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Introduction

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The role of hippocampal predictions in cognition: bridging perception and memory

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Memory allows us to use existing knowledge to understand what we are currently perceiving and what we may experience in the future. Despite these intricate links, research on perception has historically been separate from research on memory. This theme issue focuses on the hippocampus, a brain region essential for memory, to determine how hippocampal memories enable predictions that link the past to the perceptual present. The articles discuss how hippocampal memories support prediction and perception across domains, including visual exploration, learning, navigation, inference and event cognition. The research spans computational modelling, behavioural studies, animal neurophysiology and human neuroimaging. Together, this work highlights how predictions bridge the gap between memory and perception, revealing the interplay between what we see and remember.

This article is part of the theme issue 'The role of hippocampal predictions in cognition: bridging perception and memory'.

1. Introduction

The hippocampus plays a crucial role in many domains of cognition. Although it is most frequently studied for its roles in long-term memory [1–4] and navigation [5–8], recent research has established that it contributes to a diverse array of cognitive functions that were initially seen as outside the realm of the hippocampus. These functions include perception [9–14], attention [15–17], working memory [18–21], event segmentation [22,23], statistical learning [24,25], scene construction and imagery [26,27], eye movements [28–30] and inference [31–34]. What unifying set of computations might underlie these different functions [35–39]? Here, we propose that the hippocampus is exquisitely suited both to learn predictive associations [40–42] and to exploit these associations to guide perception and behaviour [43–46]. Although prediction is a ubiquitous function of the brain [47–49], the hippocampus excels in rapidly learning arbitrary associations and using those to make predictions at multiple timescales [41,50–53].

This perspective suggests a reconsideration of the link between memory and perception. We propose that memory and perception are intimately linked through prediction [54,55]. Memory is used to generate predictions of upcoming perceptual events [56,57], and mismatches between those predictions and incoming percepts determine how we update our memories [58,59]. Despite these links, memory and perception have traditionally been studied separately. An emerging trend in recent neuroscience research challenges this separation, arguing that the hippocampus is better understood not as

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a system specialized for long-term memory, but as one that sits at the interface of perception and memory, learning complex associations over space and time in the service of perception and prediction [35–39,60]. Supporting this perspective, the hippocampus generates predictions and prediction errors across diverse cognitive domains, from prospective theta phase precession in navigation [61] to successor representations in cognitive maps [62,63].

The articles in this theme issue serve to both review this burgeoning line of work and provide new empirical evidence that demonstrates how hippocampal predictions support perception, memory and memory-guided behaviours. The presented research spans the gamut of cognitive neuroscience methodology, from psychophysics to computational modelling, and from animal neurophysiology to human neuroimaging. Below, we will discuss the topics covered in this issue in more detail.

2. Overview of the theme issue

It has been suggested that the hippocampus is crucial both for (i) learning about predictive information in the environment [25,64,65], and (ii) using this information to guide cognition and behaviour [43,44,56]. Roughly the first half of the theme issue is primarily focused on *learning*, and the second half on *predicting*. Within the *learning* section, we differentiate error-driven learning and learning of regularities (i.e. statistical or sequence learning). This distinction highlights the relative focus of the articles but should not be taken to indicate a boundary between these forms of learning. Indeed, error-driven learning plays an important role in statistical learning [41]. Within the *prediction* section, we differentiate generating predictions and using predictions, recognizing that in practise these functions are tightly linked.

(a) Error-driven learning

A major trigger for learning is prediction error: when things are not as we expect, we should update our model of the world. The first three articles in this theme issue focus on the role of hippocampal prediction errors in perception, and the next three on how prediction errors modulate memory updating.

Being exposed to new information can radically alter our perception of ambiguous information, such as in the case of the famous Dalmatian dog image [66], or other so-called Mooney images [67,68]. Völler *et al.* [69] discuss how such sudden perceptual learning may trigger large prediction errors, the resolution of which leads to a new perceptual interpretation of a previously ambiguous image. They propose that the hippocampus is crucially involved in this process, particularly when it comes to the perceptual disambiguation of detail-rich images.

Prediction errors serve an important role in aligning memory and perception: when hippocampal predictions mismatch sensory inputs, the former should be updated based on this prediction error. Based on cross-species evidence, Medina *et al*. [70] propose complementary roles for the hippocampus and the claustrum, with the two structures jointly shaping the prediction error signal.

Thus, the work of Völler *et al.* and Medina *et al.* [69,70] highlights the importance of prediction errors in linking perception and memory; but how does the hippocampus compute such perceptual prediction errors in the first place? Warrington & Kok [71] present high-resolution 7T functional magnetic resonance imaging (fMRI) data investigating this question, focusing on the different hippocampal subfields and their interaction with the neocortex. They find that during statistical learning of perceptual predictions, the dentate gyrus preferentially represents unexpected rather than expected sensory inputs. This coding of perceptual prediction errors in the dentate gyrus elucidates the hippocampal circuit underlying error computation.

