Title: The role of mental maps in decision-making

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Summary: A growing body of work is investigating the use of mental maps during decision-making. Here, we will discuss how decision-making organizes experiences according to an internal model of the current task, thereby structuring memory. Likewise, we will consider how the structure of mental maps contributes to decision-making.

Keywords: hippocampus, entorhinal cortex, decision-making, medial prefrontal cortex, state space, cognitive map

Memory processes transform experiences into mental maps

In the late 1940s, the American psychologist Edward Tolman discovered that memories formed in a spatial maze were not mere reflections of an animal's experience. Rather, animals appeared to encode relations between locations that were never directly experienced [1]. Crucially, these transitive relations informed decisions when newly opened paths afforded shortcuts. Tolman hypothesized that the animals had formed a **cognitive map** (see Glossary) of the environment during encoding—a mental representation of the relative locations of objects and boundaries in their environment [1]. Decades later, this idea is still guiding our understanding of **place and grid cells**, spatially tuned neurons in the hippocampus and entorhinal cortex respectively, which encode the relations between different locations and environmental boundaries in a dynamic and continuous manner [2]. Intriguingly, recent evidence has shown that similar neural mechanisms could be involved in encoding the relationships between nonspatial conceptual representations characterized by continuous features [3,4] and also, more generally, imagination [5,6]. Here, we will discuss evidence suggesting that map-like encoding mechanisms may be a widespread phenomenon in the brain and can potentially facilitate the interaction between decision-making and memory.

How decision-making influences cognitive maps

Memory is an organism's capacity to store and retrieve previously encountered information, a function which is anatomically linked with the hippocampus in mammals. Memory durability after **encoding** is affected by factors such as time and previous knowledge. Yet, how ongoing decision-making affects our mental mapping of different experiences remains unclear. Investigating how decisions might bias memory, one study found that a decision-making task can bias which elements of an experience are stored in memory [7]. Participants were instructed to react to the location of a stimulus, but the task also featured an unmentioned relationship between stimulus color and the correct response that could be exploited to complete the instructed task. Although the color-response relation was simple and experienced over 700 times, two-thirds of participants failed to learn it. In order to understand the neural origin of this failure to learn, the authors tested whether prefrontal areas encoded color information throughout the experiment. Notably, whether medial prefrontal cortex (mPFC), an area that has been shown to be critical for decision-making [8], encoded stimulus color information predicted participants' learning and use of the uninstructed color-response relation. This suggests that aspects that are relevant for the current decision making task are mirrored in (medial) prefrontal representations of events. These representations in turn seemed to be linked to memory formation.

More recent work has explored how decision-relevant information is encoded in the brain by using a task in which decisions were based on partial information from the current and the past trial [9]. In particular, faced with ambiguous stimuli participants had to use memory of the past trial in order to decide which image category they need to pay attention to in the current trial, and then make a decision about this category only [9]. Multivariate pattern classification analyses showed that all necessary information from past and present trials was represented within orbital (ventral) mPFC and that errors during the task were preceded by a deterioration of this representation. This representation reflected the current **hidden state of the task,** and effectively signalled the 'location' of the participant in a cognitive map of the task's **state space—**analogous to a neural position signal within a spatial environment (Figure 1).

To summarize, these results suggest that decision-making is governed by dedicated task state representations encoded in the medial network of prefrontal cortex, and our ability to encode new information is highly influenced by this internal map of the current task. This idea poses questions about the precise form of interaction between memory processes and state space representations that reflect the current decision making task. This question is particularly pertinent since mPFC is highly connected to the hippocampus, contains grid-like representations of conceptual and geometric space (see below), and is known to contain economic value representations during decision-making [8].

