Navigation Theory Notes

# CognitiveTheory

## Kolarik 2017

**~~Cognitive Map Theory~~** ~~– allocentric representations (combinations of distal cues to infer location) depends on hippocampus (O’Keefe and Nadel 1978) … “~~**~~cognitive map~~**~~” as well as the results of numerous human and rodent lesion studies (Astur et al., 2002; Bartsch et al., 2010; Morris et al., 1982; O’Keefe, 1991; O’Keefe & Dostrovsky, 1971)~~

~~Hippocampal Damage does not impair performance if the cue is at the target location or the animal already learned the trajectory.~~

**~~Precision and Binding Model~~** ~~specifically says high-resolution binding via navigation performance.~~

**~~Declarative Memory Theory~~** ~~(Squire, Stark, & Clark, 2004)?~~

**~~View-matching strategy~~** ~~to overcome any deficits in allocentric memory (Banta-Lavenex, Colombo, Ribordy-Lambert, & Lavenex, 2014).~~ Question: How does view-matching work when dealing with non-spatial information?

**~~Transformation~~** **~~Theory~~** ~~(Winocur, Moscovitch, & Bontempi, 2010; Winocur, Moscovitch, & Sekeres, 2007).~~ **~~Multiple Trace Theory (MTT)~~** ~~(Moscovitch et al.,2005). Transformation Theory (Winocur et al., 2007; Winocur et al., 2010) can be seen as an extension of MTT and suggests that in- itially, all memories are dependent on the hippocampus, but that during consolidation, a memory is transformed into a fundamen- tally different form that is less detailed and more ‘gist-like’.~~

~~Past work has also frequently associated the hippocampal circuitry with a function termed~~ **~~pattern completion/separation~~**~~(Marr, 1971; for a review, see Rolls and Kesner, 2006). This is related to subfield theoretical issues outlined in~~ **~~Complementary Learning Systems~~**~~.~~

## Daugherty 2015

~~For a wide range of organisms, the ability to find a way in a complex environment is arguably a~~ **~~prerequisite for~~** **~~survival~~** ~~(Wolbers and Hegarty 2010).~~

~~Each internal cognitive process that references the cognitive map (i.e., learning, memory, generation, and application of strategy) affects the shape of the navigation path and engenders various degrees of complexity, from which one may infer about the properties of a cognitive map. In ecology, this has been recognized for some time, and the use of~~ **~~path complexity as an index of memory for locations and landmark mapping~~** ~~has been well established (Garcia et al. 2005; Gautestad and Mysterud 2010; Gautestad 2011).~~

~~Migration and~~ **~~foraging paths have a distinct commonality with patterns of human navigation~~** ~~(Hills et al. 2013), and application of FD to the latter may prove as useful as its use in the former.~~

Spatial navigation is a complex cognitive activity that depends on **allocentric and egocentric spatial cues**, **space-specific and general computational mechanisms**, and **spatial representations in real time** and in memory (Wolbers and Hegarty 2010).

## Eichenbaum 2017

~~Edward Tolman (1948) introduced the idea that behavior is driven by memory representations that are organized as a~~ **~~cognitive map~~**~~. Although Tolman’s experiments focused on rats and maze learning, his ideas extended to a broad range of normal and disordered cognition in humans (Tolman 1948), thus clarifying that cognitive maps were not solely for mapping physical space but for a broad range of “~~**~~cognitive space~~**~~.” …; and this conception of cognitive maps applies~~ **~~across domains of cognition~~**~~.~~

~~The~~ **~~connection between the hippocampus and cognitive maps~~** ~~was argued in O’Keefe and Nadel’s (1978) pioneering treatise that reviewed the literature on hippocampal function and physiology.~~

~~The discovery of “~~**~~place cells~~**~~,” neurons that fire when an animal passes through a specific location in its environment, was viewed as providing neural instantiation of the hippocampal map of space (O’Keefe and Dostrovsky 1971).~~

~~According to Gallistel (1990), “Navigation is the process of~~ **~~determining and maintaining a course or trajectory from one place to another~~**~~” (p. 35). The phenomenology of navigation has generated considerable interest in those who study how~~ **~~humans~~** ~~(e.g., Dudchencko 2010; Huth 2013; Wolbers and Hegarty 2010) and~~ **~~animals~~**~~(e.g., Poucet 1993; Trullier et al. 1997) find their way through environments and in the development of~~ **~~robots that navigate~~**~~(e.g., Franz and Mallot 2000; Levitt and Lawton 1990).~~

### Navigation Strategies

**~~local navigation~~**~~, where one can approach a directly observed goal location in the currently perceived environment~~

**wayfinding**, where the goal must be reached by moving beyond immediately perceived space via learned routes or by referring to an internalized cognitive map (Franz and Mallot 2000; Trullier et al. 1997).