Prediction errors are powerful because they provide a learning signal: when our predictions are violated, our internal models of the world have to be updated, so we can make better predictions in the future. The next three articles investigate the role of such error-driven learning in the context of long-term memory.

Previous work has shown that prediction errors can both weaken existing memories [58] and induce false ones [59]. Yang *et al*. [72] used naturalistic videos to investigate how memory change depends on the age and strength of memories. Contrary to classical systems consolidation theory, they find that prediction-error driven malleability is determined not by age but by the strength of the memory at reactivation.

Prediction errors can be defined in two ways: objective prediction error (factual mismatch between retrieved and perceived information) and subjective estimates of prediction error (how confident you are about being right). Complementing Yang *et al.*'s [72] finding that low-strength memories were most susceptible to updating after prediction errors, Shi *et al*. [73] show that larger objective errors and lower confidence independently predict memory updating. Their fMRI findings reveal dissociable neural circuits that process objective error under low and high confidence. This work, therefore, demonstrates how subjective confidence can gate which neural circuits support memory updating based on objective prediction error. These findings highlight the importance of considering subjective assessments of learning, with implications for education and memory rehabilitation.

There is an apparent paradox in the idea that prediction errors drive the greatest learning: we also remember events that closely match our expectations. This has led to the proposal of complementary roles for the hippocampus in encoding unexpected information and the medial prefrontal cortex (mPFC) encoding expected (i.e. schema-congruent) information [74]. Raykov *et al*. [75] put this 'schema-linked interactions between medial prefrontal and medial temporal regions (SLIMM)' framework to the test using fMRI. They find the expected U-shaped function linking memory encoding to expectedness, with both very unexpected and very expected events being remembered well. However, they do not find evidence for complementary roles of the hippocampus and mPFC. These null results invite a re-examination of the SLIMM framework, suggesting that the neural

basis of the behavioural U-shape may depend not only on encoding-related activity but on post-encoding consolidation and retrieval processes, as well as factors such as the nature of the expectancy violation and the stage of learning.

(b) Sequence/statistical learning

The hippocampus is especially adept at learning sequences of stimuli or events that occur with statistical regularity [24,41,76]. What are the computational mechanisms underlying this exquisite ability, and how does it relate to another canonical hippocampal function: the encoding of individual events (i.e. episodic memory)?

Earlier, we proposed that the hippocampus is particularly well suited for rapidly learning and updating associative memories to guide predictions at multiple timescales. If the structure of our environment suddenly changes (e.g. a frequently taken route is blocked), the hippocampus may support rapid updating of our internal world model, so that we can behave adaptively in the future. Tarder-Stoll *et al*. [77] used fMRI to investigate how the hippocampus updates its representations of multi-step sequences upon presentation of novel information that links previously unconnected sequences. They find that the hippocampus rapidly integrates newly connected sequences, and that this hippocampal integration is associated with individuals' ability to behaviourally update their predictions. This work demonstrates the dynamical nature of hippocampal sequence representations, and its ability to rapidly update memories to guide predictions.

Thus, the hippocampus is involved in learning sequential regularities, but this function seems to be at odds with its ability to store distinctive representations of unique events [78,79]. The next two articles focus on how the hippocampus balances learning of statistical regularities with learning of individual events (episodic memory)—functions that are thought to have opposite computational demands, emphasizing commonalities (pattern completion) versus unique features (pattern separation), respectively [80].

Singh & Schapiro [81] explore the balance between these two functions at the neural circuit level with computational modelling. Using a biologically grounded neural network model of the hippocampus, C-HORSE, they show that these functions are implemented in different hippocampal circuits. Specifically, the trisynaptic pathway (EC -> DG -> CA3 -> CA1) is ideally suited to encode the details of individual events, whereas the monosynaptic pathway (EC -> CA1) is especially adept at extracting regularities across multiple events. Next, Zhou *et al*. [82] show that the balance between these functions can be tipped by stress, which drives the hippocampus to prioritize statistical prediction over episodic encoding. Their fMRI data suggest that stress drives the hippocampal monosynaptic pathway (EC -> CA1) to perform statistical learning, in line with the computational modelling of this pathway by Singh & Schapiro [81].

(c) Generating predictions from memories; mechanisms

Having considered how the hippocampus learns predictive signals in the environment, this theme issue now turns to how the hippocampus uses this information to generate predictions. The next four articles examine the neural mechanisms by which the hippocampus generates predictions from memories.

