Neuroscience and Biobehavioral Reviews 180 (2026) 106492

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Hippocampal Revolutions

Edmund T. Rolls [a,b,1,2,*]

[a] Oxford Centre for Computational Neuroscience, Oxford, UK
[b] Department of Computer Science, University of Warwick, Coventry CV4 7AL, UK

ARTICLE INFO

Keywords:
Hippocampus
Place cells
Spatial view cells
Cognitive map
Episodic memory
Scene representations
Navigation
Primates including humans
Concept cells
Semantic representations

ABSTRACT

New concepts build on research on the rodent hippocampus, but go beyond that to understand how the hippocampal system operates in primates including humans. First, in rodents place cells and entorhinal cortex grid cells represent the place where the individual is located, but in primates including humans, many hippocampal system neurons respond to spatial view, to where the individual looks in space. Second, rodent navigation is described from place to place, but in primates including humans, the highly developed foveal visual system and hippocampal spatial view cells allow use of visual landmarks for completely different navigational strategies. Third, research in primates including humans emphasises functions of the hippocampus in episodic memory, rather than a cognitive map. Fourth, in humans the ventromedial cortical visual pathway for scenes, the ventrolateral cortical visual pathway for faces and objects, and the orbitofrontal cortex for reward provide the hippocampus with its inputs and outputs. Fifth, these discoveries in primates including humans fit with the computational theory of hippocampal CA3 circuitry for episodic memory. Sixth, in humans, the major connectivity from the hippocampal episodic memory system to the anterior temporal lobe semantic cortical regions is stimulating new approaches to how the hippocampus helps to build semantic memories.

1. Introduction and overview

Revolutions, new concepts, are underway in our understanding of hippocampal function. Research on the rodent hippocampus has uncovered much that is of great interest, but we are now in a position where we can build on and go beyond that to understand how the hippocampal system operates in primates including humans. The aim of this review is to build on the evidence from rodents, but to go beyond that by showing that key revolutions in our understanding of the primate including human hippocampal system are taking place that are very important in understanding what the primate including human hippocampus does, that is, what and how it computes. This understanding is important, for it helps in the understanding of the memory problems that can follow medial temporal lobe damage in humans.

First, research in rodents has emphasised hippocampal place cells and medial entorhinal cortex grid cells of places where the individual is located, but in primates including humans, and in some birds, hippocampal system neurons respond to spatial view, to where the individual looks in space. Second, research in rodents has emphasised navigation as moving from hippocampal encoded place to place using self-motion, which is almost 'blind' navigation. In primates including humans, the highly developed foveal visual system and hippocampal spatial view cells allow use of visual landmarks, which leads to completely different strategies for navigation. Third, research in primates including humans emphasises the role of the hippocampus in episodic memory (rather than in a cognitive map), in which objects including faces, viewed spatial locations, and rewards are associated together to form a unique episodic memory, which can later be recalled from any of its components using associations made in hippocampal CA3. Fourth, in primates including humans the pathways to and from the hippocampus are now becoming understood, with a ventromedial cortical visual pathway for scenes using spatial view cells; with the ventrolateral cortical visual pathway for visually fixated objects and faces; and with reward inputs from the highly developed orbitofrontal cortex reaching the hippocampus via the ventromedial prefrontal cortex and anterior cingulate cortex. Similar equivalent and highly developed cortical pathways in rodents are not described or are much less clear. Fifth, all of this fits well in primates including humans with the quantitative computational theory of

* Corresponding author at: Department of Computer Science, University of Warwick, Coventry CV4 7AL, UK.
E-mail address: Edmund.Rolls@oxcns.org.
[1] URL: https://www.oxcns.org
[2] https://orcid.org/0000-0003-3025-1292

https://doi.org/10.1016/j.neubiorev.2025.106492
Received 19 August 2025; Received in revised form 9 November 2025; Accepted 24 November 2025
Available online 25 November 2025

hippocampal CA3 circuitry as being useful for episodic memory, and with the highly developed backprojection pathways from the hippocampus to the neocortex being appropriate to recall the same number of episodic memories as can be stored in the hippocampus. Sixth, in humans, the major connectivity from the hippocampal episodic memory system to the anterior temporal lobe semantic cortical regions is now becoming understood, and is stimulating new approaches to how the hippocampus may help semantic cortical regions build semantic memories, with no clear equivalent yet understood in rodents.

2. Place cells in the hippocampus and grid cells for places in the medial entorhinal cortex in rodents

A key discovery is of cells in the rat hippocampus that respond to the place where the rat is located (O'Keefe and Dostrovsky, 1971; O'Keefe, 1979). These place cells should respond to a place almost independently of head direction if they are really coding for a place where the rat is located rather than where the rat is looking or facing (O'Keefe, 1979; Andersen et al., 2007; O'Keefe and Krupic, 2021). There is some visual input to these cells, in that rotating the room cues alters the place appropriately at which the cell responds, but the cells still code for the place of the rat, not the location of the room cues (Muller and Kubie, 1987; Andersen et al., 2007). Consistent with the place encoding approach to hippocampal function, lesions of the hippocampus are described as impairing navigation to a place in the water maze (Morris et al., 1982). An additional finding is that self-motion by the rat to another place updates which place cells are firing (McNaughton et al., 1996), and this idiothetic update from place to place has been developed into a theory of navigation using what are described as maps (O'Keefe and Nadel, 1978; O'Keefe, 1990; Burgess and O'Keefe, 1996) (e.g. *The Hippocampus as a Cognitive Map* (O'Keefe and Nadel, 1978)) or charts (McNaughton et al., 1996; Battaglia and Treves, 1998).

Together, the set of cells in one test environment can represent the places in that environment, and if the rat is tested in a new environment, all the places to which place cells respond reorganize in what is termed global remapping to provide a new map or chart of the new spatial environment (Leutgeb et al., 2005). If just the room cues are changed, and the spatial structure of the environment is not changed, the place cells do not need to reorganize their map, but quickly learn to the new room cues in what is termed 'rate remapping' (Leutgeb et al., 2005). A corresponding rate remapping occurs in macaques when the room cues are changed but the spatial structure of the environment and therefore the chart or map referred to above is not changed (Baraduc et al., 2019). However, as will be described below, the representation in macaques is of where the macaque is looking, and much less of the place where the macaque is located (Rolls, 2023c). The concept of place cells in the rodent hippocampus remains a key hypothesis (Moser et al., 2017; O'Keefe and Krupic, 2021), emphasised in the Spring Hippocampal Research Conference in 2025.

However, there are some inconsistencies in describing rat hippocampal cells as encoding just places. One is that the responses of some rat hippocampal 'place' cells are modulated by head direction, which implies that the cells do not just encode the place where the rodent is, but something else that could reflect what the rat is looking at in the environment, or a vestibular head direction signal (McNaughton et al., 1983; Muller et al., 1994). Another inconsistency with place coding is that hippocampal 'place' cells may respond only when a rodent is running in one direction on a linear track or in an 8-arm maze and not when running in the opposite direction but at the same place (McNaughton et al., 1983; Wiener et al., 1989; Muller et al., 1994). This implies that it is not just the place where the rodent is located that is what the coding is about, but instead something that may be influenced by visual cues visible in one direction but not the other. Another inconsistency with the place encoding theory is that a rodent 'place' cell can be activated by the sight of a bar moving past a rat that is stationary in one place (Purandare et al., 2022).

Another key discovery is of grid cells in the rodent medial entorhinal cortex, which code a hexagonally arranged set of places (Fyhn et al., 2004; Moser et al., 2015, 2017). There are theories and models about how these grid cells could be involved in setting up hippocampal place cell representations (Rolls et al., 2006b; Solstad et al., 2006; Kropff and Treves, 2008; Giocomo et al., 2011; Moser et al., 2014). But here again the place hypothesis has inconsistencies, in that the hexagonal grid cell arrangement breaks down in a hairpin maze in which the rodent is moving either in one direction, or the opposite, even though the place may be the same (Derdikman et al., 2009).