Using spatial representations to organize a decision space

Conversely, memory can guide how we make decisions. While much decision-making research has taken a 'non-episodic' perspective on memory and focused on the storage of *aggregate* information about the desirability of different choices (i.e. value representations), recent evidence has shown how map-like representations can influence decision-making. One example is **mental exploration—**the ability to evaluate the potential outcomes related to different choices before implementing a particular decision (see Box 1 for info on decision-making and replay of place representations). The dynamics of mental exploration were recently highlighted by neuroimaging studies focusing on how humans imagine the spatial layout of an environment [5,6]. These studies leveraged knowledge about the firing properties of grid cells [10] and investigated a 60 degree directional modulation of the fMRI signal in entorhinal cortex during virtual navigation. This analysis allowed the authors to test whether grid-cell like mechanisms were also involved during imagined navigation. Indeed, after training participants to learn object locations in a virtual environment [5] or building locations in a virtual city [6], these studies found that participants exhibited grid-like fMRI signals in the entorhinal cortex when imagining themselves reorienting back towards a previously visited location [5,6].

Interestingly, a recent study has indicated that grid-like neural codes may also be used to form a map of conceptual non-spatial knowledge [4]. During fMRI scanning, human participants associated a bird silhouette of varying neck and leg lengths with specific objects. Crucially, participants were unaware that bird neck and leg length-dependent stimulus-outcome relationships were organized in a two-dimensional conceptual space [4]. Providing evidence for grid-like coding of conceptual space, the authors found that entorhinal and mPFC fMRI signals responded to 60 degree modulation of the two dimensions of bird silhouette space during learning. This result supports the idea that similar neural codes are used for conceptual as well as spatial mental maps. Following previous studies relating the coherence of grid-like fMRI signals to spatial memory performance (see [10] for an example), the study also linked the robustness of grid-like responses to subjects' decision-making ability [4]. Taken together, these results implicate the use of grid-like neural representations during decision-making. Additionally, these data highlight potentially shared neural coding mechanisms between entorhinal cortex and mPFC (also see [10]), where grid-like task space representations in these regions might partition multidimensional goal-directed decisions into relevant subtasks that lead to completing the goal. However, it is still unclear whether entorhinal cortex and mPFC make separable contributions to representing complex decision spaces, and how grid-like versus non grid-like representations relate to the task state representations discussed above. Fully determining how and when memory and decision-making processes might converge in a common representational format in medial temporal and medial prefrontal brain areas will be a crucial question for future research (Figure 1).

How cognitive maps can inform decision-making in novel environments

Another emerging area is how cognitive maps might inform decision-making in novel environments. Letting participants' use their internal model of the physical world, a recent study had participants visually search novel mazes for the shortest path to a goal location [11]. Mazes contained one or two choice points and participants needed to quickly (~1-3 s) determine the correct choice(s) to follow the shortest path. When planning sequential choices, rostrodorsal mPFC (rd-mPFC) selectively responded to computationally demanding choices that were later in a sequence of choices [11]. Interestingly, hippocampal activity peaked and was synchronized with rd-mPFC during planning in mazes that afforded sequential choices and extensive deliberation [11].

Why would rd-mPFC-hippocampal interactions increase during planning in novel environments? One possibility is that we use previous experience as a template to predict novel situations [12]. Consequently, engaging mental maps in novel environments would then help restrict state space search—leading to more robust and efficient decision-making.

Concluding Remarks

In the decades since Tolman theorized that "learning consists not in stimulus-response connections but in the building up in the nervous system of sets which function like cognitive maps" [1], there has been a large body of work investigating how neurons in the hippocampal formation encode an internal map of the physical world. Here, we highlight recent studies extending the idea of cognitive maps to non-physical conceptual [3] and decision-making spaces. This evidence suggests that neurons in the mPFC and hippocampal formation (including entorhinal cortex) might employ similar neural mechanisms that contribute to decision-making processes like forming a decision state-space, vicarious evaluation of potential options, and representing conceptual relationships parametrically. Mechanistically, we suggest that cognitive map-like neural computations can help the brain extract structure from our previous experiences in order to guide future decisions, as well as impose structure on the encoding of new experiences.

