Hippocampal hierarchical networks for space, time, and memory

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The hippocampus is critically involved in both mapping space as well as the formation of memories for events. Here, we propose that common coding principles in the hippocampus enable spatial, temporal and episodic representations. We discuss recent studies employing novel cognitive tasks as well as newly developed representational analysis techniques which show that both spatial and mnemonic representations can be thought of as networks of interlinked elements, be it locations in space or events in memory. These mnemonic networks share certain characteristics, such as plasticity and hierarchical organisation, which enable structured representation of information while also allowing simultaneous assimilation of new elements. We conclude by outlining possibilities of how neural mechanisms underlying the formation of such networked representations can support the organisation of interlinked information beyond time and space.

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Introduction

The hippocampal formation has a well-established role in both episodic memory and internal representation of space [1,2]. However, the exact nature of its involvement is still under debate. At the heart of the debate is the type of information represented by the hippocampal formation, and whether identical coding mechanisms underlie the formation of these representations. According to one influential theory, the hippocampal formation codes for a detailed map-like representation of space, to which other non-spatial elements of episodic memories can be bound during encoding [2,3]. Another prominent theory posits that both spatial and non-spatial information is represented as networks of related events in the hippocampus [4,5,6•], in a so-called memory space. In line with this theoretical viewpoint, computational modelling [7] as well as experimental evidence [8] suggests that the hippocampus is involved in extracting and representing regularities that hold across episodes. Besides this, mnemonic networks may represent conceptual [9,10•,11•,12] and temporal information [13•,14–16] as well. We will briefly outline commonalities in spatial and mnemonic representations, and then discuss the mechanisms which enable their formation. We conclude by proposing that the representation of these networks is not restricted to spatial, episodic and temporal information, but rather reflects domain general computations.

Spatial representations in the hippocampal formation

It is well established that the hippocampal formation, which consists of the hippocampus and entorhinal cortex, is involved in representing space [3]. More specifically, the hippocampus contains so-called place cells, which fire when an animal enters a particular location in the environment [17]. On the other hand, the entorhinal cortex, a cortical region one synapse away from the hippocampus, contains cells that fire in response to multiple locations which are arranged in a hexagonal pattern that tiles the entire environment (the so-called 'grid cells') [1].

The same cells can represent different configurations of locations within different environments through the process of remapping [18,19]. Remapping can also be induced through changes in the task or goals, and may provide a link between coding of space and coding of events. For example, Moita *et al.* showed that, after conditioning, firing of hippocampal neurons became synchronised to the onset of a conditioned stimulus, suggesting that hippocampal neurons are also responsive to non-spatial stimuli [20]. Additionally, this provides evidence that hippocampal place cells are dynamic and can remap due to changes in experience [18,21].

Intracranial recordings in pre-surgical epilepsy patients exploring virtual reality (VR) environments, have confirmed that place [22] and grid cells [23] are also found in human hippocampus and entorhinal cortex, respectively. In addition to electrophysiological evidence, we have reported systems-level fMRI responses in participants

navigating in VR environments, which are consistent with the population response of place cells [24] and grid cells [25,26,27•,28•] in the rodent hippocampal formation. Furthermore, connectivity studies in humans are indicative of a highly similar subdivision of the entorhinal cortex in rodents and humans [29,30]. These findings not only indicate that spatial representations in humans are implemented similarly to those of rats, but also that fMRI can be a useful tool to probe such representations.

Together, the place- and grid-cell system forms the basis of the brain's navigation system [3]. This system seems to be hierarchically organised with functional subdivision along the hippocampus, corresponding to the posterior-anterior axis in humans and dorsal–ventral axis in rodents, respectively [31,32]. The size of place fields increases along the long axis of the rodent hippocampus [33,34], and the size of the grid fields, as well as the spacing between the vertices of the grid, also increase along the same axis of rodent mEC [1,35,36]. There are also differences in connectivity along the hippocampal long axis [37,38]. There are several theories regarding the function of multiple spatial scales in the hippocampal formation [31,39]. This simultaneous representation of the same location at multiple spatial resolutions may underlie our ability to represent our environments along hierarchically organised internal maps: ranging from smaller scales [24,40,41], such as our homes, to progressively larger scales [41,42], such as our neighbourhoods, and even our cities (see part b of Figure 1).

