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On the Nature of Three-Dimensional Encoding in the Cognitive Map: Commentary on Hayman, Verriotis, Jovalekic, Fenton, Jeffery

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Abstract

A recent article by Hayman, Verriotis, Jovalekic, Fenton, and Jeffery titled Anisotropic encoding of three-dimensional space by place cells and grid cells (2011) explored how place and grid cells respond when rats locomote vertically above the ground. From their results the authors concluded a number of points about rats' abilities to orient and navigate in three dimensions. Here, we review evidence revolving around several issues including: 1) what reference frame rats use when locomoting vertically, 2) whether rats can perceive their height above the ground, 3) whether rats can estimate vertical distance and have a cognitive map in the vertical domain, 4) whether rats can path integrate in the vertical domain, and 5) does processing 3-dimensional representations require a large number of neurons. We argue that the Hayman et al. results can be accounted for by considering the reference frame the animals used in the tasks. Had the rats been facing inward with their limbs in contact with the vertical surface when moving, it is possible that different patterns of place and grid cell activity would have been observed. Further, there is good evidence to indicate that rats can orient and navigate effectively in the vertical domain.

One of the challenges in the field of spatial cognition is to understand the nature of how space is encoded by neurons in the brain. In reality, this issue revolves around two separate questions. First, do humans and other animals have a 3-dimensional (3D) representation of space? And second, if so, how does the brain represent it? If humans and animals do have a 3D understanding and perception of space, then there must be a way that the brain accomplishes this representation. One of the first places to look for these neural correlates is of course the allocentric spatial cells observed throughout the hippocampus and limbic system – place cells, head direction cells, and grid cells.

A recent article by Hayman, Verriotis, Jovalekic, Fenton, and Jeffery titled Anisotropic encoding of three-dimensional space by place cells and grid cells (2011) explored how place and grid cells respond when a rat locomotes at different heights above the ground. Two different apparatuses were employed. The first was a square pegboard oriented vertically in which the rat climbed the pegs while facing parallel to the vertical board with the side of its body adjacent to the board. In the second task the rats locomoted along a continuous, flat-surfaced spiral that contained 5-6 coils and ended about 75 cm above the floor.

In the pegboard task the authors found that place cells appeared to fire across a continuum between two different modes. At one end of the spectrum, cell activity increased along one

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vertical strip of the pegboard, thus firing at different heights above the floor (e.g., the cells in the upper left and lower right in Hayman et al. Fig. 1A). At the other end, place cells maintained their location-specific firing at one circumscribed area on the pegboard, but the size of the areas were generally larger than those seen when the cell was recorded on the floor in the horizontal plane (e.g., the two cells in the third row in Heyman et al. Fig. 1A). In contrast, grid cells appeared to fire in only one manner, with a response pattern that was best characterized as one or more stripes oriented vertically along the pegboard. When there were multiple stripes, they did not appear to be organized in a regular repeating pattern – at least compared to the regular spaced-pattern on the floor. Thus, the firing pattern could be appreciated as the plane of the pegboard slicing through regularly-spaced, vertically oriented, grid columns of sensitivity (Hayman et al., Fig. 5C).

In the spiral helix, place cells continued to fire in a location-specific manner with firing usually occurring at only one location per coil, and that location was similar across coils. Normal grid cell activity also occurred along every coil, but firing occurred at more than one location for each coil and these locations were aligned with the same fields for the coils above and below their current position. Thus, for both place and grid cells, firing on the spiral helix could be represented as vertical cylindrical columns.

These results are interesting and important, but there are a number of issues to consider regarding both the findings themselves and the conclusions drawn from them. These considerations include: 1) what reference frame the animals used, 2) whether the animals perceived their height above the floor and maintained a cognitive representation, or map, in the vertical plane, 3) whether the animals have an estimation of the distance (odometer) they moved along the vertical dimension, 4) the related issue: can animals path integrate in the vertical plane, and 5) whether processing three-dimensional (3D) spatial representations requires a significantly large number of neurons.