Box 1: Influence of cognitive map reactivation on decision processes

In order for past experience to inform decision-making, different learned representations must be readily available for reactivation. **Hippocampal sharp-wave ripple** (SWRs) oscillations (~80-200 Hz) co-occur with the reactivation of place cell ensembles representing previously visited locations, in the order which they were visited. Ripples occur during slow-wave sleep and epochs of quiet wakefulness, time periods putatively linked with memory consolidation. A recent study showed that hippocampal SWRs were accompanied by selective excitation of mPFC neurons that were encoding task-relevant locations during spatial exploration [13]. Further linking the reactivation of learned spatial representations with efficient decision-making, it has been observed that **vicarious trial and error (VTE)** behavior—where a rat pauses at a choice point and turns serially toward their potential routes of travel—is inversely related to hippocampal SWRs [14]. Additionally, ripples selectively influence endogenous fMRI signal fluctuations in the default network, a collection of synchronized brain regions—including hippocampus, mPFC, posterior cingulate cortex, and temporo-parietal junction— that are also involved in decision-making and episodic memory [15]. Taken together, these findings provide evidence that endogenous neural fluctuations in the hippocampus and other regions might reflect the maintenance and modulation of cognitive maps.

Figure 1: How experiences and tasks are transformed into cognitive maps.

The figure illustrates how, for any given situation, various aspects of experience might be encoded as different configural neural representations in the hippocampal formation (including medial entorhinal cortex, MEC and hippocampus, HPC), and orbital and medial prefrontal regions (, for simplicity referred to as mPFC). In the example, a person stands at a street corner in New York, trying to cross the street. The person's relative spatial location might be represented in the hippocampal formation, whereas the current state in the ongoing task (street crossing) might be reflected in state representations in mPFC. Note that the neural basis of spatial memory representations in HPC and MEC are relatively well understood, but considerably less is known about the neural populations involved in state or conceptual representations. Given that task information and previous decisions both influence spatial representations and memory, the way different memory and decision spaces interact poses an important question in neuroscience (see text). Recent evidence suggesting that grid-like representations could be employed in mPFC for the representation of continuous non-spatial relationships [4] offer an intriguing window into the interaction of memory and decision-making related representations in the brain.

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Glossary:

Cognitive map-Mental representation that an individual uses to acquire, maintain, and retrieve about the relative locations and attributes of phenomena in their everyday or metaphorical spatial environment.

Place cell-A type of neuron within the hippocampus that becomes active when an animal enters a particular location within an environment. Place cells are thought to collectively act as a neural representation of a particular environment, known as a cognitive map.

Grid cell - A location-modulated neuron that selectively activates when an animal enters a set of periodic triangular locations covering the entire environment. Grid cells are found most commonly in the dorso-medial entorhinal cortex and are thought to form an essential part of the brain's navigation system.

Encoding- The process of converting an item of interest into a construct that can be stored or mapped in the brain.

Hidden states- A collection of information relevant to a given decision. This information is difficult to distinguish based on sensory input alone.

