Linggard, 1987; Thinus-Blanc, Durup & Poucet, 1992).

Most of the studies on spatial memory of multiple targets used targets that can be perceived from a single (learning) position, and the spatial memory is acquired directly from perception instead of using the spatial updating process. There is some evidence that targets learned across viewer movements can be incorporated into one representation (Klatzky, Loomis, Golledge, 1997; Meilinger, Berthoz, & Wiener,

2011). For example, Meilinger et al. (2011) asked people to learn three target locations from one position, then walk to another position and learn three other target locations. After learning, they were required to travel through all six targets in a shortest path. People's performance showed that they were able to integrate the targets learned from two different positions. These findings are consistent with the sequential learning by spatial updating mechanism. However, integration over spatial updating can be difficult, especially across environments (Montello & Pick, 1993; Wang, 2006; Wang & Brockmole, 2003b).

The recalibration

There are several lines of research in both humans and other animals that may involve the recalibration process. The most closely related process is reorientation. It has been shown that humans, rodents, and fish can use the shape of the environment to locate a hidden target after disorientation (Cheng, 1986; Cheng & Newcombe, 2005; Hermer & Spelke, 1996; Sovrano, Bisazza, & Vallortigara, 2002; Wang, Hermer & Spelke, 1999). It is hypothesized that the animals first use the geometric information to reorient themselves, i.e., re-establish their orientation relative to the environment, then they retrieve their memory of the target location encoded during the learning stage to find its current location (Wang & Spelke, 2003). This process is similar to the recalibration mechanism. However, reorientation corrects errors in the heading orientation instead of the position, and the relationship between heading and position calibration is not clear yet.

The second line of research is target localization using landmarks. In these studies, animals learn a target location in the presence of other landmarks. During testing, the landmarks are moved, and the animals are shown to be able to locate the target according to the landmarks' new positions (e.g., Eichenbaum, Stewart, & Morris, 1990; Burgess, Spiers, & Paleologou, 2004). These studies showed that animals can encode distinctive features of the environment in their spatial memory and use them to solve spatial localization tasks. However, it is unclear whether spatial localization using landmarks relies on direct relational coding or involves recalibration of the spatial updating system. For example, an animal may encode the locations of the landmarks in addition to the target. When the landmarks are moved, it will generate an error signal between its representation in the spatial updating system and the perceptual information, and this error signal can be used to correct the representation of the target locations in a recalibration process. As a result, the animals can locate the targets according to the new landmark position, even though they do not directly encode the spatial relationship between the target and the landmarks.

The majority of the studies using the landmark manipulation paradigm did not examine the spatial updating process,

and therefore were ambiguous about whether the landmark usage is due to direct association between landmarks and the target, or due to indirect influence of the landmarks in a recalibration process. There is some evidence that spatial localization using landmarks affects the path integration system. For example, Etienne et al. (1990, 2000) trained hamsters to forage on a circular platform in the presence of visual cues. During testing, the home was rotated to a new location in the dark, and the animals were lured along an outbound journey. In the middle of the journey, the light was switched on briefly to reveal the familiar cues, which defined a different home location than the one they were updating in their path integration system. Unlike in traditional landmark manipulation tasks, the animals were not asked to locate their home in the presence of the landmarks. Instead, they continued their foraging journey in the dark for an additional segment before returning to home. The data showed that the animals used the cues to correct/recalibrate their homing vector, and updated this new vector during their last segment.

The place cells, head direction cells, and grid cells

A large and rapidly growing literature has been focused on the neural basis of path integration and cognitive maps (e.g., Brun, et al., 2008; McNaughton et al., 1996; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006). The most important findings are the hippocampal place cells which fire when the animal is at a specific location in the environment (McNaughton, Knierim, & Wilson, 1995; O'Keefe & Burgess, 1996; O'Keefe & Nadel, 1978; O'Keefe & Speakman, 1987; Taube, 1995), the head direction cells which fire when the animal is facing a specific direction (Taube, Muller, & Ranck, 1990a,b), and the grid cells which have receptive fields organized along triangular grids (Fyhn, Hafting, Witter, Moser, & Moser, 2008; Hafting, Fyhn, Molden, Moser, & Moser, 2005). Because different place cells have different place fields, as an ensemble they "map out" an external space, and therefore have been referred to as a "cognitive map" that serves as a representation of an animal's own location in space (O'Keefe & Nadel, 1978). According to this conventional interpretation, the place cells form a representation of "where I am." In contrast, a cognitive map should be a spatial representation of "where things are." Therefore the place cell system is not a real cognitive map. Instead, it is a complementary system for a cognitive map. That is, one will need a separate, real cognitive map that contains spatial information about the environment, and use the place cell information to define where the animal is on that map in order to navigate to different destinations (for more discussion see Wang, 2012).