3. A revolution: spatial view cells in primates including humans

A revolution in our understanding of hippocampal function is now occurring, in that evidence is now accumulating that many macaque and now also human hippocampal neurons respond to the spatial location being viewed, and not to the place where the individual is located.

The first discoveries were that some macaque hippocampal neurons respond to some but not other locations 'out there' in space on a screen when the macaque is performing an object-location memory task in which the location at which an object had appeared on a screen must be remembered (Cahusac et al., 1989; Rolls et al., 1989).

Another discovery was that in a simple model of episodic memory in which what-where associations must be formed between 'what' the stimulus is and 'where' it is located, macaque hippocampal neurons contribute to solving the task by forming combinations of the object and where it is located on a screen, responding for example primarily to object 1 in spatial location 1 on the screen (Rolls et al., 2005b). Similar combination or conjunctive neurons have now been described in the human hippocampus / medial temporal lobe when humans are performing a similar object-viewed location episodic memory task (Kolibius et al., 2023). Consistent with this neurophysiology, damage to the hippocampal system in primates impairs the ability to remember where objects are in scenes that are being viewed (Gaffan and Saunders, 1985; Gaffan, 1994; Gaffan and Parker, 1996; Murray et al., 1998).

Another discovery was that in another simple model of episodic memory, hippocampal neurons responded to locations in scenes being viewed on a screen at which a high value juice reward could be obtained by a touch, or for other neurons the location in a viewed scene at which a low value juice reward was available (Rolls and Xiang, 2005). In this case it was the location in each viewed scene at which a particular type of reward could be obtained that was encoded, and not the location on the monitor. The monkey had to remember for every scene which were the high and low reward locations. These neurons could also reverse the location to which they responded in a viewed scene when the rewards available were reversed (switched between the two locations). Moreover, these neurons do not just code for reward per se, for these hippocampal neurons do not respond in an object-reward task, which is implemented by a different brain region, the orbitofrontal cortex (Rolls and Xiang, 2005).

We followed up our early discoveries by recording from macaque hippocampal neurons while monkeys were performing an object-spatial location task, and showed that the majority of the spatial view cells coded in allocentric coordinates, in that their response occurred at the same location on a large screen when the screen was moved to different locations relative to the monkey (Feigenbaum and Rolls, 1991).

We next recorded from these hippocampal neurons in a cue controlled spatial environment (i.e. with cues hung on the wall of the enclosure) in which the monkey could be moved to different places. The monkey used the cues on the walls of the enclosure to determine in which of four cups on the walls food would be found. We found that the majority of the hippocampal neurons responded to where the monkey was looking in space (in the enclosure), relatively independently of the place where the monkey was located, and these were now termed 'spatial view neurons' (Rolls and O'Mara, 1995). In addition, a few primate neurons responded to the place where the macaque was located

(Rolls and O'Mara, 1995), so I do not exclude the possibility that some primate hippocampal neurons code for the place where an individual is located.

Because rodent hippocampal place cells are typically recorded during locomotion, we next analysed the activity of macaque hippocampal neurons while the monkey was freely locomoting on all four feet on the floor of a large laboratory that provided a rich spatial environment, and was freely foraging for food on the floor to be comparable with a standard test situation in which rodent hippocampal place cells are found. In this rich spatial environment during walking and running the spatial hippocampal neurons fired to a location in space at which the monkey was looking, and the neurons conveyed considerable information (measured with Shannon information theory) about where the monkey was looking, and much less information about place or head direction or eye position (Rolls et al., 1997, 1998; Georges-François et al., 1999) (Fig. 1).

Moreover, in this test situation it was also possible to stop the monkey locomoting, and to show that it was indeed where the monkey was looking in the room, and not the place where the monkey was located, nor the head direction, and nor the eye position (Fig. 2) (Rolls et al., 1997, 1998; Georges-François et al., 1999). (Eye position refers to the horizontal and vertical angles of the eye relative to the head.)

Interestingly, self-motion update of spatial view was shown, in that in the dark and with curtains completely obscuring the lab, these neurons (especially in CA1) updated their representations in that the neurons fired only when the monkey moved his eyes to look towards the spatial view field (Robertson et al., 1998). This was self-motion update, in that after a few minutes the path integration failed, and at about the same time, the experimenters became lost in the dark environment (Robertson et al., 1998). The idiothetic update of spatial view neurons is a direct parallel to the idiothetic update found in rodents (McNaughton et al., 1996), though in rodents the update is for place and not for spatial view.

Recently, evidence for representations in primates of spatial view by neurons in the hippocampus has accumulated.

In an investigation of navigation towards a goal in a virtual reality star maze with room cues, some macaque hippocampal neurons were found to respond to where the monkey was looking (Wirth et al., 2017). It was in this test situation that it was found that replacing the room cues with new room cues resulted in just rapid rate remapping (Baraduc et al., 2019), with no global remapping as the chart or map (or schema as it was termed here) of the star maze and the goal location etc had not changed (Baraduc et al., 2019), so a new map or chart was not needed (McNaughton et al., 1996; Battaglia and Treves, 1998; Leutgeb et al., 2005).

In another investigation, it was shown that many macaque neurons fire for where the monkey is facing (or, it turns out, probably was looking (Rolls, 2026b)) during locomotion (Mao et al., 2021). Interestingly, it has been found that hippocampal neurons fire much better when macaques locomote in a real spatial environment than in virtual