Before we discuss each of these issues, it is important to consider whether animals have a means to detect motion in 3D space. Because gravity holds us to the floor/ground, much of our navigation can be approximated by a two-dimensional (2D) plane, making it difficult to assess how the brain defines our sense of height in a larger environment. While visual and auditory stimuli provide information about vertical translation to different heights above ground, the accuracy of these stimuli for defining height depends to a large extent upon the distance of the stimulus from the animal. The best candidate to continuously detect motion in 3D space is of course the vestibular system. The vestibular system is certainly designed to detect how the head moves in 3D space, and it is well-known that this system is sensitive to movement of the head either by linear translation or rotation in three dimensions. The horizontal semi-circular canals are most sensitive to rotation of the head in the azimuthal plane as defined by the rat. Thus, if an animal locomotes a vertical wall, this set of canals will be just as activated when the animal turns its head laterally, as when the animal moves around on the floor, even though the plane of movement with respect to the Earth is different. However, for the otolith organs, the saccule and utricular hair cells would respond differently depending on which planar surface the animal was on – this situation follows from the fact that these organs use an Earth-based reference frame, detecting tilt relative to gravity as well as linear translation. Taken together, mammals contain a set of organs that are ideally suited for detecting how the head is moving in 3D space.

It is also noteworthy, that humans generally have a good sense of where their limbs are located with respect to their body in 3D space. This ability is important for being able to make reaching and reorienting movements to or away from objects near the body. Similarly, most vertebrates, as well as invertebrates, move various body parts in 3D and indicates that motor systems must be representing space in 3D. At the perceptual level, when we are in a

multi-storied building, we have contextual information, as well as the experience of the vertical up/down movements from floor to floor, to provide us with the awareness that we are in a different place in the vertical dimension than when we entered the building on the first floor. We have a perception of our height above the ground, which is similar to how far we might feel from a distal object that is in our 2D planar (horizontal) space. Given all these circumstances, one might ponder why it should be difficult to conceptualize one's perceived spatial orientation or navigate in 3D? Yet, Hayman et al. appear to question just such a notion by suggesting that “our own internal representation of space may be planar and that our sense of having a complete 3D spatial map may be an illusion” (p. 1188).

1) What reference frame were the animals using in the vertical domain?

The rats in the Hayman et al. study appeared to consistently use the room floor, the base of the pegboard, or the first coil of the helix, as their reference frame. On the pegboard task, the animals likely remained in a horizontal or near-horizontal position while they climbed the pegs, with their body's longitudinal axis aligned to the room's floor. Thus, yaw rotations of the head (left and right head turns relative to the egocentric frame) were similar to those made if the rat was on the ground. Note also that the rats' bodies were generally aligned parallel to the pegboard with their four limbs usually oriented toward the floor surface, which was perpendicular to the vertical pegboard surface. With the reference frame as the room and the floor defined as the ‘ground’ surface, then it is not surprising that grid cells may have continued to fire in a hexagonal pattern by extending each of the floor's grid fields vertically to form cylindrical columns. In this way, it is easy to see how a vertical striped pattern was observed, as shown by Hayman et al. in Figure 5B. By extension the same pattern of grid cell firing was seen when the rats traversed the helix and can be accounted for again by extending the grid cell firing pattern on the floor vertically into cylindrical columns. Thus, in both tasks, grid cell firing patterns can be accounted for by simply extending the pattern of firing seen on the floor vertically.

In contrast, place cells appeared to have firing patterns that cannot be accounted for by this simple extension, because about half of the cells fired in an area on the peg board surface that was smaller than a stripe (Hayman et al., Fig. 1f: cells with field sizes of three layers and less, and estimated by pooling the cells in Suppl. Fig. 2). If place cell firing on the vertical pegboard was simply an extension of the floor firing pattern, then fields along the floor at the base of the pegboard should have extended their fields in a stripe-like pattern vertically. While many cells appeared to fire in this manner, many of the cells did not, but rather had well-defined circular fields that resembled those typically seen on the floor. Thus, while place cells that fired in a stripe-like pattern may be extending the horizontal surface vertically, the cells that had discrete fields on the pegboard were mapping the pegboard surface and chamber floor differently.

Place cell firing on the helix appeared more consistent with the vertical column extension hypothesis, as place cells usually fired at discrete locations in the equivalent position on each coil. The spatial representation of the place cells probably reflected the fact that the rats perceived they were either ascending or descending the helix (as opposed to locomoting in continuous circles) because firing was direction dependent, although it is possible the rats were simply distinguishing between clockwise vs. counter-clockwise runs around the helix. Nonetheless, because the incline (or decline) was not substantial (14.4 cm per lap), the rats most likely treated the helix coil floor as the horizontal surface.

