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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

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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.

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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.

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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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References

1. Scoville WB, Milner B. 1957 Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* **20**, 11–21. (doi:10.1136/jnnp.20.1.11)
2. Squire LR. 1992 Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol. Rev.* **99**, 195–231. (doi:10.1037/0033-295x.99.2.195)
3. Eichenbaum H. 2004 Hippocampus: cognitive processes and neural representations that underlie declarative memory. *Neuron* **44**, 109–120. (doi:10.1016/j.neuron.2004.08.028)
4. Bonnici HM, Chadwick MJ, Lutti A, Hassabis D, Weiskopf N, Maguire EA. 2012 Detecting representations of recent and remote autobiographical memories in vmPFC and hippocampus. *J. Neurosci.* **32**, 16982–16991. (doi:10.1523/JNEUROSCI.2475-12.2012)
5. O'Keefe J, Nadel L. 1978 *The hippocampus as a cognitive map*. Oxford, UK: Clarendon Press.
6. Burgess N, O'Keefe J. 1996 Neuronal computations underlying the firing of place cells and their role in navigation. *Hippocampus* **6**, 749–762. (doi:10.1002/(SICI)1098-1063(1996)6:6%3C749::AID-HIPO16%3E3.0.CO;2-0)
7. Moser EI, Kropff E, Moser MB. 2008 Place cells, grid cells, and the brain's spatial representation system. *Annu. Rev. Neurosci.* **31**, 69–89. (doi:10.1146/annurev.neuro.31.061307.090723)
8. Maguire EA, Gadian DG, Johnsrude IS, Good CD, Ashburner J, Frackowiak RSJ, Frith CD. 2000 Navigation-related structural change in the hippocampi of taxi drivers. *Proc. Natl Acad. Sci. USA* **97**, 4398–4403. (doi:10.1073/pnas.070039597)
9. Martin CB, Barense MD. 2023 Perception and memory in the ventral visual stream and medial temporal lobe. *Annu. Rev. Vis. Sci.* **9**, 409–434. (doi:10.1146/annurev-vision-120222-014200)
10. Graham KS, Barense MD, Lee ACH. 2010 Going beyond LTM in the MTL: a synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia* **48**, 831–853. (doi:10.1016/j.neuropsychologia.2010.01.001)
11. Aly M, Ranganath C, Yonelinas AP. 2013 Detecting changes in scenes: the hippocampus is critical for strength-based perception. *Neuron* **78**, 1127–1137. (doi:10.1016/j.neuron.2013.04.018)

[1]https://www.sciencedirect.com/special-issue/326685/the-constructive-mind-commemorating-eleanor-maguire

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12. Kok P, Turk-Browne NB. 2018 Associative prediction of visual shape in the hippocampus. *J. Neurosci.* **38**, 6888–6899. (doi:10.1523/JNEUROSCI.0163-18.2018)
13. Ruiz NA, Meager MR, Agarwal S, Aly M. 2020 The medial temporal lobe is critical for spatial relational perception. *J. Cogn. Neurosci.* **32**, 1780–1795. (doi:10.1162/jocn_a_01583)
14. Billig AJ, Lad M, Sedley W, Griffiths TD. 2022 The hearing hippocampus. *Prog. Neurobiol.* **218**, 102326. (doi:10.1016/j.pneurobio.2022.102326)