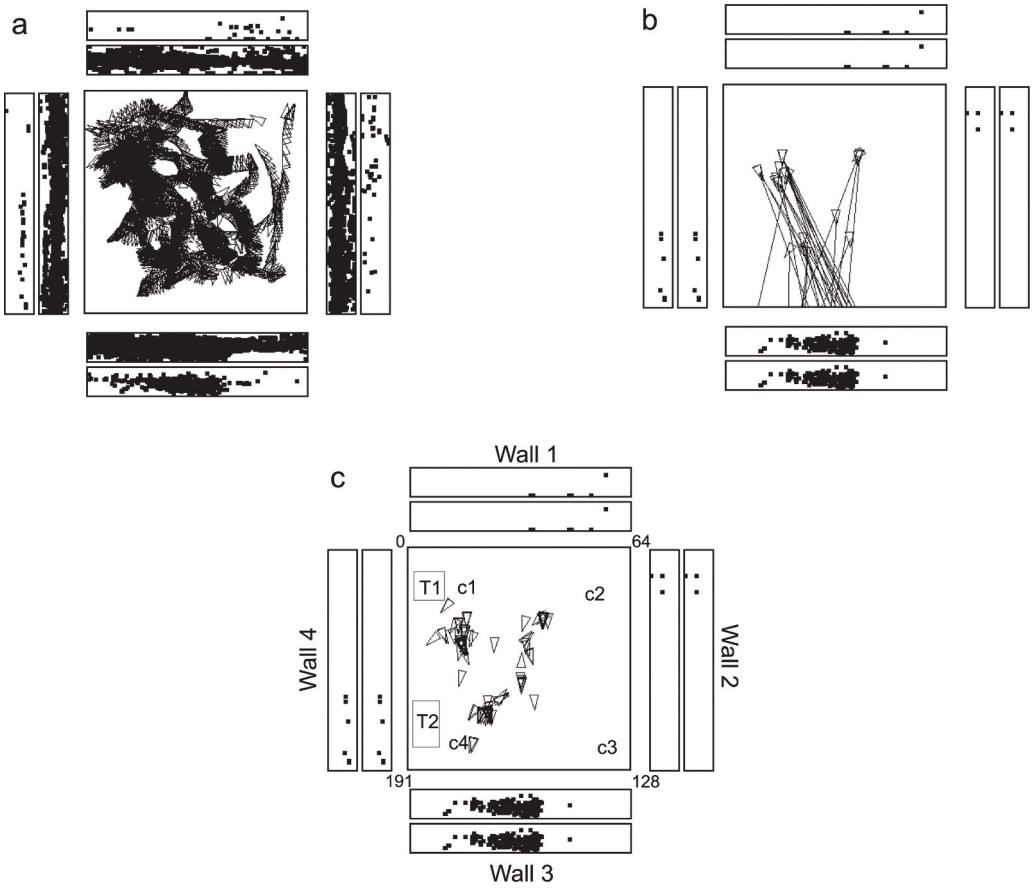

Fig. 1. A hippocampal spatial view cell (az033) recorded while a monkey walked around in an open field area 2.5 × 2.5 m shown as the square within a rich and large laboratory environment. In (a) every time that the cell fired is shown by a spot in the outer rectangles each of which represents one of the four walls of the room. The inner rectangles show where the monkey looked on the walls. The neuron has a spatial view field on wall 3. The places to which the monkey walked are shown by the triangles, with the pointed end showing the head direction. (b) shows some of the many different places at which the monkey was located when the neuron fired, and the lines show where the monkey was fixating when the spatial view cell fired. (c) provides more evidence about the places where the monkey was located when the cell fired because he was looking at the view field on wall 3. This helps to show that the neuron responds to spatial view, and not to the place where the monkey was located. C1 to c4 are cups containing food to encourage the monkey to forage. T1 was a trolley and T2 a table. Details are provided by Georges-François et al., (1999). Videos to illustrate the firing of spatial view neurons are described in the Data and Code Availability statement.

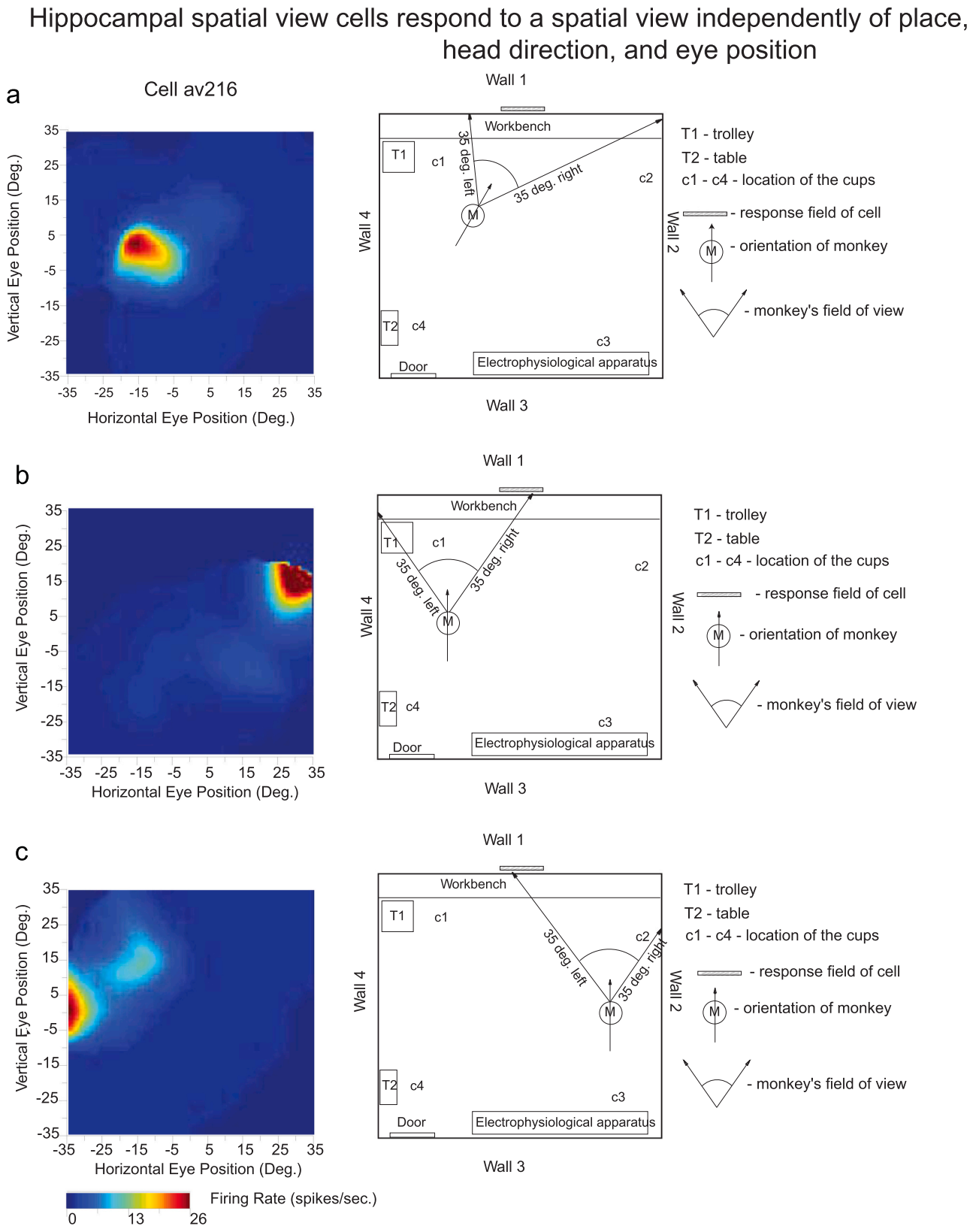

Fig. 2. Testing of a hippocampal spatial view neuron (av216) to show that it has allocentric encoding, and that the response does not depend on where the monkey is located. The firing rate is shown as a function of the horizontal and vertical eye position, where positive values indicate right or up. The neuron responded when the monkey looked towards its view field (indicated with a hatched bar) relatively independently of place, eye position, or head direction. ANOVAs and information theory analyses performed on the same data cast in different ways confirmed this: for spatial view, the ANOVA was $p < 0.001$ with 0.217 bits in a 500 ms period for the average Shannon mutual information; for place $p = 0.9$ with 0.001 bits; for head direction $p = 0.5$ with 0.0 bits; and for eye position $p = 0.8$ with 0.006 bits. (Modified from Georges-François et al., 1999).

reality in the same environment (Yan and Mao, 2024). The hippocampal neuronal responses in these free moving test situations (Mao et al., 2021; Mao, 2023; Yan and Mao, 2024) was very similar to the activity recorded when our macaques were freely locomoting on all four legs in our rich lab environment with the head free to rotate in the horizontal plane (Rolls et al., 1997, 1998; Robertson et al., 1998; Georges-François et al., 1999), which is useful validation. As shown in Fig. 2, an advantage of our testing was that we could stop the monkey and measure neuronal responses for different eye positions with particular combinations of place and head direction to define the responses of the neurons as being related to the location in the environment at which the monkey was looking, independently of head direction, facing direction, and place (Rolls et al., 1997, 1998; Georges-François et al., 1999).

In another investigation, it has been found that during unrestrained navigation in a 3D environment, many hippocampal neurons in marmosets respond to where the marmoset is looking (Piza et al., 2024).

Further, in a virtual reality experiment involving navigation towards goals, some macaque hippocampal neurons responded to where in space the macaque was looking like spatial view cells, rather than the place where the macaque was located (Buffalo, 2025).

In an investigation of navigation in a virtual reality environment, hippocampal neurons recorded were described as "landmark cells" (Vericel et al., 2024), consistent with proposals and a model for how spatial view cells could be useful in navigation by coding for landmarks (Rolls, 2021b).