It is interesting to contrast these results with those of head direction (HD) cells that have also been tested in the vertical plane, but one where the animal faced into the plane of locomotion, thus having the vertical surface act as a horizontal surface beneath the rat's feet

(Stackman et al., 2000). Under these conditions, the rats either treat the vertical surface as their 'new horizontal' plane (also see Calton and Taube, 2005, Figs. 3 and 6) or HD cell responses remain gravitationally anchored to the Earth's reference frame even as the rat traverses surfaces that are aligned to different orientations. Previous work postulated that HD cell firing rates could be modeled as the surface of a hemi-torus (see Fig. 5C in Stackman et al., 2000; Taube et al., 2004). However, how the hemi-torus is oriented to account for directional firing as the rat traverses different surfaces depends on which of two different reference frames the HD cell uses. In one scheme, the hemi-torus would remain fixed to the animal and when the animal traverses onto a different surface oriented orthogonal to the one it was currently traversing, the hemi-torus rotates with the animal, thus maintaining the same orientation with respect to the rat (Fig. 1A). Alternatively, in the second scheme, the hemi-tours remains gravitationally anchored to the Earth's reference frame and does not shift when the animal changes surfaces and locomotes into differently oriented planes (Fig. 1B). Although each scheme has certain advantages, which one is correct remains to be determined, as present data do not favor one scheme over the other. Returning to how HD cells fired when the rat is locomoting on a vertical wall, Stackman et al. (2000) showed that HD cell tuning curves were identical to those seen when rats locomoted on the floor. Similar findings were also reported both when rats traversed a square-shaped ring that was positioned vertically (Calton & Taube, 2005), and when rats traversed a spiral track that was positioned vertically (Taube et al., 2012).

If the rats in the Hayman et al. study were to treat the pegboard as their horizontal plane by ascending it with their limbs on the vertical surface, it is quite possible that a hexagonal grid firing pattern might have been observed when the animals locomoted the vertical surface. However, if the rats were using the room as their reference frame with the horizontal surface corresponding to the room floor, then the grid cell firing pattern would remain as stripes. Thus, a key experiment would be to monitor grid cells when rats are locomoting on a vertical surface while facing it. Such an experiment makes clear predictions about how grid cells might fire. If they continue to fire in striped patterns (similar to the current results), then this result would be consistent with the view that the grid cell firing is anchored to the room's floor as its horizontal reference frame, as depicted in Hayman et al.'s Figure 5B. However, if grid cell firing reverts to a tessellated grid pattern normally seen on the floor, then this result would suggest that the animals can rotate their horizontal reference frame to align with their plane of locomotion, and has implications for the ability to estimate distance and path integrate in the vertical domain.

Another issue to consider is how the rats arrived on the pegboard. The pegboard was positioned above the floor and the rats had to be placed on it by carrying them from their holding cage. Thus, they were unable to continuously locomote from one environment to the next. In contrast, in both HD cell studies mentioned above, the rats locomoted under their own volition onto the vertical surface – making it relatively easy for them to perceive the transition between the horizontal and vertical surfaces. If the horizontal reference frame is oriented in the plane of the animal's locomotion, then active motion between the two planes may allow the animals to change their defined horizontal reference frame from the floor to the vertical plane. If the reference frame is to the room (and thus the room's floor remains as the horizontal reference frame), then the response on the floor should represent a continuation of the firing rate pattern on the wall sampled in an orthogonal plane. Therefore, if the rats in the Hayman et al. study been allowed to actively locomote from the floor onto the vertical pegboard, they may have defined their reference frame differently.

2) Did the animals perceive their height above the floor? Do they have a cognitive map in the vertical domain?

Hayman et al. suggested that rats might lack a volumetric representation of 3D space because they did not find an accurate allocentric representation of it on the pegboard and helix tasks. This view implies that the rats did not have an accurate representation of their height above the floor surface because the height above the floor was not encoded in the same way as horizontal distance across the floor. However, this view appears to neglect the finding that a significant number of place cells had fields confined to a small region on the pegboard that encompassed only 2 out of the 5 vertical levels, and Hayman et al. indeed noted in their discussion that both place and grid fields were partially height-modulated on both apparatuses, with place cells being more modulated than grid cells. Thus, in theory, this cell population could have been encoding either the height of the animal above the floor or its location on the pegboard in a pegboard-based coordinate frame. Without further manipulations it is difficult to distinguish between these two possibilities. Nonetheless, the finding that there appeared to be two modes for place cell responses (discrete location-specific firing and patches of vertical striped firing) suggests that these two populations of cells may be encoding different aspects of space at the same time – with one population firing based on room coordinates with the floor as the horizontal plane, and the other population encoding discrete locations on the pegboard in a pegboard-based coordinate frame that, in essence, equates to representing the height above the floor.