15. Aly M, Turk-Browne NB. 2016 Attention stabilizes representations in the human hippocampus. *Cereb. Cortex* **26**, 783–796. (doi:10.1093/cercor/bhv041)
16. Mack ML, Love BC, Preston AR. 2016 Dynamic updating of hippocampal object representations reflects new conceptual knowledge. *Proc. Natl Acad. Sci. USA* **113**, 13203–13208. (doi:10.1073/pnas.1614048113)
17. Günseli E, Aly M. 2020 Preparation for upcoming attentional states in the hippocampus and medial prefrontal cortex. *eLife* **9**, e53191. (doi:10.7554/eLife.53191)
18. Olson IR, Page K, Moore KS, Chatterjee A, Verfaellie M. 2006 Working memory for conjunctions relies on the medial temporal lobe. *J. Neurosci.* **26**, 4596–4601. (doi:10.1523/JNEUROSCI.1923-05.2006)
19. Wu Z, Buckley MJ. 2022 Prefrontal and medial temporal lobe cortical contributions to visual short-term memory. *J. Cogn. Neurosci.* **35**, 27–43. (doi:10.1162/jocn_a_01937)
20. Yonelinas A, Hawkins C, Abovian A, Aly M. 2024 The role of recollection, familiarity, and the hippocampus in episodic and working memory. *Neuropsychologia* **193**, 108777. (doi:10.1016/j.neuropsychologia.2023.108777)
21. Daume J *et al*. 2024 Control of working memory by phase-amplitude coupling of human hippocampal neurons. *Nature* **629**, 393–401. (doi:10.1038/s41586-024-07309-z)
22. Baldassano C, Chen J, Zadbood A, Pillow JW, Hasson U, Norman KA. 2017 Discovering event structure in continuous narrative perception and memory. *Neuron* **95**, 709–721. (doi:10.1016/j.neuron.2017.06.041)
23. Ben-Yakov A, Henson RN. 2018 The hippocampal film editor: sensitivity and specificity to event boundaries in continuous experience. *J. Neurosci.* **38**, 10057–10068. (doi:10.1523/JNEUROSCI.0524-18.2018)
24. Turk-Browne NB, Scholl BJ, Chun MM, Johnson MK. 2009 Neural evidence of statistical learning: efficient detection of visual regularities without awareness. *J. Cogn. Neurosci.* **21**, 1934–1945. (doi:10.1162/jocn.2009.21131)
25. Schapiro AC, Gregory E, Landau B, McCloskey M, Turk-Browne NB. 2014 The necessity of the medial temporal lobe for statistical learning. *J. Cogn. Neurosci.* **26**, 1736–1747. (doi:10.1162/jocn_a_00578)
26. Zeidman P, Maguire EA. 2016 Anterior hippocampus: the anatomy of perception, imagination and episodic memory. *Nat. Rev. Neurosci.* **17**, 173–182. (doi:10.1038/nrn.2015.24)
27. Barry DN, Barnes GR, Clark IA, Maguire EA. 2019 The neural dynamics of novel scene imagery. *J. Neurosci.* **39**, 4375–4386. (doi:10.1523/JNEUROSCI.2497-18.2019)
28. Hannula DE, Ranganath C. 2009 The eyes have it: hippocampal activity predicts expression of memory in eye movements. *Neuron* **63**, 592–599. (doi:10.1016/j.neuron.2009.08.025)
29. Nau M, Julian JB, Doeller CF. 2018 How the brain's navigation system shapes our visual experience. *Trends Cogn. Sci.* **22**, 810–825. (doi:10.1016/j.tics.2018.06.008)
30. Ryan JD, Shen K. 2020 The eyes are a window into memory. *Curr. Opin. Behav. Sci.* **32**, 1–6. (doi:10.1016/j.cobeha.2019.12.014)
31. Koster R, Chadwick MJ, Chen Y, Berron D, Banino A, Düzel E, Hassabis D, Kumaran D. 2018 Big-loop recurrence within the hippocampal system supports integration of information across episodes. *Neuron* **99**, 1342–1354. (doi:10.1016/j.neuron.2018.08.009)