Episodic memory representations

The distinction between local and global is not only relevant for representation of space, but also for episodic memory because it is important to have detailed memories as well as memories at a coarser mnemonic resolution. The range of mnemonic resolutions may serve to organise memories into hierarchical memory networks. For such memory networks to arise, incoming information needs to be integrated with pre-existing knowledge [43,44], or otherwise linked with other information, which can occur through both shared spatial context [45•,46•], and shared temporal context [13•,14,15,45•]. Additionally, episodic memories can be linked through shared event context [16,47] shared narrative context [48,49•,50•], or through shared features (e.g. people involved, types of activities, similar objects) [9,49•,51,52•,53] while being far apart in space and time.
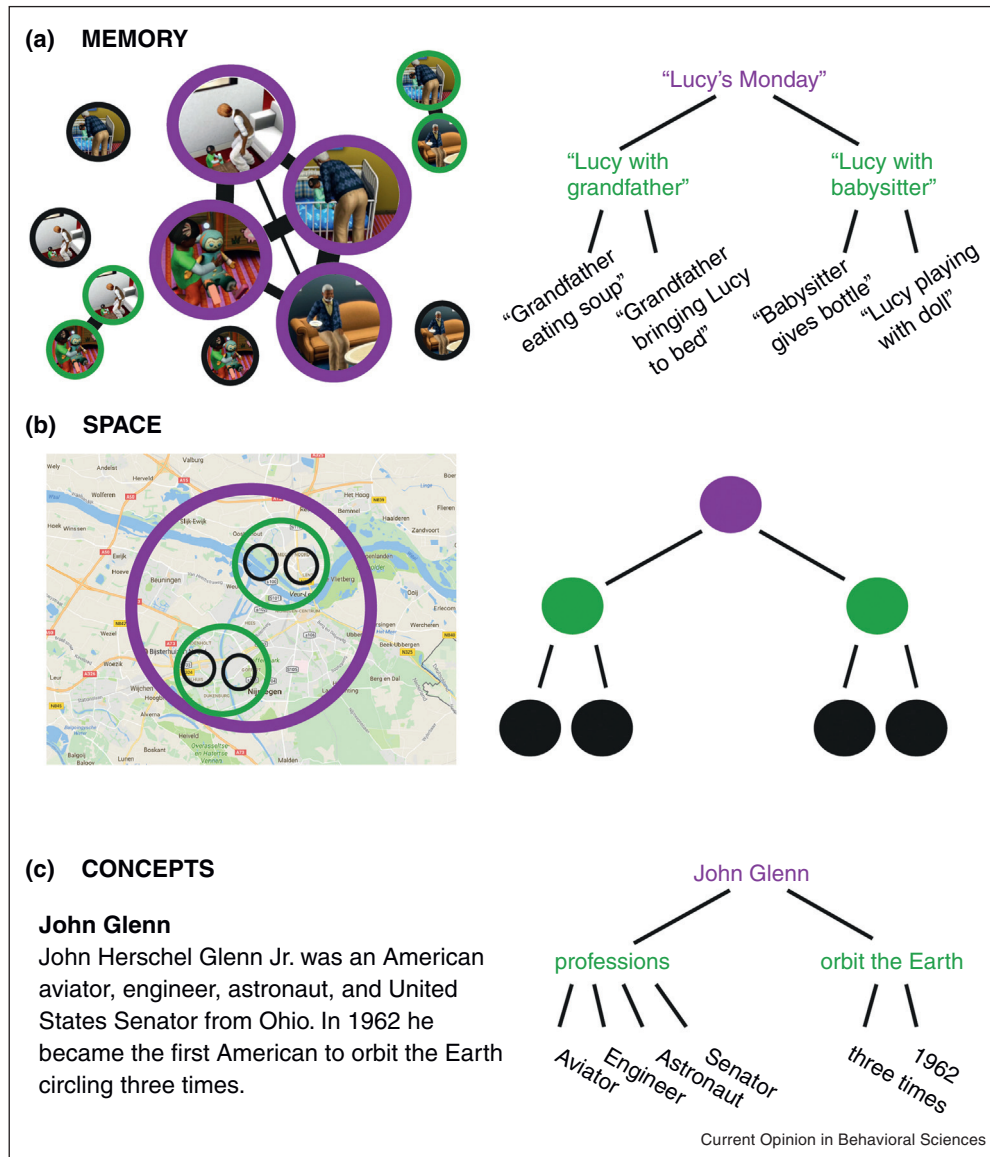
Even though we cannot visualise neural representations of memories (i.e. 'engrams') using noninvasive neuroimaging in humans, we can visualise the organisational structure of the relationships between different mnemonic representations and a number of recent studies have made large strides at mapping the structure of emerging representations in both memory [48,50•,53–57] and space [19,28•]. These studies have used