Several studies have indicated that the place cell population can split and encode two difference reference frames simultaneously (Shapiro et al., 1997; Zinyuk et al., 2000; Knierim & Rao, 2003). For example, Zinyuk et al. (2000) showed how simultaneously recorded place cells fired to different aspects of a spatial task with some cells firing in relation to the rotating platform they were on, while other cells fired in relation to the stationary room reference frame. Moreover, Hayman et al. report that place fields on the pegboard, which were elongated and often vertically spanned most of the pegboard, were rate modulated based on the animal's height above the pegboard bottom (Hayman et al., Suppl. Fig. 3). This finding would suggest that even the elongated responses of these cells may be encoding some information about height. Indeed, Hayman et al. appear to be aware of this issue because in the Discussion section they mention “that height is encoded by these [place] cells, but in a different way.” But if height is being encoded (at least to some extent), then the animals may have a true volumetric representation of space - it just may not be symmetric or linear across dimensions, at least based on these data.

In terms of the spiral helix task, the finding that place cells repeated their firing at the same location on each coil suggests one of two possibilities. First, as suggested by Hayman et al. it is possible the animals lacked a volumetric representation of 3D space and were unable to differentiate which coil they were on. In this case they may not have perceived their height above ground. These results are reminiscent of those reported by Knierim and McNaughton (2001) who reported that hippocampal place cells did not encode the 3D aspects of space when rats traversed a 45° tilted rectangular platform. However, because the helix was transparent (i.e., the rats could see through it) and open on the sides, thus allowing a view of the room, the rats had visual cues available for them to perceive that they were increasing their height above the room floor with each coil traverse. Even assuming place cells were not encoding vertical height information, it is possible that cells in another brain area encoded this variable. We will return to this possibility below.

The second possibility is that the rats used each coil as a reference frame. Consequently, the place cells encoded the rat's position on each coil in a coil-based reference frame, rather than in 3D, and therefore place cells fired in the same equivalent position on each coil. In this

scenario, the apparatus becomes a strong local reference frame for the animals and the cells may have ignored more global height cues. However, closer scrutiny of the results (Hayman et al., Suppl. Fig. 11) indicates that a similar rate modulation based on coil height was also found for place cells on the helix. Taken together, the rate modulations on both the pegboard and helix is indicative that the cells were encoding information about the animal's vertical height, which the authors suggest when they state that 'place cells seemed to be partially modulated by vertical travel distance on the helix, as they were on the pegboard.' Thus, if we assume that these cells play a role in the animal's perception of space, then the animals appear to have some sense of their location in the vertical domain. If this vertical domain perception is true, then it follows that they should also have some conception of 3D space.

In comparison to motion in the vertical plane, it is clear that rats do not have a good representation of space when they are inverted. In the vertical-square-ring track task mentioned above, Calton & Taube (2005) showed that HD cells generally lost their direction-specific firing when the rats locomoted in an inverted orientation. With HD cell firing disrupted, one would expect that the grid cell signal would also be disturbed, since lesions of the ADN, where HD cells are abundant, disrupts the grid cell signal (Clark et al., 2011). More recently, Valerio et al. (2010) used an inverted spatial task where inverted rats were required to locomote along a suspended wire mesh in order to escape into one of four holes where they could right themselves and avoid remaining in an inverted position. They reported that rats were unable to learn this task when released randomly from one of four entry points spaced equally around the periphery. In contrast, the rats were able to learn the goal location when they were started from only one or two entry points, but probe trials revealed that their performance immediately returned to chance when they were released from the platform center (a novel start position). Additional probe trials revealed that the rats were using a directional strategy (Skinner et al., 2003) from the familiar entry points that depended on viewing nearby visual cues. These studies indicate that the rats lacked a flexible, cognitive map-like representation of space, and had a poor, if any, representation of 3D space when they were in an inverted position. Confirming this view, Gibson et al., (2011) in a preliminary report showed that even when rats were able to find the goal when inverted and released from one of the two entry points, HD cells did not show any direction-specific firing on the task. Taken together, HD studies indicate that while it is unlikely that rats contain an accurate representation of space when inverted, it seems probable that they can adequately represent a specific directional heading within the vertical domain, as well as orient toward a goal or landmark when inverted.

