

environment which are then used for predicting future inputs, a hypothesis which requires feedback [9] and permits the (re)appearance of representations [10]. Memory in this sense is not for processing the past, but for predicting the future. In this context, the data of van Kerkoerle and colleagues open up challenging questions, including: When is working memory encoded and retrieved and what is the temporal capacity of the neuronal mechanisms? How could this activity support a complex stimulus that is represented invariantly in higher cortex but represented retinotopically in early visual cortex? How does this activity shape the processing of new sensory signals? There are multiple memory systems in the brain; what function does cortical memory support? Which mechanisms underlie working memory and which ones allow for longer-term storage? Do the observed activity traces contribute to the divergent reconstruction of memory [6] or are they part of storage? Cortical areas engaged in perception may retain the information that they initially represent in a feedforward manner. However, the data of van Kerkoerle *et al.* [5] imply something more complex than a mere persistence of sensory representation because the working memory activity they observed was both fed back and reappeared after a mask. Internal models could use memory to reinstate a sensory representation, as if drawing lines in the sand after a wave of sensory inputs. Ultimately, these lines drawn into the sand might hold clues to understanding one's mind.

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## Forum

# The Role of Mental Maps in Decision-Making

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

## 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 still guides our understanding of **place** and **grid cells** – spatially tuned neurons in the hippocampus and entorhinal cortex, respectively, that 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 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.

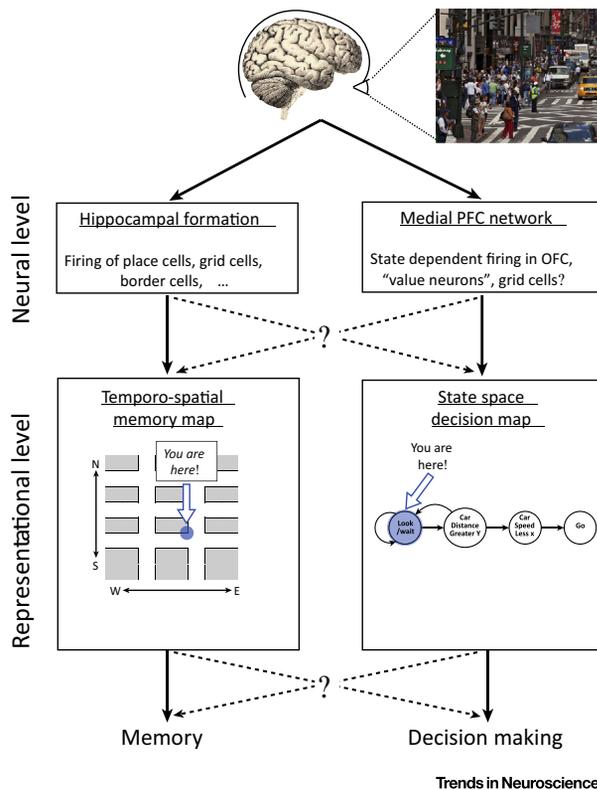
## How Decision-Making Influences Cognitive Maps

Memory is an organism's capacity to store and retrieve previously encountered information, a function that is anatomically linked with the hippocampus in mammals. Memory durability after encoding is affected by factors such as time and previous knowledge. However, 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. To understand the neural origin of this failure to learn, the authors tested whether prefrontal areas encoded color information throughout the

experiment. Notably, whether the 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 to decide which image category they needed 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 the orbital (ventral) mPFC and that errors during the task were preceded by deterioration of this representation.



**Figure 1. How Experiences and Tasks Are Transformed into Cognitive Maps.** The figure illustrates how various aspects of experience might be encoded as different configural neural representations in the hippocampal formation [including the medial entorhinal cortex (MEC) and the hippocampus (HPC)] and orbital and medial prefrontal regions [for simplicity referred to as the medial prefrontal cortex (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 the mPFC. Note that the neural basis of spatial memory representations in the HPC and MEC are relatively well understood, but considerably less is known about the neural populations involved in state and conceptual representations. Given that task information and previous decisions both influence spatial representations and memory, the way that 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 the mPFC for the representation of continuous nonspatial relationships [4] opens an intriguing window onto the interaction of memory- and decision-making-related representations in the brain.

## Glossary

**Cognitive map:** a mental representation that an individual uses to acquire, maintain, and retrieve information about the relative locations and attributes of phenomena in their environment.

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

**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 dorsomedial entorhinal cortex and are thought to form an essential part of the brain's navigation system.

**Hidden states:** a collection of information relevant to a given decision. This information is difficult to distinguish based on sensory input alone and therefore 'hidden'.

**Hippocampal sharp-wave ripple (SWR):** 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.

**Mental exploration:** planning or imagining a sequence of actions to achieve a novel goal.

**Place cell:** a type of neuron in 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.

**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.

**Vicarious trial and error (VTE):** a behavior observed in rodents that occurs when the animal is stopped at a choice point in a maze, where it frequently pauses and turns serially towards its potential routes of travel.

This representation reflected the current **hidden state** of the task and effectively signaled 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 orbitofrontal/medial network of the PFC, 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 the 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 information 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° directional modulation of the fMRI signal in the entorhinal cortex during virtual navigation. This analysis allowed the authors to test whether grid-cell-like mechanisms were also involved during imagined navigation. 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 2D conceptual space [4]. Providing evidence for grid-like coding of conceptual space, the authors found that entorhinal and mPFC fMRI signals responded to 60° modulation of the two dimensions of bird silhouette space during learning. This result supports the idea that similar neural codes are used for conceptual and spatial mental maps. Following previous studies relating the coherence of grid-like fMRI signals with 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 the entorhinal cortex and the 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 completion of the goal. However, it remains unclear whether the entorhinal cortex and mPFC make separable contributions to representations of complex decision spaces and how grid-like versus non-grid-like representations relate to the task state representations discussed above. Full determination of 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 choices to follow the shortest path. When planning sequential choices, the rostradorsal 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 the 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

#### Box 1. Influence of Cognitive Map Reactivation on Decision Processes

For past experience to inform decision-making, different learned representations must be readily available for reactivation. **Hippocampal sharp-wave ripple** (SWR) 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 towards its 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 the hippocampus, mPFC, posterior cingulate cortex, and temporoparietal 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.

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 nonphysical conceptual [3] and decision-making spaces. This evidence suggests that neurons in the mPFC and hippocampal formation (including the 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 to guide future decisions as well as to impose structure on the encoding of new experiences.

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