Cells that respond to viewed locations out there, not to the place where the individual is located, have also been found in humans (who have a fovea very like that of macaques (Rolls and Cowey, 1970)). In fact, apart from some Virtual Reality studies, most research on neuronal activity in humans has been with the human in one place, and any spatial component has been related to where the stimuli are "out there" in space, on for example a screen (Ekstrom et al., 2003; Miller et al., 2013). For example, in the study by Ekstrom and colleagues, some medial temporal lobe neurons were found to represent views of landmarks (Ekstrom et al., 2003). In another study of human medial temporal lobe neurons, it was found that in a Treasure Hunt game, some neurons respond to the sight of remote locations rather than the subject's own place (Tsitsiklis et al., 2020). Just like macaque spatial view cells, these neurons in humans respond when the spatial location is seen with different bearings. Some parahippocampal cortex neurons in humans respond to the bearing and distance of viewed locations (Kunz et al., 2021). Also in humans some medial temporal lobe neurons reflect the learning of paired associations between views of locations, and people or objects (Ison et al., 2015), or between an animal and for example a viewed location in a scene (Kolibius et al., 2023), and this implies that views of scenes are important for human hippocampal function. Consistent with this, human functional neuroimaging studies do show hippocampal or parahippocampal cortex activation when scenes or parts of scenes are viewed even when the human is fixed in one place for neuroimaging (Epstein and Kanwisher, 1998; O'Keefe et al., 1998; Burgess, 2008; Hassabis et al., 2009; Chadwick et al., 2010, 2013; Maguire, 2014; Brown et al., 2016; Zeidman and Maguire, 2016; Rolls et al., 2024a, 2024d) (Fig. 3).

Our hypothesis is that the primate fovea is important in enabling primate hippocampal neurons respond to a particular location in space at which a primate is looking, by enabling cortical neurons to respond to a combination of visual features in the small part of space being fixated (De Araujo et al., 2001; Rolls, 2025a). The spatial view neurons are bound together in the correct spatial relationship to each other by the recurrent collateral connections between the neurons in hippocampal CA3 and/or the medial parahippocampal gyrus which form a continuous attractor network due to the overlap of the view fields of co-active neurons (Stringer et al., 2005; Rolls, 2025a). Consistent with this hypothesis that the fovea with its limited angle for a high resolution view is important in forming spatial view cells, in birds with a fovea such as the chickadee, neurons with spatial view fields useful for food caching have now been described (Chettih et al., 2024). Moreover, just like macaque spatial view cells which respond to a viewed location depending on the reward value at that location (Rolls and Xiang, 2005), the chickadee neurons only respond to a viewed cache when it still has food in it and is therefore rewarding (Chettih et al., 2024). Also consistent with the hypothesis that animals with a fovea or auditory equivalent can represent locations "out there" in space is that some bat hippocampal neurons can respond to the location of another bat "out there" (Omer et al., 2018). In contrast, in rodents with a very wide field of view of approximately 270 degrees and no fovea, the neurons in responding to a place where the rodent is located may be responding to a combination of visual features over a wide angle of space, which would encode the place where the

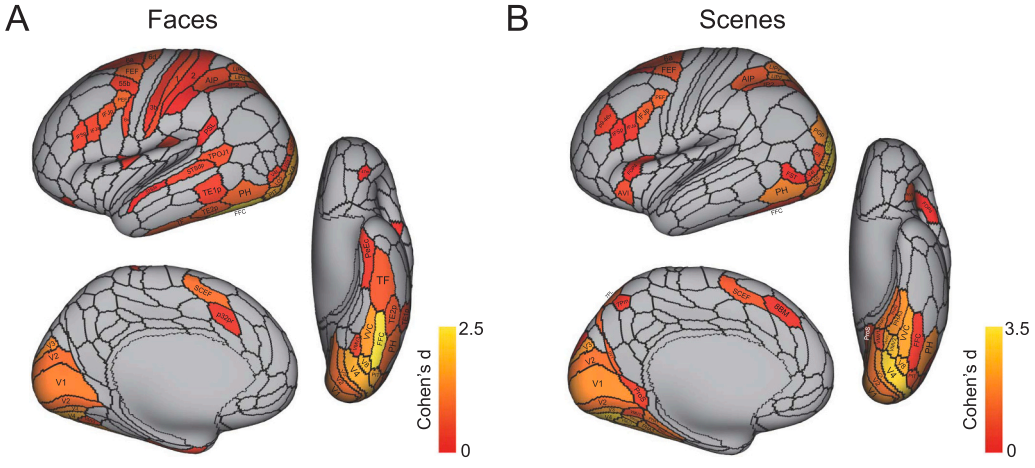

Fig. 3. Activations in visual cortical pathways to the human hippocampus. Faces activate the ventrolateral temporal regions including FFC, lateral parahippocampal TF, and the perirhinal cortex PeEc. Scenes activate ventromedial cortical regions including the ProStriate Cortex (ProS), ventromedial cortical regions VMV1–3, and medial parahippocampal regions PHA1–3. The cortical regions exhibiting significant differences in the average BOLD signal between the baseline prestimulus period preceding the 0-back blocks (shown in Fig. 1 of (Rolls et al., 2024a)) before the BOLD signal had responded to the stimuli, and the last 20 timepoints within the 0-back blocks (when the BOLD signal response to the visual stimuli was occurring) for each of the two stimulus types (faces and scenes) after Bonferroni correction (α=0.05) across 956 Human Connectome Project participants. The effect size as indicated by Cohen's d is indicated. The activations are shown in red to yellow. The top 50 cortical regions with significant increases in the BOLD signal are shown out of the 180 cortical regions in the left hemisphere using the HCP Multimodal Parcellation (Glasser et al., 2016a). The abbreviations for each cortical region are provided in Table S1, and the cortical regions are illustrated in Fig. S1. (After (Rolls et al., 2024a)).

rodent is by a process like triangulation (De Araujo et al., 2001).

4. A revolution in mechanisms of navigation

In rodents, the hippocampal place cells that are active are updated by self-motion, using path integration over head direction and speed (McNaughton et al., 1983, 1996). Head direction cells are found in the primate presubiculum (Robertson et al., 1999), as well as in many hippocampal system regions in rodents (Taube et al., 1990; Butler et al., 2017; Cullen and Taube, 2017; Clark et al., 2024). Speed cells were discovered in the primate hippocampus (O'Mara et al., 1994; Rolls, 2025b) and can respond to angular or linear velocity sensed by vestibular and/or optic flow signals (O'Mara et al., 1994; Rolls, 2025b), and have more recently also been found in the rodent medial entorhinal cortex (Kropff et al., 2015; Spalla et al., 2022). The place cells are said to respond to a particular place by using boundary vector cells, each one of which responds maximally when the boundary of the rodent's environment is at a particular distance and allocentric angle (Burgess et al., 2000). Place cells in rodents and their idiothetic (self-motion) path integration update have been the basis for many approaches to navigation, involving navigation from place to place using place cells (McNaughton et al., 1991, 1996; Hartley et al., 2014; Edvardsen et al., 2020). The medial entorhinal cortex grid cells may be involved in the path integration from place to place (McNaughton et al., 2006; Giocomo et al., 2011; Moser et al., 2014, 2017). In rodents the environmental cues such as room cues or landmarks can be used to help reset the path integration of the place being represented, which typically fails within 2 - a few minutes, and indeed idiothetic path integration in humans without vision (e.g. when blindfold) typically fails within a very few minutes, and participants quickly lose their bearings and become lost (Israel et al., 1993, 1997; Wiener et al., 2011). Thus some resetting of rodent place cell representations by visual cues such as those encoded by boundary vector cells is needed for these place cell based models of navigation to work for more than a short time (Burgess et al., 2000).