Finally, in addressing whether animals, and in particular rats, have a sense of height and a cognitive map in the vertical domain, it is important to recall findings from Stackman and Taube (1998) who reported cells in the lateral mammillary nuclei that were sensitive to the animal's head pitch. These 'pitch' cells encoded the amount the head was tilted in the vertical dimension relative to the horizontal (yaw) plane. All of them were tuned in a manner that their maximal response occurred when the animal's head was pointing straight up. It should be noted that the lateral mammillary nuclei also contain HD cells and is one of the sites that is believed to be the origin of the directional signal (Sharp et al., 2001; Taube, 2007). Theoretically, cells that receive inputs from HD cells and these pitch cells would be capable of representing a direction in the vertical domain.

3) Can animals estimate distance (odometer) in the vertical domain?

Given the absence of a 3D metric, Hayman et al. questioned whether rats have the ability to estimate the distance (odometer) they move in the vertical domain. A behavioral study by Grobety & Schenk (1992) addressed this issue and concluded that rats were aware of the vertical dimension (i.e., height). The authors tested rats' spatial performance in a 3D cubic

maze and in a simplified planar version that was positioned either horizontally, vertically, or at a 45° tilt. The authors found that on probe trials in the cubic maze, the rats searched in the x-y (horizontal) plane at a particular vertical level, rather than going to the proper horizontal plane coordinate and then searching vertically above or below that location. It was as if they knew the correct height above the floor in which to search for the food reward. In the planar versions of the maze the authors also found a similar trend for the rats to search in the correct vertical position and varied their searches within the horizontal dimension. These results strongly suggest that the rats were aware of their height above ground and knew where to search along the vertical axis (although this data would also be consistent with the Hayman et al. notion of context-modulated, planar representations, in which the context is the height of the current level of the rat). Comparable findings in humans were also reported by Hölscher et al. (2006), who showed that subjects seeking a goal in a multi-storied building used a 'floor-first' strategy, where they relied on routes that first sought out the vertical position of the goal (vertical way-finding) before searching for the correct horizontal position.

One important caveat to this discussion is that active motor outflow appears critical for tracking perceived movement in the vertical domain. Whereas both position and velocity estimation are readily accomplished during active and passive motion in the horizontal plane when subjects are gravitationally upright (Israel et al., 1993; Mittelstaedt & Mittelstaedt, 2001; Seidman, 2008), this ability is compromised in the vertical domain during passive transport. For example, humans that are moved vertically in a computer-controlled helicopter or in a vertical motion simulator are unable to judge the correct vertical distance (Malcolm & Melvill Jones, 1974). They perceive that they are moving vertically, but it is difficult for them to determine by how much, particularly at certain frequencies (Melvill Jones & Young, 1978).

Another point to note regarding whether rats have a vertical odometer is that Hayman et al. base their position on a hippocampo-centric view of spatial cognition. In such a view, the hippocampal system lies at the center for spatial cognitive abilities. While it is certainly true that the hippocampus is critically involved in spatial cognition, as well as associative and episodic mnemonic processes, it is well-established that other brain areas play important roles in spatial cognition – particularly with path integration. For example, Shrager et al. (2008) reported that blindfolded human subjects with extensive hippocampal and entorhinal damage were still able to accurately perform a simple path integration task that involved estimating both directional heading and distance. Alyan and McNaughton (1999) showed that animals with hippocampal lesions were still able to perform a homing task that required path integration (cf., Golob & Taube, 1999; Maaswinkel et al., 1999) and Packard & McGaugh (1996) demonstrated the importance of the caudate nucleus for correct spatial responses when the hippocampus was inactivated in rats performing a T-maze task. These findings suggest that other brain areas, including possibly the parietal cortex (Calton and Taube, 2009; Save et al., 2001; Whitlock et al., 2008) or subcortical areas (Frohardt et al., 2006), must be performing these functions. Consistent with these findings, Clark and Taube (2011) reported that HD cells recorded in rats with entorhinal lesions were able to maintain their preferred firing directions when the animals locomoted to a novel environment, suggesting that these animals were still capable of accurate angular path integration (cf., Parron & Save, 2004). While this study does not speak to linear path integration (i.e., one based on location), it nonetheless points out that other brain areas are capable of performing such integrative processes, which are required for angular path integration. Thus, the Hayman et al. animals may have an odometer in the vertical domain (or a sense of their height above the ground), despite whatever conclusions are drawn from the hippocampal recordings.