multivariate pattern-based analyses (such as representational similarity analysis [58] or pattern component modelling [59]) or repetition suppression paradigms [10•,25,57] to define the structure of internal representations of events and event elements. The analysis logic for multivariate pattern analyses is based on the idea that mnemonic elements which are closer together in the memory 'space' would also evoke more similar patterns of neural activity. Thus, by examining the patterns evoked by different experimental conditions (e.g. different events), we can visualise the distance between conditions in an internal representational space.

The hypothesised memory networks are comprised of partially overlapping events, where the nodes of the networks consist of mnemonic elements, such as people, objects, spatial or temporal contexts [4,6•,9,60]. In our recent study, participants watched a movie with two interleaved narratives in the MRI-scanner. We examined whether overlapping event elements in those narratives also evoke more similar internal representations of those events. We showed that events which featured particular characters or locations were associated with more similar hippocampal activity patterns than other events. Those results suggest that characters and locations in a movie indeed form nodes of memory networks. In addition to nodal representations, we also found evidence that hippocampal representations of separate storylines from the movie gradually diverge over time [49•]. These results suggest that the hippocampus also represents larger groupings of events, akin to narrative contexts, in separate networks. These findings may relate to how different hippocampal cell assemblies represent different spatial contexts, whereas the process of remapping allows for switches between the contexts as a consequence of pattern separation processes [18,61].

We have also tracked the emergence of small-scale narrative event networks in the posterior hippocampus in a study where participants saw initially unrelated events that, over the course of the experiment, became linked through a new event. The formation of those networks of events was triggered by insight into how previously unrelated events fit together [48]. We showed that patterns of hippocampal event representations became more similar between non-overlapping events once they became linked through a new event [48]. To investigate more complex narratives, we presented participants with multiple unrelated events which were linked into larger narratives. Here we discovered that, in addition to the small-scale networks in the posterior hippocampus, the scale of these event networks increased along the long axis of the hippocampus, with anterior hippocampus providing coarser event representations corresponding to the multi-event narratives. These results suggest that memories may indeed be organised into networks of related events, and follow a similar hierarchical

Figure 1

We propose that multiple cognitive domains rely on similar mechanisms for organising information in the brain. **(a)** Episodic memories can be organised as a hierarchy with an entire experience as highest hierarchical level, and more specific events within these experiences as lower levels of the hierarchy. **(b)** Space can be organised as a hierarchy, with large sections of the environment as highest hierarchical level, and more detailed sections of the environment as lower levels of the hierarchy. **(c)** Also conceptual knowledge can be organised as a hierarchy, with an entire concept as highest level of the hierarchy, and more specific facts related to this concept as lower levels of the hierarchy.

organisation like space (see part a of Figure 1) [5,50•,53]. This is consistent with a global versus local spatial distinction along the hippocampal long axis as proposed in Poppenk *et al.* [39]. Thus, the same neural mechanisms that create hierarchical representation of space may also underlie our ability to think of past events at different memory scales, ranging from the smallest meaningful units — such as accidentally spilling coffee during breakfast — through progressively coarser scales — such as having breakfast, what we did in the morning, and how we spent the day.