A revolution is now taking place in theories of navigation in primates including humans, which need no longer be based on the rodent models of navigation from place to place, but which can now use spatial view cells that code for viewed locations "out there" in space of, for example, landmarks, to guide navigation (Rolls, 2020, 2021b, 2023b, c). There are many strategies that can be used for navigation (Vijayabaskaran et al., 2025), and spatial view cells open up strategies involving for example viewed landmarks in space "out there" for use in navigation, rather than navigation being primarily from place to place as typically envisaged for rodents in the context of rodent place cells (O'Keefe, 1990; O'Keefe et al., 1998; Hartley et al., 2014; Edvardsen et al., 2020). The last part of navigation to a goal is made very straightforward in this approach, by associating a viewed location represented by spatial view cells with reward, which has been demonstrated for hippocampal spatial view cells in macaques in a spatial view location-with-reward association task (Rolls and Xiang, 2004). Earlier stages of navigation towards a goal could involve route following from viewed landmark to viewed landmark with the hippocampus involved in remembering the sequence of landmarks, as illustrated in a computational model which can also incorporate turns to be made at each landmark to help find the next landmark (Rolls, 2021b). This may provide a model of much human navigation when a set of instructions is given, which typically involve references to visual landmarks such as particular buildings, streets with their names, and visual features such as rivers, bridges, roads, and paths (Rolls, 2021b, 2023b). Moreover, the associatively modifiable recurrent collateral connections in regions such as hippocampal CA3 and the medial parahippocampal cortex where the parahippocampal scene (or place) area is found enable spatial view neurons with overlapping spatial view fields that are therefore co-active and near to each other to be associated to form a continuous attractor network of viewed space, which is a cognitive map (Stringer et al., 2005; Rolls, 2023b). However, this cognitive map is made of viewed spatial location in primates including humans (Stringer et al., 2005; Rolls, 2023b), and not of places where the individual is located as in rodents (O'Keefe and Nadel, 1978). Almost none of human navigation would be simple and would occur without being able to represent these visual features at particular locations in the viewed environment as implemented by spatial view cells (Rolls, 2025a).

The ventromedial visual cortical pathway for scene representations in humans described later includes a retrosplenial place or scene area in the ProStriate cortex (Rolls, 2023c; Rolls et al., 2023a). The hippocampal spatial view cells that receive inputs via this pathway (Rolls, 2025a) may be computationally especially useful in navigation compared to the retrosplenial scene area because computationally the hippocampus receives reward inputs (Rolls et al., 2022b) that can be associated with spatial view representations (Rolls and Xiang, 2005) to guide navigation towards a goal.

Thus there is a revolution in our understanding of navigation in primates and humans compared to rodents. Rodents typically are nocturnal animals with poor vision which live underground in tunnels, and idiothetic navigation from place to place with errors in the path integration being corrected when possible by visual cues may be what their hippocampal system has evolved to implement. Primates including humans are not limited by a poor visual system, and can fixate distant landmarks, and use these for navigation, which has therefore evolved to use visual cues wherever possible, using spatial view cells, so that navigation can be much better than just moving from place to place with the eyes closed, which provides for only poor navigation.

5. A hippocampal episodic memory system in primates including humans, not just a cognitive map for navigation

Another revolution is that emphasis is now on the functions of the primate including human hippocampus in episodic memory (Rolls, 2023c, b; Rolls and Treves, 2024), which does receive support from some complementary research on functions of the rodent hippocampus in episodic memory (Kesner and Rolls, 2015; Eichenbaum, 2017; Sugar and Moser, 2019), rather than the emphasis that has been placed by some on the hippocampus as a cognitive map with a focus on research on place cells in rodents (O'Keefe and Nadel, 1978; Morris et al., 1982, 2025; O'Keefe, 1990; McNaughton et al., 1996; Hartley et al., 2014; Takeuchi et al., 2014; Moser et al., 2017; Morris, 2025). (Although there has been this emphasis by some on place / grid cell encoding in the rodent hippocampus, it is noted that some parts of the rodent extended hippocampal system have boundary-vector cells (Lever et al., 2009; Shine et al., 2019; Alexander et al., 2020) and object-vector cells (Hoydal et al., 2019); and that some rodent hippocampal neurons code time or distance (Eichenbaum, 2014, 2017; Howard and Eichenbaum, 2015; Salz et al., 2016; Abramson et al., 2023). Moreover, rodent hippocampal place cells may respond to local tactile or odor cues, and can be directional so may be influenced by visual room cues (McNaughton et al., 1983; O'Keefe and Burgess, 1996; Hartley et al., 2000; Itskov et al., 2011).)

There is much evidence from humans that the hippocampal system is involved in episodic memory (Scoville and Milner, 1957; Smith and Milner, 1981; Zola-Morgan et al., 1986; Squire and Wixted, 2011; Dede et al., 2016; Moscovitch et al., 2016; Renoult et al., 2019; Kolibius et al., 2023). In investigations of episodic-like memory in macaques, it has been shown that damage to the hippocampal system impairs 'What'-'-Where' memory for where objects have been seen in scenes (Gaffan and Saunders, 1985; Gaffan, 1994; Gaffan and Parker, 1996; Murray et al., 1998; Waters et al., 2023), and Reward-'Where' memory (Hampton et al., 2004). Space, and probably time, are key aspects of hippocampal computation for episodic memory as shown by the effects of brain damage in these and other investigations including some in rodents (Kesner and Rolls, 2015), whereas in contrast object-reward associations and their reversal involve instead the orbitofrontal cortex (Rolls, 2023b, a), and recognition memory involves the perirhinal cortex (Murray and

Mishkin, 1998; Buckley and Gaffan, 2000; Baxter and Murray, 2001; Buckley, 2005; Waters et al., 2023).

Given this background, we recorded from macaque hippocampal neurons in an object-spatial location memory task, and found that some hippocampal neurons responded to a conjunction (combination) of object and viewed spatial location (for example to object 1 in viewed location 1, but not to a different object or location, which provides a solution to this task (Rolls et al., 2005b). Spatial view cells can thus learn associations between objects and their spatial locations, with the CA3 autoassociation or attractor network being the obvious network for this association to form 'what'-'where' episodic memories (Rolls, 2023b; Rolls and Treves, 2024). Similar conjunctive object-location learning has been reported in the human hippocampus (Kolibius et al., 2023).

A key feature of episodic memory is that it must be learned fast, in essentially one trial, so that an episodic memory formed now can be separated from one learned even a few minutes earlier. It is like a 'snapshot' form of memory. Another key feature of an episodic memory is that the whole memory can be recalled from any part in the process called completion, for example the 'what' can be recalled from a 'where' recall cue, and 'where' can be recalled from a 'what' recall cue. We showed that both these properties apply to some macaque hippocampal neurons, in a one-trial object-viewed location memory task, in which the neuronal recall could be of 'what' from 'where', or of 'where' from 'what' (Rolls and Xiang, 2006).

The episodic memory system is also important in primates including humans for remembering where rewards have been seen in the spatial environment. An example might be remembering where one had seen ripe fruit on a tree. Indeed, associations of spatial locations with reward value is a key function potentially support by the major inputs to the human hippocampal system from the orbitofrontal cortex and anterior cingulate cortex, via the perirhinal and entorhinal cortex (Rolls, 2022; Rolls et al., 2022b). We showed that some primate hippocampal neurons can implement this type of episodic memory, with some neurons associating a viewed location with a high reward value, and other neurons associating a different viewed location with a low reward value (Rolls and Xiang, 2005). Moreover, the neurons could rapidly reverse the location to which they respond when the reward locations were reversed (Rolls and Xiang, 2005). The chickadee neurons that respond to viewed cache locations only when they contain a reward are analogous (Chettih et al., 2024). The primate hippocampal neurons were not simply responding to reward, for they hardly responded in an object-reward association memory task (Rolls and Xiang, 2005), a task that is not hippocampal dependent but which is implemented in the primate including human orbitofrontal cortex (Thorpe et al., 1983; Rolls, 2023b, a). The reward or affective or emotional value is a key component of an episodic memory which is also implicated in memory consolidation (Rolls, 2022), and this evidence shows how the primate hippocampus implements this type of episodic memory.

The evidence just described on the primate including human hippocampus indicates that it plays a fundamental role in episodic memory, for what has been seen where and what the reward value was on a particular occasion (Rolls, 2023b, c), with considerable supporting evidence in rodents (Kesner and Rolls, 2015), rather than with the view that the hippocampus is a cognitive map. This fits well with the human literature, that humans with hippocampal / medial temporal lobe damage cannot remember what they saw where yesterday or even a few minutes ago, which looks like a memory deficit, not a navigation deficit (Scoville and Milner, 1957; Smith and Milner, 1981; Zola-Morgan et al., 1986; Corkin, 2002; Squire and Wixted, 2011; Dede et al., 2016; Moscovitch et al., 2016). Of course, the ability to implement episodic memory may be useful to navigation, by helping to remember the sequence of landmarks to follow to reach a goal (Rolls, 2021b, 2023c). Further, the primate including human hippocampus appears to be well connected and to contain useful internal network architecture to implement these computations for episodic memory, as described in the next two sections.