Nalluru *et al*. [83] put forward the intriguing proposal that the hippocampus can be characterized as a generative model of sensory information. Perception is often characterized as an inferential process that involves estimating the hidden causes underlying the sensory data we receive [47,84]. That is, we need to infer from the spatial pattern of retinotopic activation what kind of object may have caused that pattern. Nalluru *et al*. [83] propose that the hippocampus represents such latent, unobserved causes of sensory data, and crucially is able to invert them to generate hypothetical sensory samples that would have been observed should these causes be present—predictions, effectively. This exciting proposal has implications for the role of the hippocampus in cognition and adaptive behaviour. It also yields clinically relevant predictions by discussing how disruptions to latent cause inference may underlie some of the symptoms observed in psychosis.

Bein & Davachi [85] discuss the neural circuit whereby the hippocampus generates predictions, as well as prediction errors, focusing on high-resolution fMRI research studying the hippocampal subfields. They discuss that different types of predictions may be generated by different subfields, and that the generation of prediction errors depends on goal relevance. Ultimately, this leads to a view whereby the hippocampal subregions promote adaptive predictive processing.

There is a puzzle at the heart of the proposal that the hippocampus generates predictions about future inputs. Namely, memories of associations are generally symmetric: I associate hearing a siren with seeing an ambulance, and seeing an ambulance with hearing a siren. However, to predict forward in time, this symmetry needs to be broken in order to generate a directed sequence of events in time. Wagner *et al*. [86] present a computational model of how the hippocampus balances stable, symmetric memories with symmetry breaking in service of generating predictive sequences.

(d) Using predictions to guide cognition and behaviour

The preceding section examined how the hippocampus generates predictions; the next asks how those predictions are used to guide cognition and behaviour.

The next two articles discuss the use of hippocampal predictions in planning future behaviour, specifically in the context of navigation. That is, using predictions to generate plausible simulations allows one to consider the best path going forward. A particular focus in this field has been the role of hippocampal theta oscillations [61]. Damphousse *et al*. [87] propose that each hippocampal theta cycle starts with a representation of the present state followed by sweeps along possible future paths. These future paths are then evaluated in the ventral striatum and orbitofrontal cortex, enabling optimal decision-making.

Robinson *et al*. [88] similarly consider how the hippocampus and entorhinal cortex may scan future trajectories. They explain the role of episodic memories in generating such trajectories and avoiding collisions with known objects and boundaries in the environment. This perspective also explains several types of representations recently observed in the human hippocampus, such as boundary cells and egocentric bearing cells. Together, these two papers offer mechanistic insights into how known hippocampal coding schemes—theta sweeps and trajectory scanning—may link simulated paths with current sensory input to guide navigation.

In addition to enabling simulations, hippocampal predictions may also directly influence overt behaviour. Ladyka-Wojcik *et al*. [89] propose an intimate link between hippocampal predictions and eye movements. Specifically, they suggest that eye movements are a means by which the hippocampus generates, tests and updates predictions about the visual world in real time. The authors bring to bear evidence from computational modelling, neurophysiology and neuroimaging to outline the neural mechanisms whereby the hippocampus and oculomotor control systems can engage in bidirectional interactions. This intriguing perspective suggests that eye movements do not merely guide visual processing but also play a central role in memory updating and prediction.

To make optimal predictions, we need to know which set of memories best applies to our current situation. This requires us to identify and select the correct 'cognitive map' to guide decisions. Although the notion that the hippocampus generates predictions based on cognitive maps is not new [50,62], Shi & Garvert [90] argue that in complex and ever-changing real-world environments a single cognitive map is insufficient. Rather, the brain must maintain multiple maps and decide which one to use depending on the context. The authors propose that the hippocampus and orbitofrontal cortex work together to arbitrate between these cognitive maps, and that this process may be disrupted by anxiety.

(e) Meaning

Ultimately, cognitive neuroscience aims to shed light not only on how the brain generates behaviour, but also on how it gives rise to the subjective mental states that characterize the human mind. The final, and perhaps most interdisciplinary, article of this theme issue bridges neuroscience and philosophy to propose a novel perspective on how meaning emerges in the brain. Maurer *et al*. [91] consider how the crucial role of the hippocampus in sensory processing may not only optimize behaviour but also imbue sensory signals with meaning. Specifically, they propose that meaning is an emergent property of large-scale, recurrently connected networks in which the hippocampus acts as a key hub linking information across modalities, timescales and contexts. The authors outline the core principles required for meaning to arise and show how neural systems—particularly hippocampal–cortical interactions—instantiate these principles.