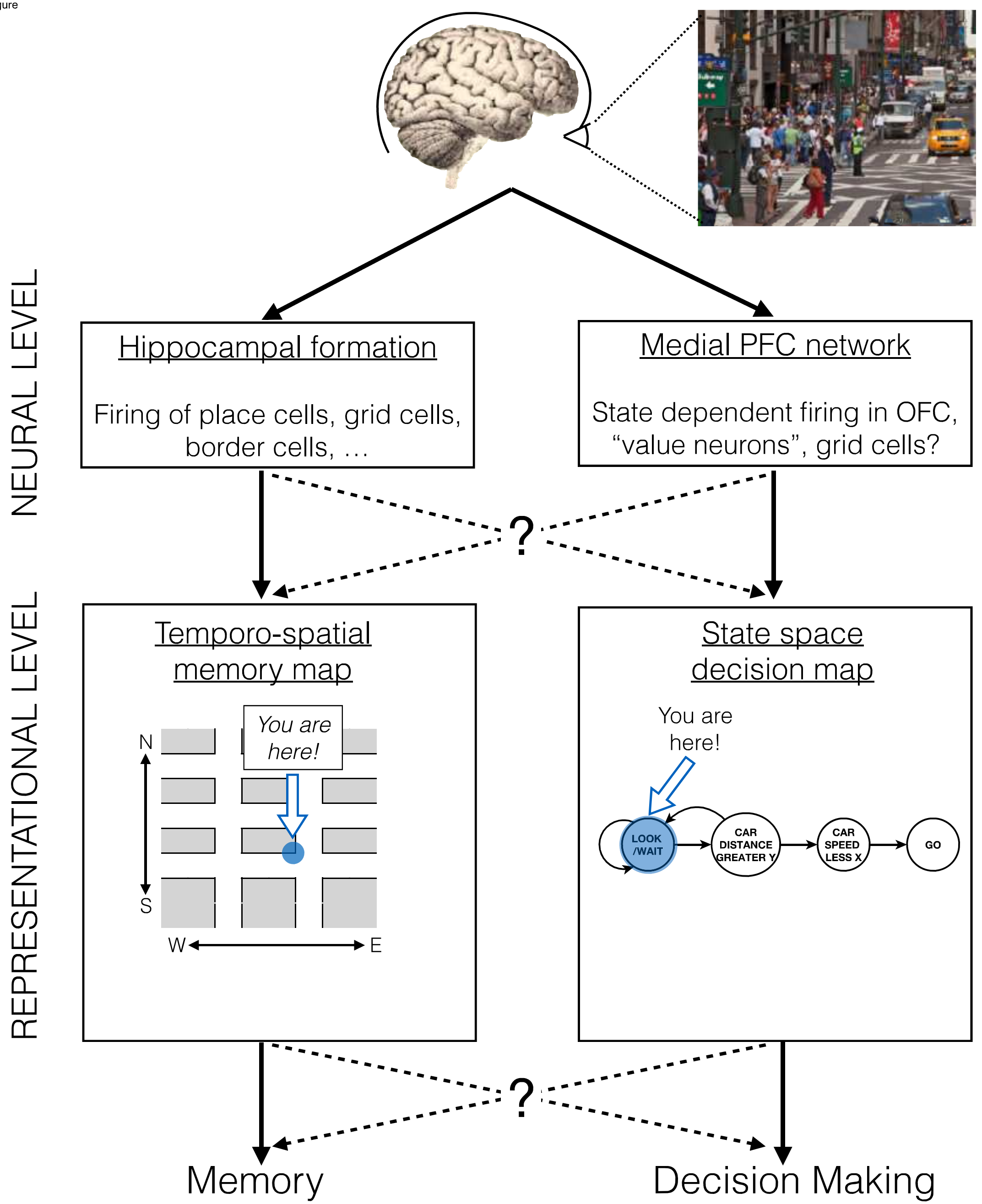
State-space - The set of all possible states of the environment that are relevant for a given task, including the relations or possible transitions between these states.

Mental exploration-Planning or imagining a sequence of actions in order to achieve a novel goal.

Hippocampal sharp-wave ripple-A large deflection in the hippocampal local field potential that is accompanied by a high frequency oscillation (typically >100 Hz) lasting approximately 200 ms during epochs of quiet wakefulness and slow-wave sleep. Notably, rapid reactivation of hippocampal place cell ensembles co-occurs with ripples and is associated with mental exploration and memory consolidation.

Vicarious trial and error- A behavior typically observed in rodents that occurs when the animal is stopped at a choice point in a maze, where they frequently pause and turn serially toward their potential routes of travel.-

Figure


NEURAL LEVEL
REPRESENTATIONAL LEVEL
Hippocampal formation
Firing of place cells, grid cells, border cells, …
Medial PFC network
State dependent firing in OFC, “value neurons”, grid cells?
?
Temporo-spatial memory map
You are here!
N
S
W
E
State space decision map
You are here!
LOOK /WAIT
CAR DISTANCE GREATER Y
CAR SPEED LESS X
GO
?
Memory
Decision Making