In addition to its functions in episodic memory, it has been suggested that the hippocampus is involved in relational/associative memory, again going beyond primarily spatial functions (Eichenbaum and Cohen, 2014). They proposed that the representational schemes that underlie relational processing of ongoing experiences include: the representation of events as the relations among objects within the context in which they occur; and the interleaving of events and episodes into relational networks, supporting the ability to draw novel inferences from memory. It has also been argued that the hippocampal system is involved in imagining future events by a process described as 'scene construction' (Hassabis et al., 2007; Hassabis and Maguire, 2007), which does imply spatial scene components.

Some key points in this section can be emphasized as follows. The rodent hippocampal place cell and entorhinal grid cell systems have been described as "an "inner GPS" in the brain that makes it possible to orient ourselves in space". What is argued in this section is that a revolution is due, for advances in understanding the hippocampus show that we can go beyond that for in primates including humans the hippocampus is involved in representing space being viewed "out there", and is involved in episodic memory, an example of which is to associate a viewed location in space (not the place where we are) with the object or reward at that location in viewed space, which has great adaptive value.

6. A revolution: cortical pathways to the human hippocampus for spatial view ('where'), objects and faces ('what'), and reward

In rodents, the pathways to the hippocampal system include subcortical for head direction (Cullen and Taube, 2017; Taube, 2017; Graham et al., 2023; Clark et al., 2024); medial entorhinal cortex with grid cells computed using head direction and speed cells that may be useful in the idiothetic update of hippocampal place cells (Moser et al., 2017); allocentric boundary vector cells that may be useful for correcting place cells (Burgess et al., 2000); and time ramping cells in the medial entorhinal cortex (Tsao et al., 2018) that may be useful for generating hippocampal time cells (Rolls and Mills, 2019) and human time sequence cells (Umbach et al., 2020; Khazali et al., 2024).

But none of that is useful for generating primate including human spatial view cells for viewed locations "out there"; nor for hippocampal face and object cells for single visually fixated faces and objects that can be associated with viewed spatial locations; nor for the highly developed reward system in the primate including human orbitofrontal cortex that allows face expressions, other face-related social signals, monetary rewards, food rewards, touch rewards, etc to reach the primate including human hippocampus. A revolution is now in progress in that the cortical pathways for these inputs are now starting to be understood in primates including humans. Some of the evidence for humans is new, and comes from fMRI and magnetoencephalography investigations with Human Connectome Project participants from diffusion tractography, functional connectivity, and effective connectivity which by using time delays can provide information about the directionality of the connectivity from resting state or task-related data (Rolls, 2023b).

First, a ventromedial visual 'Where' cortical pathway for scenes connects from V1 to the prostriate cortex (ProS) where the retrosplenial scene area is located, via ventromedial cortical regions VMV1–3 and VVC to the medial parahippocampal gyrus PHA1–3 where the parahippocampal place area (PPA, (Epstein and Baker, 2019)) (or, better, parahippocampal scene area) is located, and thus (via the medial entorhinal cortex) to the hippocampus (Huang et al., 2021; Rolls et al., 2022c, 2023a, 2024b; Rolls, 2024; Rolls and Turova, 2025) (Fig. 4). This pathway is selectively activated by scenes, relative to faces, body parts, and tools (Rolls et al., 2024a) (Fig. 3), and is also selectively activated during an episodic memory task for object-scene location memory and for reward-scene location memory (Rolls et al., 2024d). An especially interesting feature of this pathway is that it is a ventral cortical stream pathway for 'Where', which operates computationally by forming