Besides these theories in the literature, there is an alternative interpretation of the place cell's behavior that is compatible with the dynamic cognitive map in the spatial updating system. Although a place cell fires when the animal is at a

specific location in space, it is not necessarily a representation of the animal's own location. In fact, a cell will show exactly the same type of behavior if it represents a target's location relative to the animal itself, using certain directional reference frames.³ For example, if a place cell encodes the location of a target relative to the animal (e.g., the tree is 20 m north of me), then it will fire whenever the animal is at a specific location in space (e.g., 20 m south of the tree). A different place cell may signal the target at a different location (e.g., the tree is 30 m west of me). The place cells encoding the same target at different locations will become a dynamic representation of where that target is as the animal moves around. Moreover, different groups of place cells may encode the locations of different targets, with each group representing the vector of a different target dynamically as the animal moves. In this way, the place cells become a spatial updating system described in the section *Path integration to spatial updating*, and form a cognitive map in the real sense (albeit a dynamic one). Whether the place cell system is a representation of the location of the animal as traditionally assumed (i.e., a self-locator and not the cognitive map itself) or a representation of the target locations relative to the animal (i.e., a real, dynamic cognitive map) awaits further empirical research.

In summary, the dynamic multiple vector representation, the snapshot of the spatial updating system, and the recalibration of spatial updating system are all relatively new theories that are different from traditional conceptualizations of spatial memory and navigation. Although there are some related lines of research providing evidence that is consistent with these mechanisms, currently experimental data on these representations and processes are limited, and more direct empirical research is needed to examine these hypotheses in both humans and other animals.

A possible evolutionary origin

The fact that a cognitive map system can be constructed from multiple copies of the basic path integration processors in three relatively simple, straight forward steps suggests a possibility that despite their apparent drastic difference, cognitive maps may have evolved from the path integration system, as most complex, advanced systems evolve from more basic, primitive systems. The exact evolutionary sequence does not necessarily follow the order of the three steps laid out in the section *Building a cognitive map from path integrators*. For example, the resetting-to-recalibration mechanism must come

after the single-to-multiple-target extension, because recalibration is a process specific for multiple targets by definition. However, the long-term memory snapshot does not have to wait for the spatial updating system to appear. It can occur anywhere along the sequence, even for the basic path integration system, and play some functional role. Therefore the evolutionary paths may differ for different species.

There can also be different evolutionary origins for different types of cognitive maps. For example, a cognitive map that consists of a set of locations (nodes) and routes connecting them (edges) is a different type of representation than the basic cognitive map discussed in the proceeding sections. This network type of representation probably did not come from the path integration system, since the path integration system generally does not encode trajectory information (e.g., routes and route distances).⁴ Similarly, a cognitive map that consists of a list of spatial relationships in propositional form is also unlikely a descendant of the path integration system. These types of spatial representations are more likely related to the visual representation, the semantic network and/or the linguistic system.

Despite the large literature on spatial memory and navigation in both humans and other animals, critical experimental evidence for understanding the evolution of navigation systems is still much needed, and systematic examination of each of the spatial processing components across a wide variety of species may identify special intermediate forms of the navigation systems to help answer the important question of how spatial representations for navigation evolved.

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³ Both an external reference direction (e.g., a compass direction) and an egocentric direction (e.g., defined by an animal's initial heading when entering an environment) will work, and both require a separately updated orientation system (e.g., the head direction system) to convert the reference direction used for the self-displacement vector (generally relative to the current self orientation) to that of the target vectors.

⁴ There is evidence that humans can retain movement profile and path information during navigation (Berthoz et al., 1995; Loomis et al., 1993); however, this may be outside of the path integration system and occur primarily for short routes (Wan et al., 2013).

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