Memories in time

It is well established that the hippocampus represents temporal context [13•,14,15], and since the discovery of phase precession of place cells [62] and hippocampal time cells [63], it has become clear that both the hippocampus and medial entorhinal cortex code for time as well as space [64]. Furthermore, representations of items presented close together in predictable temporal sequences have more similar neural patterns than items presented in unpredictable sequences [14], suggesting that known temporal context binds those items together. The role

of the hippocampus for integration of information across time is also suggested by increased hippocampal activity, positively correlated with subsequent memory, at event offsets [65]. Interestingly, shared event context can override temporal context for item grouping [47]. Nevertheless, when the across-event items were judged to be closer in time, their neural patterns were also more similar [47,66[•]], perhaps suggesting that temporal and event contexts are partially independent but can interact. Similarly, we have shown that although items linked through spatial or temporal context vary in representational similarity as a function of spatial or temporal distance, these two types of contexts also interact with each other [45[•]]. Comparable effects have been reported for real-life autobiographical memories [46[•]].

However, what remains to be seen is whether temporal scales are also represented in a similar manner in the hippocampal formation. One might predict that anterior hippocampus in humans or the ventral hippocampus in rodents may code for a global temporal context, while more posterior/dorsal regions code for shorter time scales [63,64]. In the example above, we effectively described progressively wider event contexts in the temporal domain, however, it is not clear whether these memory scales indeed represent temporal context in the same way as narrative context, the topic of the research reported in recent work [49[•],50[•]]. When it comes to sensory information, different brain regions accumulate information differently across time, with early visual cortex representing short time scales while higher-order visual areas represented longer time scales, while no variation with temporal scales was reported in the hippocampus [13[•]]. However, even naturalistic stimuli used in an experimental setting do not match true temporal scales, which leave the question about potential hippocampal involvement in hierarchical temporal processing of episodic memory unanswered.

Networks beyond the memory domain
In this review we have discussed leading theories, computational modelling, and recent neuroimaging work that suggest that the hippocampus does not only represent memories of individual events but also represents memories as networks of related events [2,4,5,45[•],48,49[•],50[•], 51,52[•],67–69]. This suggests that spatial and episodic memory rely on similar coding principles necessary for the formation of hierarchical networks in the hippocampus (Figure 1). We propose that these coding principles may also support formation of networked representations unrelated to events or space. A particularly interesting question is whether these neural mechanisms, which lead to hierarchically organised spatial and mnemonic representations, also provide a neural metric for other types of related information, for example the structure of conceptual knowledge in the brain (Figure 1). Research has indeed shown critical involvement of the hippocampus in the emergence of conceptual knowledge [10[•],11[•],12].

However, the exact structure of knowledge representations in the brain is still under debate. Some evidence suggests that neural mechanisms underlying navigation through space also underlie navigation through conceptual space (of bird stimuli) that are defined through two continuous dimensions [10[•]].

An efficient representation of knowledge needs to be dynamic to enable flexible switching between building new entries and integrating information into existing structures. Furthermore, knowledge should transfer to new situations. Thus, knowledge systems need to rely on efficient organisational principles. One such organisational principle could be hierarchical coding which use the same underlying neural populations and can remap between different contexts (or concepts). Future research needs to focus on whether representing knowledge in network structures, similarly to how the brain represents spatial and event maps, reflects the actual mechanisms by which the brain can efficiently store and update knowledge. Additionally, future research should address whether the hippocampus is primarily necessary for the formation of conceptual knowledge as hierarchical networks, and which other brain regions play a role in the retrieval and long-term storage of these hierarchical networks [70].

Concluding remarks
In this review, we discussed hippocampal computational mechanisms that are known to be important for representing the environment as well as representing experiences. Research on space and episodic memory indicates that the hippocampus can represent small-scale, detailed information, and larger-scale, more general information in parallel. All available information about the environment, as well as our experiences, is structured into dynamic networks that can flexibly incorporate new information through mechanisms such as remapping. We proposed that these computational mechanisms are combined to enable the brain to organise space as well as episodic memories into dynamic hierarchical structures. We concluded with reviewing recent literature on the emergence of conceptual knowledge and proposed that these computational mechanisms might not only underlie spatial and episodic representations, but could reflect neural mechanisms for organisation of interlinked information more generally. This has the potential to significantly increase our understanding about the coding mechanisms of the brain for cognition in general.

Conflict of interest statement
Nothing declared.

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