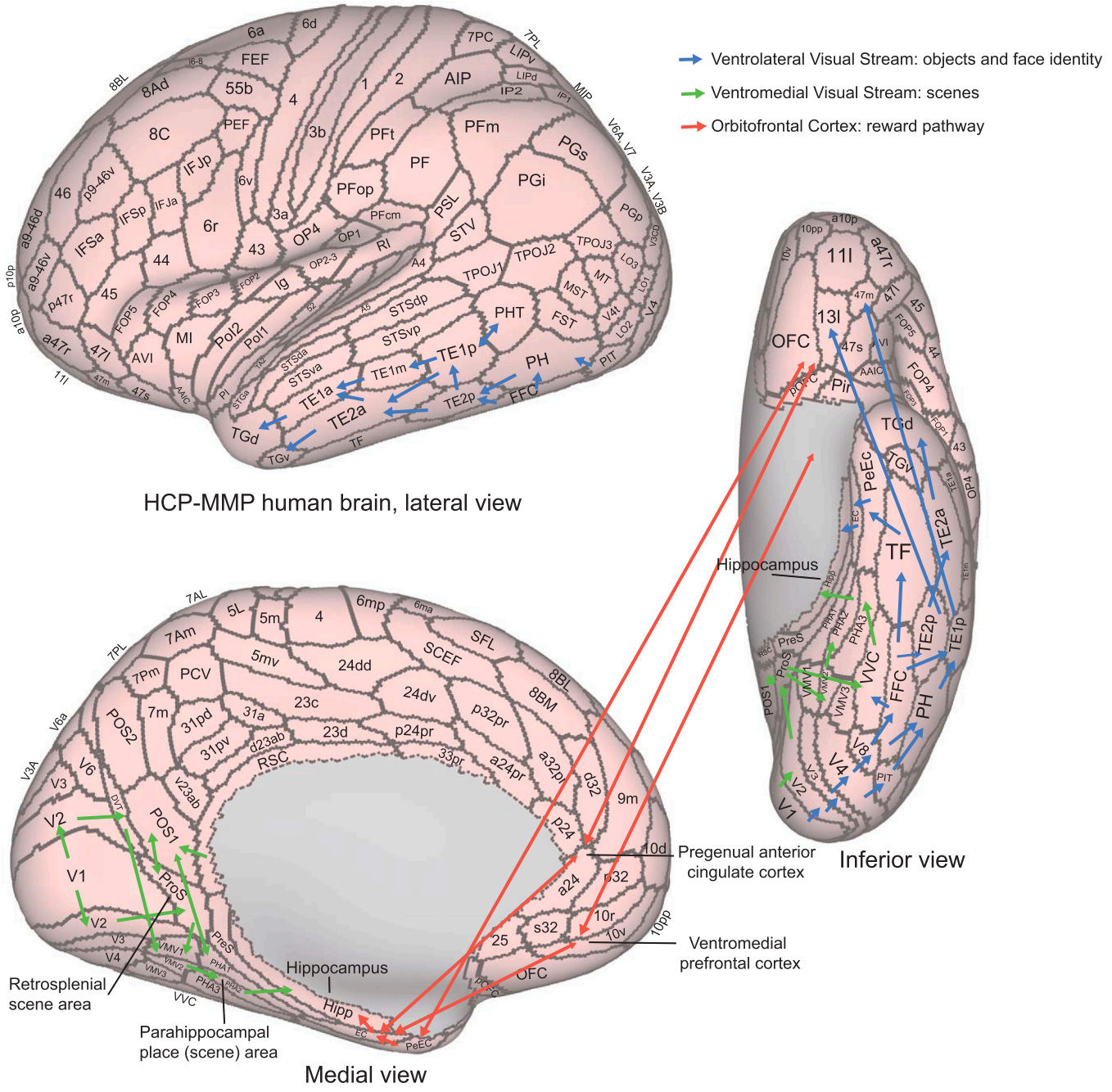

Fig. 4. Three key pathways to the human hippocampus for 'where', 'what', and reward. A ventromedial visual cortical pathway for scenes (green arrows) connects from V1 and V2 to the ProStriate Cortex (Pros) where the retrosplenial scene area is located, and then via ventromedial visual cortical regions VMV1–3 and VVC, and then to the medial parahippocampal gyrus where the parahippocampal place (or, better, scene) area is located, and then in part via the entorhinal cortex to the hippocampus (Huang et al., 2021; Rolls et al., 2022c, 2023a, 2024b). The ventrolateral visual cortical pathway for objects and faces (blue arrows) connects from V1 then V2 and V4 to the fusiform face cortex (FFC) and then via the lateral parahippocampal gyrus (TF), perirhinal cortex (PeEC), and entorhinal cortex to the hippocampus (Rolls et al., 2023a, 2023b). The reward-related medial orbitofrontal cortex (red arrows) connects especially from OFC and pOFC to the perirhinal cortex, then entorhinal cortex to the hippocampus, with in addition routes via the pregenual anterior cingulate cortex and ventromedial prefrontal cortex (Rolls et al., 2022b). In addition, the lateral orbitofrontal cortex 47 m has similar connectivity to reach the hippocampus (Rolls et al., 2022b) (see Fig. 6). The pathways were analysed with effective connectivity and functional connectivity with fMRI and magnetoencephalography, and diffusion tractography in 171 Human Connectome Project participants. The pathways are shown on the parcellation of the human cortex in the HCP-MMP atlas (Glasser et al., 2016a), and in its extended version HCPex (Huang et al., 2022). The regions are shown on images of the human brain in inflated form with the sulci expanded sufficiently to allow the regions within the sulci to be shown. The abbreviations for each cortical region are provided in Table S1, and the cortical regions are illustrated in Fig. S1.

feature combinations for spatial features close together in scenes, and then linking these using recurrent collateral connections and associative learning to form a continuous attractor model of a scene, assisted by gain modulation by gaze direction to link visual fixation patches across saccades (Rolls, 2025a) (Fig. 5). Because the system utilises visual features in scenes, it is locked to allocentric space (Rolls, 2025a). This pathway produces spatial view cells that represent the location in space being viewed, which in the hippocampus can be associated with the object and/or reward at the viewed location, to implement an episodic memory as described in the next section.

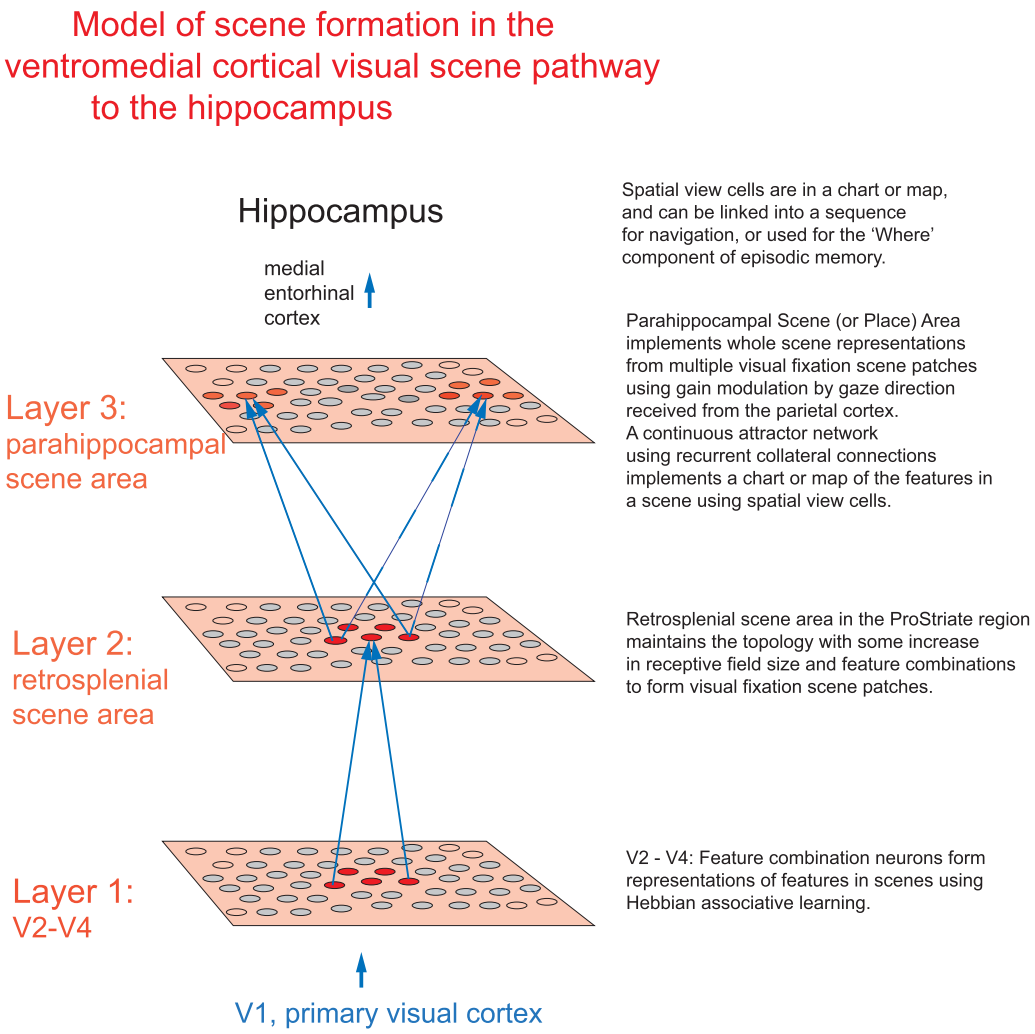

Fig. 5. The theory and model VisSceneNet for building hippocampal spatial view cells and scene representations along the ventromedial cortical visual scene pathway. This is a three-layer feedforward network, with competitive learning implemented using the forward synaptic connections at each layer, and short-range convergence from layer to layer. The input is from V1, and is produced from a scene by Gabor filtering to produce a V1-like representation. Visual fixation scene patches for a single fixation of a scene are produced by Layer 2. Layer 3 implements gain modulation by world-based gaze direction to map visual fixation scene patches into a whole scene representation in Layer 3. The whole scene representation in Layer 3 makes use of associatively modifiable recurrent collateral connections to form a continuous attractor network for the whole scene. Nearby features in a scene are more strongly linked in the continuous attractor because they are more likely to be co-active, but no topographical organization of space on the surface of the cortex is needed in Layer 3.

Second, the ventrolateral visual 'What' cortical pathway for faces and objects connects from V1 via V2, V3 and V4, to the fusiform face cortex FFC and then to inferior temporal visual cortex TE1p and TE2p and then the lateral parahippocampal cortex TF which connects via perirhinal (PeEc) and entorhinal (EC) cortex to the hippocampus (Rolls et al., 2023a, 2023b) (Fig. 4). In this pathway we discovered transform including view invariant neuronal representations of faces (Perrett et al., 1982; Rolls, 1984, 2025c) and objects (Booth and Rolls, 1998) in macaques, which are ideal as a 'What' input to the hippocampus because any episodic memory formed will generalize to other views of the people or objects (Rolls, 2021e). This pathway is selectively activated by faces, relative to scenes, body parts, and tools (Rolls et al., 2024a) (Fig. 3), and is also activated during an episodic memory task for object-scene location memory (Rolls et al., 2024d).

Third, the very highly developed primate including human orbitofrontal cortex where the reward and emotional value of objects, faces, money and social stimuli are represented (Rolls, 2019a, 2023a, 2026a) connects in part via the ventromedial prefrontal cortex and anterior cingulate cortex, then perirhinal and entorhinal cortex, to the hippocampus (Figs. 4 and 6) to provide the reward inputs to the hippocampus which are an important part of episodic memories, and which are implicated in memory consolidation. The extent of this output from the orbitofrontal cortex to the hippocampus is quite remarkable (Fig. 6). Moreover, the human orbitofrontal cortex has connectivity to the basal forebrain cholinergic systems (Rolls et al., 2022b) (Fig. 6) that release acetylcholine in the neocortex and hippocampus to rewarding, punishing, and novel stimuli, and are implicated in memory consolidation (Rolls, 2022). In contrast, the rodent orbitofrontal cortex is far less developed (Wise, 2008) and operates very differently from the primate orbitofrontal cortex in that the rodent orbitofrontal cortex is not involved only in rewards but contains movement-related neurons (Wilson et al., 2014; Sharpe et al., 2015; Izquierdo, 2017), so is computationally quite different (Rolls, 2023b).