32. Barron HC *et al*. 2020 Neuronal computation underlying inferential reasoning in humans and mice. *Cell* **183**, 228–243. (doi:10.1016/j.cell.2020.08.035)
33. Schwartenbeck P, Baram A, Liu Y, Mark S, Muller T, Dolan R, Botvinick M, Kurth-Nelson Z, Behrens T. 2023 Generative replay underlies compositional inference in the hippocampal-prefrontal circuit. *Cell* **186**, 4885–4897. (doi:10.1016/j.cell.2023.09.004)
34. Bakermans JJW, Warren J, Whittington JCR, Behrens TEJ. 2025 Constructing future behavior in the hippocampal formation through composition and replay. *Nat. Neurosci.* **28**, 1061–1072. (doi:10.1038/s41593-025-01908-3)
35. Aly M, Turk-Browne NB. 2018 Flexible weighting of diverse inputs makes hippocampal function malleable. *Neurosci. Lett.* **680**, 13–22. (doi:10.1016/j.neulet.2017.05.063)
36. Cowell RA, Barense MD, Sadil PS. 2019 A roadmap for understanding memory: decomposing cognitive processes into operations and representations. *eNeuro* **6**, ENEURO.0122-19.2019. (doi:10.1523/ENEURO.0122-19.2019)
37. Eichenbaum H, Cohen NJ. 2014 Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron* **83**, 764–770. (doi:10.1016/j.neuron.2014.07.032)
38. Olsen RK, Moses SN, Riggs L, Ryan JD. 2012 The hippocampus supports multiple cognitive processes through relational binding and comparison. *Front. Hum. Neurosci.* **6**, 146. (doi:10.3389/fnhum.2012.00146)
39. Ranganath C. 2010 A unified framework for the functional organization of the medial temporal lobes and the phenomenology of episodic memory. *Hippocampus* **20**, 1263–1290. (doi:10.1002/hipo.20852)
40. Schapiro AC, Kustner LV, Turk-Browne NB. 2012 Shaping of object representations in the human medial temporal lobe based on temporal regularities. *Curr. Biol.* **22**, 1622–1627. (doi:10.1016/j.cub.2012.06.056)
41. Schapiro AC, Turk-Browne NB, Botvinick MM, Norman KA. 2017 Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning. *Phil. Trans. R. Soc. B* **372**, 20160049. (doi:10.1098/rstb.2016.0049)
42. Aitken F, Kok P. 2022 Hippocampal representations switch from errors to predictions during acquisition of predictive associations. *Nat. Commun.* **13**, 3294. (doi:10.1038/s41467-022-31040-w)
43. Eichenbaum H, Fortin NJ. 2009 The neurobiology of memory based predictions. *Phil. Trans. R. Soc. B* **364**, 1183–1191. (doi:10.1098/rstb.2008.0306)
44. Turk-Browne NB. 2019 The hippocampus as a visual area organized by space and time: a spatiotemporal similarity hypothesis. *Vision Res.* **165**, 123–130. (doi:10.1016/j.visres.2019.10.007)
45. Hindy NC, Ng FY, Turk-Browne NB. 2016 Linking pattern completion in the hippocampus to predictive coding in visual cortex. *Nat. Neurosci.* **19**, 665–667. (doi:10.1038/nn.4284)
46. Warrington O, Graedel NN, Callaghan MF, Kok P. 2025 Communication of perceptual predictions from the hippocampus to the deep layers of the parahippocampal cortex. *Sci. Adv.* **11**, eads4970. (doi:10.1126/sciadv.ads4970)
47. Friston K. 2005 A theory of cortical responses. *Phil. Trans. R. Soc. B* **360**, 815–836. (doi:10.1098/rstb.2005.1622)
48. den Ouden HEM, Kok P, de Lange FP. 2012 How prediction errors shape perception, attention, and motivation. *Front. Psychol.* **3**, 548. (doi:10.3389/fpsyg.2012.00548)