4) Can animals path integrate in the vertical domain?

Hayman et al. suggested that if odometry is impaired in the vertical domain, then by implication animals should also be unable to path integrate in the vertical plane. Although the findings certainly cast doubt on the extent to which grid cells can represent 3D space, the Hayman et al. results do not address rats' abilities at the behavioral level to path integrate in the vertical plane. As discussed above, rats are capable of keeping track of their angular directional heading within the vertical plane and are also capable of moving about in the vertical dimension accurately to find a food source. But more unequivocal behavioral experiments, which directly test their path integration abilities in the vertical plane awaits future experimentation.

Because of the anisotropic, and less defined place and grid cell response relative to the height of the animal, Hayman et al. suggested that path integration is planar – that is, it only functions within a two-dimensional plane and is a general feature across all terrestrial animals in all settings. This view is difficult to evaluate given current studies, although the absence of identifying a good 3D volumetric spatial representation amongst the different hippocampal spatial cell types would be consistent with this view. If HD cells rotate their horizontal plane of reference to the plane the animals are locomoting in when climbing vertical surfaces, then directional heading remains planar as well and this finding is also consistent. However, if HD cells remain anchored to an Earth-based reference frame, then, as was suggested above for place cells responding in three or fewer layers or having 3D rate coding, the spatial reference may not be planar. In essence, if it can be shown that animals can derive a novel (short-cut) route to a goal in a 3D environment, it would support the view that animals' conception of space is more volumetric and less planar.

Like the pegboard experiment, the fact that human subjects and astronauts in micro-gravity have difficulty in orienting in 3D space (Oman, 2007) is consistent with both the planar and volumetric views of path integration. Under 0-g conditions, the consequent loss of tonic otolith input concerning the position of the head relative to an external reference (usually Earth gravitational) limits the ability to resolve non-planar head movements into their constituent planar components, and makes it difficult to maintain a sense of orientation with the environment. Accordingly, with planar reference, what may be important is which surface is defined as the horizontal reference plane, no matter how this plane is situated with respect to the Earth's reference frame. Therefore, it is possible that path integration is planar, but definitive conclusions await a better definition of the spatial reference frame used by the brain in these conditions.

5) Does processing 3D spatial representations require a large number of neurons?

Hayman et al. contend that forming and maintaining 3D representations require significant more computational power than 2D ones. Any planar subdivision of 3D space requires a way to align and connect the different 2D planes in order to create a representation for volume. As environments become larger and more complex, there are more individual planes needed to represent all the associated landmarks within and across each planar environment. Therefore, a 2D view of spatial representation necessitates a much larger set of neurons to accomplish the representation of a complex 3D environment. Yet, in both marine and terrestrial animals there are numerous examples of organisms that 'make a living' in a 3D world, which have brains that, at least at first glance, do not appear to be any more complex than humans, or for that matter, organized significantly different from rats in areas that are involved in spatial processing. For example, many species of monkeys spend their lives in arboreal environments, where height above ground is a major component of their

spatial representations. To date, we are not aware of any studies showing that arboreal primate brains are dramatically different from other primate species that spend most of their time on the ground (e.g., baboons). Tree squirrels are rodents that live in a 3D world and there are no studies reporting that their brain size (and hippocampus) is different from rats. Indeed, Lavenex et al. (2000a,b) reported that food-caching squirrels showed no seasonal variation in the size of their hippocampus as a function of spatial demand. Moreover, marine mammals, such as otters, seals, and dolphins, are not known to have brains that are organized significantly different from other terrestrial mammals.