3. Conclusion and future directions

Together, the articles in this theme issue converge on an emerging view of the hippocampus as a predictive system that uses spatiotemporal structure to support diverse cognitive functions. Its influence pervades our interactions with the world, from the moment-to-moment sampling of sensory input via our eye movements to higher order representations of the causes, consequences and meaning of sensory events. Hippocampal memories are not merely records of the past: they allow us to adaptively behave in the present and plan for the future, showing the intimate links between memory, perception and prediction. By virtue of lying at the interface between perception and memory, the hippocampus serves as a cornerstone of flexible behaviour, with disruptions to the hippocampus having widespread consequences for adaptive functioning.

This new lens on the hippocampus yields many exciting directions for future work. Recognizing that the hippocampus may have more in common with its visual inputs than initially conceived [44], recent work has used visual neuroscience methods to examine retinotopic coding in the hippocampus itself [92–95]. Such work can build on studies exploring hippocampal representations of future navigational paths [87,88] and guidance of eye movements [89] by exploring how hippocampal coding for relevant regions of visual space can guide selective attention, perception and planning. Applying a more expansive view of hippocampal function can also motivate the use of biologically inspired computational models of the hippocampus [81] to better understand functions beyond memory, such as perception [96]. Finally, recent technological advances in mobile neuroimaging [97], including in intracranial electroencephalography [98] and optically pumped magnetometer-based magnetoencephalography [99,100], allow tracking of hippocampal activity as human participants walk around. Such advances can allow unprecedented insights into the moment-by-moment dynamics by which the hippocampus uses memory to inform perception, and vice versa, to support adaptive predictions and goal-directed behaviour. Importantly, this predictive framework may also inform the development of novel interventions for individuals with memory disorders, by focusing on supporting the dynamic use of memory to generate predictions that guide perception and behaviour. Such approaches could use external aids, computational models, or neurostimulation techniques to scaffold predictive processing in everyday contexts. For example, interventions that capture and replay structured representations of everyday experiences—such as wearable or smartphone-based memory augmentation tools (e.g. [101])—may help scaffold the use of past experience to generate predictions about ongoing and future events, thereby supporting adaptive behaviour even when memory is impaired.

To conclude, in this theme issue, we aimed to use hippocampal prediction as a means to bridge the gap between memory and perception, revealing the interplay between what we see and what we remember. We expect this will allow researchers in different fields to interact and learn from each other, promoting new understanding and novel research avenues.

4. In memoriam – Eleanor Maguire

At the core of this theme issue is the view that perception and memory are inherently intertwined, and that to understand cognition one must investigate the dynamic interplay of perception and memory as they unfold over space and time. These principles were exemplified in the pioneering work of Eleanor Maguire (1970–2025), whose creative and innovative work pushed the boundaries of the field's knowledge of the hippocampus and invited novel conceptualizations of its function. Here, we share a brief tribute in honour of her work and how much she inspired us, both with her research and with her exuberant passion for the field. We also refer readers to heartwarming tributes written by close colleagues (e.g. [102,103]) and a forthcoming special issue of *Neuropsychologia*[1].

Throughout her career, Eleanor's work constantly challenged traditional views of the role of the hippocampus in cognition. Her contributions range from creative studies of unique populations such as her world-famous investigations of hippocampal structure in London taxi drivers [8,104,105] to methodological innovations like studying hippocampal signals using OP-MEG [99,106]. Her diverse methods, tasks and findings led to comprehensive theoretical proposals outlining hippocampal contributions to novelty detection [107], construction of imagined future experiences [108], autobiographical memory [4] and scene perception and imagery [26,109,110]. Ultimately, she put forward the intriguing and unifying view that the hippocampus contributes to these myriad cognitive processes because of its essential role in scene construction [111,112]. In recent years, Eleanor emphasized the need for understanding memory in the wild [113], leading her to establish a novel research programme in which she used OP-MEG to study hippocampal activity in mobile participants [99]. In embracing new techniques, she was always led by objective scientific evidence rather than subjective preferences. For instance, having long been sceptical of automated labelling of hippocampal subfields in MRI, she was ultimately convinced when robust inter-rater reliability measures demonstrated the accuracy of modern automated protocols [114]. That willingness to be changed by evidence, even on questions she had long settled in her own mind, was the mark of her rigorous scientific character.

Beyond her science, Eleanor was a rare kind of colleague—one who asked you about your life outside the laboratory, who made time for those facing professional as well as personal challenges and who championed women in science not just in word but in deed. Her keen scientific mind improved countless experimental designs, papers and research programmes, often without fanfare. In her understated and generous way, she became one of the most influential voices in the cognitive neuroscience of memory. Her influence on the field, and on the researchers she inspired, will be felt for generations.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.A.: conceptualization, writing—original draft, writing—review and editing; M.B.: conceptualization, writing—original draft, writing—review and editing; P.K.: conceptualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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