49. Clark A. 2013 Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* **36**, 181–204. (doi:10.1017/S0140525X12000477)
50. Stachenfeld KL, Botvinick MM, Gershman SJ. 2017 The hippocampus as a predictive map. *Nat. Neurosci.* **20**, 1643–1653. (doi:10.1038/nn.4650)
51. Patai EZ *et al*. 2019 Hippocampal and retrosplenial goal distance coding after long-term consolidation of a real-world environment. *Cereb. Cortex* **29**, 2748–2758. (doi:10.1093/cercor/bhz044)
52. Brunec IK, Momennejad I. 2022 Predictive representations in hippocampal and prefrontal hierarchies. *J. Neurosci.* **42**, 299–312. (doi:10.1523/JNEUROSCI.1327-21.2021)

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53. Tarder-Stoll H, Baldassano C, Aly M. 2024 The brain hierarchically represents the past and future during multistep anticipation. *Nat. Commun.* **15**, 9094. (doi:10.1038/s41467-024-53293-3)
54. Nadel L, Peterson MA. 2013 The hippocampus: part of an interactive posterior representational system spanning perceptual and memorial systems. *J. Exp. Psychol. Gen.* **142**, 1242–1254. (doi:10.1037/a0033690)
55. Barron HC, Auksztulewicz R, Friston K. 2020 Prediction and memory: a predictive coding account. *Prog. Neurobiol.* **192**, 101821. (doi:10.1016/j.pneurobio.2020.101821)
56. Clarke A, Crivelli-Decker J, Ranganath C. 2022 Contextual expectations shape cortical reinstatement of sensory representations. *J. Neurosci.* **42**, 5956–5965. (doi:10.1523/JNEUROSCI.2045-21.2022)
57. Mynick A, Steel A, Jayaraman A, Botch TL, Burrows A, Robertson CE. 2025 Memory-based predictions prime perceptual judgments across head turns in immersive, real-world scenes. *Curr. Biol.* **35**, 121–130. (doi:10.1016/j.cub.2024.11.024)
58. Kim G, Lewis-Peacock JA, Norman KA, Turk-Browne NB. 2014 Pruning of memories by context-based prediction error. *Proc. Natl Acad. Sci. USA* **111**, 8997–9002. (doi:10.1073/pnas.1319438111)
59. Sinclair AH, Manalili GM, Brunec IK, Adcock RA, Barense MD. 2021 Prediction errors disrupt hippocampal representations and update episodic memories. *Proc. Natl Acad. Sci. USA* **118**, e2117625118. (doi:10.1073/pnas.2117625118)
60. Lee ACH, Yeung LK, Barense MD. 2012 The hippocampus and visual perception. *Front. Hum. Neurosci.* **6**, 91. (doi:10.3389/fnhum.2012.00091)
61. George TM, de Cothi W, Stachenfeld KL, Barry C. 2023 Rapid learning of predictive maps with STDP and theta phase precession. *eLife* **12**, e80663. (doi:10.7554/eLife.80663)
62. Garvert MM, Dolan RJ, Behrens TE. 2017 A map of abstract relational knowledge in the human hippocampal-entorhinal cortex. *eLife* **6**, e17086. (doi:10.7554/eLife.17086)
63. Ekman M, Kusch S, de Lange FP. 2023 Successor-like representation guides the prediction of future events in human visual cortex and hippocampus. *eLife* **12**, e78904. (doi:10.7554/eLife.78904)
64. Chun MM, Phelps EA. 1999 Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nat. Neurosci.* **2**, 844–847. (doi:10.1038/12222)
65. Bianco R, Magami K, Pearce M, Chait M. 2026 Discovery, interruption, and updating of auditory regularities in memory: evidence from low-frequency brain dynamics in human MEG. *J. Neurosci.* **46**, e0629252025. (doi:10.1523/JNEUROSCI.0629-25.2025)