~~“~~**~~search~~**~~” without an active orientation toward the goal, which involves simply locomotion and goal recognition without any need for spatial representation (Franz and Mallot 2000).~~

~~“~~**~~target approaching~~**~~” (Trullier et al. 1997) or “~~**~~taxis~~**~~” (O’Keefe and Nadel 1978), which involves~~ **~~orienting and maintaining a body orientation~~** ~~while reaching toward an observable goal (e.g., a visible escape platform in the water maze) or proximal landmark as a surrogate of the goal (e.g., a visible flag over a submerged platform). O’Keefe and Nadel (1978) and Morris (1981) considered taxis as sup- ported by stimulus-response behavior, falling short of consideration as true navigation, although it is kept within the hierarchy of navigational strategies discussed here.~~

~~When the~~ **~~goal itself is not directly observable~~** ~~but instead its location is defined by a spatial configuration of observable non- proximal cues, navigation can be accomplished at the next level by “~~**~~guidance~~**~~” toward the precalculated goal location. … a goal that lies at a particular~~ **~~distance between two landmarks~~** ~~that are not contiguous with the goal (Collett et al. 1986) and the submerged escape~~ **~~platform in a water maze~~** ~~that lies at a location defined by distant cues on the walls of the room (Morris 1981).~~

~~“~~**~~recognition-triggered responses~~**~~” wherein the goal is reached by~~ **~~recognizing and approaching sequential landmarks~~** ~~or places within local environments (Franz and Mallot 2000; Trullier et al. 1997).~~

~~a concatenation of multiple recognition-triggered responses called a “~~**~~route~~**~~,” and when multiple distinguishable routes intersect while maintaining their distinctive paths, they can support “~~**~~topological navigation~~**~~” or “~~**~~route following~~**~~.”~~

~~“~~**~~survey~~**~~” or “~~**~~metric~~**~~” navigation, which requires embedding all known places and their~~ **~~spatial relations~~** ~~into a~~ **~~common frame of reference~~**~~, and can support navigation through~~ **~~novel routes~~**~~, including detours and shortcuts to a goal (Franz and Mallot 2000; Trullier et al. 1997). Survey navigation involves precisely the~~ **~~relational organization of a cognitive map~~** ~~described by Tolman (1948) and adopted by O’Keefe and Nadel (1978).~~

In addition, a recent study of the phenomenon of “**reorientation**” also indicates that the hippocampus employs a survey map even when a simpler strategy based on memory for individual landmarks is sufficient (Keinath et al. 2017). Reorientation refers to t**he ability of navigators to regain their sense of direction after becoming disoriented**. By one view, reorientation is accomplished by **employing a** **cognitive map based on available cues** (Cheng 1986; Gallistel 1990), whereas by another view reorientation can be accomplished by **matching the current view to a remembered, egocentrically defined landmark** (Pecchia and Vallortigara 2010).

Notably, the creation of **distinct representations for overlapping maze routes** is not universally observed, and specifically is **not observed when rats are trained to run in both forward and reverse directions in a Y-maze** (Lenck-Santini et al. 2001), when each leg of a journey is guided by signals and rewards (Bower et al. 2005), and when rats are trained only on delayed alternation (Ainge et al. 2007a).

~~O’Keefe and Nadel (1978) viewed the~~ **~~rodent hippocampus as dedicated to mapping physical space~~**~~; they allowed that the~~ **~~human left hemisphere evolved to map semantic space~~**~~. Buzsáki and Moser (2013) raised a similar argument, suggesting that the~~ **~~hippocampus~~** ~~and closely associated areas~~ **~~originally evolved as a dedicated spatial navigational system, but in humans was co-opted to support a broader role in mapping memories~~**~~. However, there is substantial evidence that hippocampus is essential to~~ **~~creating cognitive maps of physical and abstract space in nonprimates~~**~~, including~~ **~~birds~~** ~~(Lazareva et al. 2015) as well as~~ **~~rats~~** ~~(Bunsey and Eichenbaum 1996) and mice (Devito et al. 2010), indicating a general role in cognitive mapping across spatial and nonspatial domains among diverse mammalian species.~~