Interestingly, it is noteworthy that when these animals navigate their 3D world, it is usually done with their heads in an upright (erect), or near-upright (within 90° of Earth vertical), position. Animals seldom navigate with their heads inverted 180° relative to Earth horizontal. Keeping the head in an upright position might be useful if, as Hayman et al. suggest, the cognitive map is truly planar in nature (although there was no apparent attempt for the rats to keep their heads in an upright position when locomoting on the vertical walls in our HD cell experiments). On the other hand, keeping the head in the upright position may more easily aid the organism in maintaining the alignment of 'up' derived from vestibular otolith information with the visual vertical 'up'. Keeping the head in an upright position also allows for more simpler mechanisms to be used when resolving complex 3D self-motion into horizontal and vertical plane components relative to gravity (Mittelstaedt, 1999; Kaptein & Van Gisbergen, 2005; Clemens et al., 2011).

In addition, birds, which certainly live in 3D environments and contain relatively small sized brains, do not appear to have circuits within the homologous hippocampal region that are significantly more complex or larger (by percentage comparison to the rest of the brain) than mammals, although it is true that food-storing birds, which need to remember where they cached food, have a larger hippocampal complex compared to non-food-storing birds (Krebs et al., 1989; Lucas et al., 2004). But this larger hippocampal size may be more a function of mnemonic requirements than spatial processing ones. Finally, one might argue that because animals that live in an ecologically 3D world do not have significantly larger or differently organized brains than animals that live in more 2D worlds, it might support the notion that no vertebrates truly have a fully developed 3D map. On the other hand, one could also argue just the opposite – that because of this circumstance, all vertebrate brains are capable of handling 3D representations should the need arise. We note that it is not *a priori* that a neural solution for encoding 3D metrics necessarily requires a significantly larger number of neurons. In sum, we urge caution when suggesting that representations of 3D space require larger numbers of neurons and more complex computations to process this type of representation.

Conclusions

In summary, the Hayman et al. findings on the pegboard and spiral coil tasks are interesting and important. To fully appreciate such findings several issues should be considered including 1) the reference frame that the spatial information is related to, 2) whether spatial representations are volumetric or planar, and 3) whether height or vertical distance contributes to the spatial representation. Hayman et al. found that place and grid cells displayed different spatial sensitivities in horizontal and vertical dimensions, but many aspects of the results can be accounted for by considering that the rats were using the room's floor as its horizontal reference plane. In essence, the rats moved about the pegboard with the ventral portion of their body axes aligned with the floor. If the rats had locomoted the pegboard facing inward with their limbs in contact with the pegboard surface, it is possible that different patterns of place and grid cell activity may have been observed. Such a task would also provide insight into how the rats defined their spatial reference frame. By using

the floor as the horizontal reference frame, place and grid cell responses appeared to be vertical extensions of their floor patterns along the vertical pegboard. Finally, before concluding that animals lack an odometer and the ability to path integrate in the vertical plane, it will be important to demonstrate these impairments at the behavioral level, as anisotropic hippocampal representations of space may or may not reflect an impairment in encoding 3D space.

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Figure 1.

Schematic models of HD cell firing when an animal locomotes in the vertical plane. Previous studies have proposed that HD cell firing in 3D can be represented as the surface of a hemi-torus by taking the 2D polar plot and pitching it $\pm 90^\circ$. The model predicts that cell firing will cease abruptly as the animal pitches forward or backward $> 90^\circ$, or for rolls $> 90^\circ$ to the right or left. However, there are two ways in which this model can be anchored to a reference frame. In *A* the model is anchored to the animal and its plane of locomotion. Thus, when the animal moves onto a wall as in *C*, the hemi-torus rotates with the rat and maintains the same spatial orientation to it as it had on the floor. In *B* the model is anchored to the surrounding room and the Earth's gravitational frame. Thus, when the animal moves onto the vertical wall, the hemi-torus does not rotate and remains fixed to the external environment. The red arrow represents the cell's preferred firing direction, which in this case is to the left when the animal is on the floor. When the animal moves onto the left wall (*C left*) the cell's preferred firing direction is oriented straight up, and this occurs for both models. When the animal moves onto the right wall (*C right*) the cell's preferred firing direction is oriented straight down, and also occurs for both models. Thus, both models can account for how a HD cell fires when an animal locomotes in a vertical plane. The two models can be distinguished by monitoring cell firing when the animal traverses a ceiling in an inverted position (Calton & Taube, 2005) and from studies when an animal actively locomotes, or is passively placed, into the vertical plane (Taube et al., 2012). The former study supports an Earth-based reference frame, while the latter study supports a reference frame based on the animal's plane of locomotion.