66. Gregory RL. 1970 *The intelligent eye*. New York, NY: McGraw-Hill.
67. Hsieh PJ, Vul E, Kanwisher N. 2010 Recognition alters the spatial pattern of FMRI activation in early retinotopic cortex. *J. Neurophysiol.* **103**, 1501–1507. (doi:10.1152/jn.00812.2009)
68. Becker M, Sommer T, Cabeza R. 2025 Insight predicts subsequent memory via cortical representational change and hippocampal activity. *Nat. Commun.* **16**, 4341. (doi:10.1038/s41467-025-59355-4)
69. Völler J, Linde-Domingo J, Ortiz-Tudela J, González-García C. 2026 From sudden perceptual learning to enduring engrams: a representational perspective. *Phil. Trans. R. Soc. B* **381**, 20250245. (doi:10.1098/rstb.2025.0245)
70. Medina C, Fernández RS, Krawczcyk MC, Boccia MM. 2026 Hippocampal prediction errors and claustral control at the perception–memory crossroads. *Phil. Trans. R. Soc. B* **381**, 20250253. (doi:10.1098/rstb.2025.0253)
71. Warrington O, Kok P. 2026 Dentate gyrus encodes prediction errors during learning of perceptual predictions. *Phil. Trans. R. Soc. B* **381**, 20250241. (doi:10.1098/rstb.2025.0241)
72. Yang CM, Duncan K, Barense M. 2026 Memory strength at reactivation, not memory age, governs prediction error-driven updating of naturalistic event memory. *Phil. Trans. R. Soc. B* **381**, 20250244. (doi:10.1098/rstb.2025.0244)
73. Shi A, Liu Y, Liu XL. 2026 Neural mechanisms of error-driven learning in retrieval practice: confidence gates memory and metamemory networks. *Phil. Trans. R. Soc. B* **381**, 20250240. (doi:10.1098/rstb.2025.0240)
74. van Kesteren MTR, Ruiter DJ, Fernández G, Henson RN. 2012 How schema and novelty augment memory formation. *Trends Neurosci.* **35**, 211–219. (doi:10.1016/j.tins.2012.02.001)
75. Raykov P, Gurunandan K, Moniri M, Jain A, Greve A, Henson R. 2026 Predictions and declarative memory encoding: two fMRI paradigms provide slim pickings for SLIMM. *Phil. Trans. R. Soc. B* **381**, 20250250. (doi:10.1098/rstb.2025.0250)
76. Davachi L, DuBrow S. 2015 How the hippocampus preserves order: the role of prediction and context. *Trends Cogn. Sci.* **19**, 92–99. (doi:10.1016/j.tics.2014.12.004)
77. Tarder-Stoll H, Baldassano C, Aly M. 2026 The hippocampus rapidly integrates sequence representations during novel multistep predictions. *Phil. Trans. R. Soc. B* **381**, 20250237. (doi:10.1098/rstb.2025.0237)
78. Poskanzer C, Tarder-Stoll H, Javid R, Spolaore E, Aly M. 2025 Successful prediction is associated with enhanced encoding. *Open Mind.* **9**, 959–991. (doi:10.1162/opmi.a.15)
79. Sherman BE. 2026 How prediction of the future affects encoding of the present: cooperation or competition? *Open Mind.* **10**, 79–90. (doi:10.1162/OPMI.a.329)
80. Sherman BE, Graves KN, Huberdeau DM, Quraishi IH, Damisah EC, Turk-Browne NB. 2022 Temporal dynamics of competition between statistical learning and episodic memory in intracranial recordings of human visual cortex. *J. Neurosci.* **42**, 9053–9068. (doi:10.1523/JNEUROSCI.0708-22.2022)
81. Singh D, Schapiro AC. 2026 Evidence for complementary learning systems within the hippocampus. *Phil. Trans. R. Soc. B* **381**, 20250243. (doi:10.1098/rstb.2025.0243)