~~navigation in humans and animals … use of~~ **~~both topological navigation (route following) and survey navigation (cognitive maps).~~** **Brain imaging studies** have identified **hippocampal activation in London taxi drivers** as they employ learned maps of the city to navigate (Maguire et al. 1997; Maguire et al. 1998), and these experiments have distinguished the activation of the **hippocampus in** wayfinding by survey navigation from activation of the **caudate nucleus in route following** (Hartley et al. 2003; Iaria et al. 2003). … **human hippocampus is preferentially involved in survey navigation**. … primarily … during the **building and updating of cognitive maps rather than the expression of well-learned maps** (Rosenbaum et al. 2000; Suthana et al. 2009; Teng and Squire 1999; Wolbers and Büchel 2005; see McNamara and Shelton 2003), and these findings are **confirmed in studies on rats** (Tse et al. 2007; Winocur et al. 2005).

# Technical Issues

## Kolarik 2017

~~High~~ **~~sampling rate~~** ~~of navigation is critical for more advanced analyses (See last paragraph of p7).~~

~~Target proximity is a good measure but may miss information.~~

## Daugherty 2015

~~To answer a question of potential influence of path geometry on navigation time, a common practice has been a~~ **~~visual inspection of individual paths~~**~~(i.e., Sei et al. 1992; Moffat and Resnick 2002).~~

~~Based on variable definitions, a~~ **~~search path may be classified~~** ~~as direct or indirect, spatial or nonspatial~~ ~~(Davis et al. 2010), or assigned to any category depending on the researcher’s interest. Such an approach is subjective, and creating nominal classes produces little statistical variability, thus limiting options for analysis and interpretation.~~

~~Counting the number of~~ **~~path crossings~~**~~(Buzsaki 2005) is a third alternative that offers more statistical flexibility. The sum of path crossings is thought to reflect path tortuosity, with a larger number indicating compromised spatial cognition.~~

**~~Heading error~~** ~~is not an index of search path complexity but has been used to infer decision-making processes in the MWM based on navigation accuracy~~ ~~(i.e., Smith et al. 2013).~~

~~Since the introduction of~~ **~~fractal geometry~~**~~(Mandelbrot 1967), FD has been applied to the study of many natural and behavioral phenomena, including patterns of animal migration and~~ ~~grazing (Garcia et al. 2005; Gautestad and Mysterud 2010; Gautestad 2011).~~

## Eichenbaum 2017

~~Notably, a~~ **~~major exception to the focus on simple behavioral tasks~~** ~~is recent work on firing properties of hippocampal neurons in~~ **~~bats as they navigate long distances to find food in a real-world environment~~**~~(e.g., Geva-Sagiv et al. 2015; Sarel et al. 2017).~~

# Neuroanatomical

## Kolarik 2017

Indeed, some models suggest a gradient for representational precision along the **long axis of the ~~hippocampus~~** ~~with higher precision being represented more posteriorally and coarse representations anteriorally~~ ~~(Fanselow & Dong, 2010; Nadel, Hoscheidt, & Ryan, 2013).~~

~~There are also models that would predict that right hippocampal damage would disproportionately impair per- formance compared to left hippocampal damage (Burgess, Maguire, & O’keefe, 2002).~~

~~Our findings are thus consistent with previous data showing that after right hippocampal lesions, some spatial memory can persist even after a delay (Bohbot et al., 1998).~~

## CLS 2016

~~Indeed, information about the spatial (e.g.,~~ **~~place~~**~~) and non-spatial (e.g.,~~ **~~what~~** ~~happened) aspects of an event are thought to be processed primarily~~ **~~by parallel streams~~** ~~before~~ **~~converging in the hippocampus~~** ~~at the level of the~~ **~~DG/CA3 subregions~~** ~~[Knierim, J.J. and Neunuebel, J.P. (2016) Tracking the flow of hippocampal computation: pattern separation, pattern comple- tion, and attractor dynamics. Neurobiol. Learn. Mem. 129, 38–49].~~

~~Evidence suggests that the~~ **~~dentate gyrus (DG) subregion of the hippocampus performs pattern separation~~**~~, orthogonalizing incoming inputs before~~ **~~auto-associative storage in the CA3~~** ~~region [131–137].~~

~~the~~ **~~CA3 subregion is crucial for pattern completion~~** ~~– allowing the output of an entire stored pattern (e.g., corresponding to an entire episodic memory) from a partial input consistent with its function as an attractor network [138,139]~~