82. Zhou I, Bai Z, Huang Y, Wijaya EG, Sherman BE, Turk-Browne NB, Goldfarb EV. 2026 Stress drives the hippocampus to prioritize statistical prediction over episodic encoding.Phil. *Trans. R. Soc. B* **381**, 20250238. (doi:10.1098/rstb.2025.0238)
83. Nalluru S, Glitz L, Przygodda X, Mancini V, Barron HC. 2026 The hippocampus as a generative model. *Phil. Trans. R. Soc. B* **381**, 20250247. (doi:10.1098/rstb.2025.0247)
84. Shams L, Beierholm UR. 2010 Causal inference in perception. *Trends Cogn. Sci.* **14**, 425–432. (doi:10.1016/j.tics.2010.07.001)
85. Bein O, Davachi L. 2026 Adaptive processing of predictions and prediction errors in hippocampal subregions. *Phil. Trans. R. Soc. B* **381**, 20250239. (doi:10.1098/rstb.2025.0239)
86. Wagner M, Chen Y, Karuvally A, Cameron M, Sejnowski T. 2026 Balancing stability and flow in hippocampal networks via inductive bias and learned symmetry breaking. *Phil. Trans. R. Soc. B* **381**, 20250260. (doi:10.1098/rstb.2025.0260)
87. Damphousse CC, Gagliardi CM, Peterson JG, Feng C, Schmidt B, Mugan U, Redish AD. 2026 The vicarious nature of hippocampal theta sequences. *Phil. Trans. R. Soc. B* **381**, 20250242. (doi:10.1098/rstb.2025.0242)
88. Robinson JC, LaChance PA, Malmberg S, Fang J, Sankaranarayanan S, Stern CE, Hasselmo ME. 2026 Trajectory scanning as a predictive coding mechanism for goal-directed navigation, obstacle avoidance and episodic memory. *Phil. Trans. R. Soc. B* **381**, 20250251. (doi:10.1098/rstb.2025.0251)
89. Ladyka-Wojcik N, Flick G, Liu ZX, Ryan JD. 2026 Where we look, what we know: how hippocampal predictions shape, and are shaped by, eye movements. *Phil. Trans. R. Soc. B* **381**, 20250248. (doi:10.1098/rstb.2025.0248)
90. Shi Y, Garvert MM. 2026 Forming, selecting and updating cognitive maps to support flexible behaviour: relevance for anxiety. *Phil. Trans. R. Soc. B* **381**, 20250246. (doi:10.1098/rstb.2025.0246)
91. Maurer AP, Burke S, Peterson MA, Nadel L. 2026 A neural framework for the origin of meaning: network dynamics, context and the hippocampus. *Phil. Trans. R. Soc. B* **381**, 20250249. (doi:10.1098/rstb.2025.0249)

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92. Angeli PA, Steel A, Silson EH, Robertson CE. 2024 Positive and negative retinotopic codes in the human hippocampus. *bioRxiv* 2024.09.27.615397. (doi:10.1101/2024.09.27.615397)
93. Knapen T. 2021 Topographic connectivity reveals task-dependent retinotopic processingthroughout the human brain. *Proc. Natl Acad. Sci. USA* **118**, e2017032118. (doi:10.1073/pnas.2017032118)
94. Leferink CA, DeKraker J, Brunec IK, Köhler S, Moscovitch M, Walther DB. 2024 Organization of pRF size along the AP axis of the hippocampus and adjacent medial temporal cortex is related to specialization for scenes versus faces. *Cereb. Cortex.* **34**, bhad429. (doi:10.1093/cercor/bhad429)
95. Silson EH, Zeidman P, Knapen T, Baker CI. 2021 Representation of contralateral visual space in the human hippocampus. *J. Neurosci.* **41**, 2382–2392. (doi:10.1523/JNEUROSCI.1990-20.2020)
96. Elfman KW, Aly M, Yonelinas AP. 2014 Neurocomputational account of memory and perception: thresholded and graded signals in the hippocampus. *Hippocampus* **24**, 1672–1686. (doi:10.1002/hipo.22345)