~~inputs from neocortex produces a pattern of activation in the~~ **~~ERC~~** ~~that may be thought of as a~~ **~~compressed description of the patterns in the contributing cortical areas~~**

~~Several studies point to differences between the CA3 and~~ **~~CA1~~** ~~regions in how their neural activity patterns respond to changes to the environment [37]: broadly, the~~ **~~CA1 region tends to mirror the degree of overlap in the inputs from the ERC~~**

## Daugherty 2015

~~The Hc has been traditionally considered a neural substrate of MWM navigation, in which~~ **~~smaller volumes account for longer distances and time traveled by older adults~~**~~(see Maguire et al. 1999 and Moffat 2009 for reviews).~~

## Eichenbaum 2017

~~Some studies have shown that~~ **~~hippocampal damage impairs path integration~~** ~~(Whishaw and Maaswinkel 1998; Whishaw et al. 2001), and others have reported~~ **~~intact path integration in animals with hippocampal damage~~** ~~(Alyan and McNaughton 1999; Benhamou 1997). It is important to acknowledge that~~ **~~path integration is not advised in real-world navigation~~**~~, precisely for the reason that it is so~~ **~~prone to accumulated error~~** ~~(Dudchencko 2010; Huth 2013). Notably,~~ **~~humans with hippocampal damage were not impaired in path integration, whereas rats with hippocampal damage were,~~**

Moreover, **grid cell firing patterns degrade in the dark**, indicating their activity does not solely reflect self-generated cues argued to be the basis of path integration (Chen et al. 2016). ~~Cells that signal a~~ **~~vector toward an intended goal~~** ~~have been observed in~~ **~~bats~~**~~(Sarel et al. 2017)~~

The results show that **humans with hippocampal damage perform as well as normal control subjects** in guiding movements through space **by reading from maps**, using online spatial computations that successfully orient them from the map to the real world (Urgolites et al. 2016).

~~neurons that fire in association with~~ **~~head direction~~**~~(Ranck 1984; Taube et al. 1990) and~~ **~~grid cells~~** ~~in the~~ **~~medial entorhinal cortex (MEC)~~** ~~that fire when rats traverse a~~ **~~spatially periodic array of locations~~**~~, as well as~~ **~~MEC head-direction cells~~** ~~and~~ **~~cells that signal~~****~~borders and speed~~**~~(see Hartley et al. 2013; Kropff et al. 2015).~~

Amnesic patients also succeeded in **tests of memory for previously seen targets** from **new viewpoints** (Shrager et al. 2007), memory for a **start location and distance from the start location** (Shrager et al. 2008), and **computations supporting path integration** (Kim et al. 2013; discussed above), as long as the accumulated spatial information could be **held in working memory**.

**~~recording studies~~** ~~in~~ **~~animals~~** ~~showing that hippocampal networks link associations among object memories by both~~ **~~spatial and nonspatial dimensions in rats~~** ~~(McKenzie et al. 2014) and organize memories via a mappin~~**~~g of the time course of events in a memory independent of space in rats, monkeys, and humans~~** ~~(Kraus et al. 2013, 2015; Naya and Suzuki 2011; Pastalkova et al. 2008; Paz et al. 2010; Spiers et al. 2001). …~~ hippocampal networks also **map an auditory space** in rats trained to identify a specific frequency in a signal composed of a tone ramping in pitch (Aronov et al. 2017).

### Temporal Order and Hippocampus

~~There is also compelling evidence that the~~ **~~hippocampus plays an essential role in organizing memories in time~~**~~. In humans,~~ **~~hippocampal damage results in a greater deficit in memory for the order of events than in memory for the events themselves~~**~~(Dede et al. 2016).~~

~~Also, several~~ **~~functional imaging studies~~** ~~have shown that the~~ **~~hippocampus is activated~~** ~~during~~ **~~encoding~~** ~~and~~ **~~retrieval~~** ~~of the~~ **~~order of events~~** ~~in memories, independent of memories for the events themselves (reviewed in Eichenbaum 2014).~~

~~Similarly, in rats,~~ **~~selective hippocampal lesions result in impairments in memory for the order~~** ~~of a sequence of~~ **~~nonspatial stimuli~~**~~, even when memory for the stimuli themselves is spared~~ ~~(Fortin et al. 2002; Kesner et al. 2002).~~