97. Stangl M, Maoz SL, Suthana N. 2023 Mobile cognition: imaging the human brain in the 'real world'. *Nat. Rev. Neurosci.* **24**, 347–362. (doi:10.1038/s41583-023-00692-y)
98. Maoz SLL *et al*. 2023 Dynamic neural representations of memory and space during human ambulatory navigation. *Nat. Commun.* **14**, 6643. (doi:10.1038/s41467-023-42231-4)
99. Seymour RA, Alexander N, Mellor S, O'Neill GC, Tierney TM, Barnes GR, Maguire EA. 2021 Using OPMs to measure neural activity in standing, mobile participants. *Neuroimage* **244**, 118604. (doi:10.1016/j.neuroimage.2021.118604)
100. O'Neill GC *et al*. 2025 Combining video telemetry and wearable MEG for naturalistic imaging. *Imaging Neurosci.* **3**, imag_a_00495. (doi:10.1162/imag_a_00495)
101. Martin CB, Hong B, Newsome RN, Savel K, Meade ME, Xia A, Honey CJ, Barense MD. 2022 A smartphone intervention that enhances real-world memory and promotes differentiation of hippocampal activity in older adults. *Proc. Natl Acad. Sci. USA* **119**, e2214285119. (doi:10.1073/pnas.2214285119)
102. Price CJ, Zeidman P, Callaghan MF. 2025 Eleanor Maguire (1970–2025). *Nat. Neurosci.* **28**, 1113–1114. (doi:10.1038/s41593-025-01974-7)
103. Frith CD. 2025 Eleanor Maguire. *Biogr. Mems Fellows Br. Acad* **22**, 727–744. (doi:10.5871/mem/022.727)
104. Maguire EA, Woollett K, Spiers HJ. 2006 London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. *Hippocampus* **16**, 1091–1101. (doi:10.1002/hipo.20233)
105. Maguire EA, Nannery R, Spiers HJ. 2006 Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* **129**, 2894–2907. (doi:10.1093/brain/awl286)
106. Barry DN *et al*. 2019 Imaging the human hippocampus with optically-pumped magnetoencephalography. *Neuroimage* **203**, 116192. (doi:10.1016/j.neuroimage.2019.116192)
107. Kumaran D, Maguire EA. 2007 Which computational mechanisms operate in the hippocampus during novelty detection? *Hippocampus* **17**, 735–748. (doi:10.1002/hipo.20326)
108. Hassabis D, Maguire EA. 2007 Deconstructing episodic memory with construction. *Trends Cogn. Sci.* **11**, 299–306. (doi:10.1016/j.tics.2007.05.001)
109. Mullally SL, Intraub H, Maguire EA. 2012 Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. *Curr. Biol.* **22**, 261–268. (doi:10.1016/j.cub.2012.01.001)
110. Zeidman P, Lutti A, Maguire EA. 2015 Investigating the functions of subregions within anterior hippocampus. *Cortex* **73**, 240–256. (doi:10.1016/j.cortex.2015.09.002)
111. Maguire EA, Mullally SL. 2013 The hippocampus: a manifesto for change. *J. Exp. Psychol. Gen.* **142**, 1180–1189. (doi:10.1037/a0033650)
112. Barry DN, Maguire EA. 2019 Remote memory and the hippocampus: a constructive critique. *Trends Cogn. Sci.* **23**, 128–142. (doi:10.1016/j.tics.2018.11.005)
113. Maguire EA. 2022 Does memory research have a realistic future? *Trends Cogn. Sci.* **26**, 1043–1046. (doi:10.1016/j.tics.2022.07.006)
114. Hickling AL, Clark IA, Wu YI, Maguire EA. 2024 Automated protocols for delineating human hippocampal subfields from 3 Tesla and 7 Tesla magnetic resonance imaging data. *Hippocampus* **34**, 302–308. (doi:10.1002/hipo.23606)

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