Thus overall the primate including human hippocampus receives key information about spatial view for locations in space out there via a ventromedial 'Where' visual cortical pathway; about what face or object is present at the fixated location (Rolls et al., 2003; Aggelopoulos and Rolls, 2005) via the highly developed ventrolateral 'What' visual cortical pathway; and about reward value including for face identity and expression (Rolls et al., 2006a), and social (Kringelbach and Rolls, 2003) and monetary (O'Doherty et al., 2001; Rolls et al., 2020) rewards from the orbitofrontal cortex (Rolls, 2019a, 2023b, 2025d), with no closely

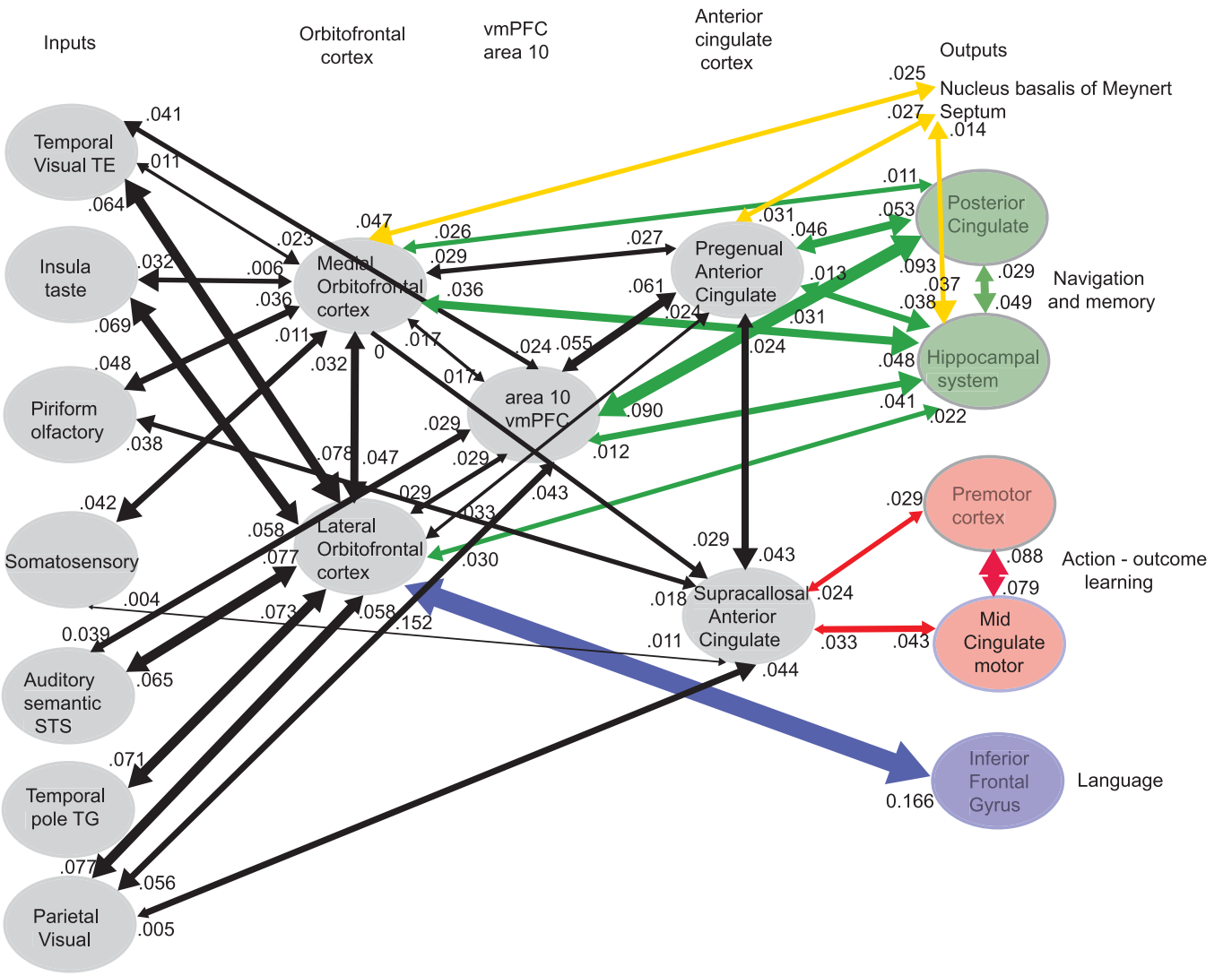

Fig. 6. Effective connectivity of the orbitofrontal cortex, vmPFC, and anterior cingulate cortex shown in the middle, with inputs on the left and outputs including to the hippocampal formation via perirhinal and entorhinal cortex on the right. The cortical regions included for each of the 5 central ellipses are defined by Rolls et al. (2022b). The width of the arrows is proportional to the effective connectivity in the highest direction, and the size of the arrows reflects the strength of the effective connectivity in each direction. The effective connectivities shown are for the strongest link where more than one link between regions applies for a group of brain regions. Effective connectivities with hippocampal memory system regions are shown in green; with premotor / mid-cingulate regions in red; with inferior prefrontal language system in blue; and in yellow to the basal forebrain nuclei of Meynert which contains cholinergic neurons that project to the neocortex and to the septal nuclei which contain cholinergic neurons that project to the hippocampus. The Somatosensory regions include 5 and parietal PF and PFop, which also connect to the pregenual anterior cingulate but are not shown for clarity; and the Parietal regions include visual parietal regions 7, PGi and PFm. The connectivity with dorsolateral prefrontal cortex is not included here for clarity. Connectivity is shown for the five groups in the centre of the Figure, and does not include for example connectivity between somatosensory and premotor cortical regions. (After Rolls et al. 2022b).

equivalent pathways in rodents.

7. The computational architecture of the primate / human neocortical – hippocampal system for episodic memory

Fig. 7 shows that the computational architecture of the primate / human neocortical – hippocampal system fits it well for episodic memory. The hippocampus receives 'Where', 'What', and Reward / Emotion inputs from neocortical regions, and via the entorhinal cortex inputs enable these three key components of episodic memory to be associated together in hippocampal CA3 (Rolls and Treves, 2024). Our theory is that the dentate mossy fibre inputs select a random new set of CA3 neurons for each new episodic event / memory, and that the perforant path inputs to CA3 show associative long-term potentiation during the learning, and are used to trigger recall (Treves and Rolls, 1992; Rolls and Treves, 2024) (see also (Borzello et al., 2023)). The CA3 recurrent collaterals which extend throughout the primate hippocampus (Kondo et al., 2009) form an autoassociation or attractor network with associative synaptic plasticity to link the random set of CA3 neurons selected for a memory to be associated together, so that later during recall any part of the memory presented as a recall cue (e.g. the 'what' component) will retrieve the whole set of neurons in CA3 in the process of completion (Treves and Rolls, 1992; Rolls and Treves, 2024) as explained in *Brain Computations and Connectivity* (Rolls, 2023b). The same idea of a random new set of CA3 neurons for each new episodic memory (Treves and Rolls, 1992) has been described as a 'barcode' in the food-caching chickadee (Chettih et al., 2024). Neurogenesis in the dentate granule cells (Deng et al., 2010; Gage, 2025) can help to generate a new random set of CA3 neurons to be active for new episodic events / memories (Rolls, 2016a, 2023b; Rolls and Treves, 2024).

This computational theory of the hippocampus also provides the only quantitative theory of how information is recalled from the

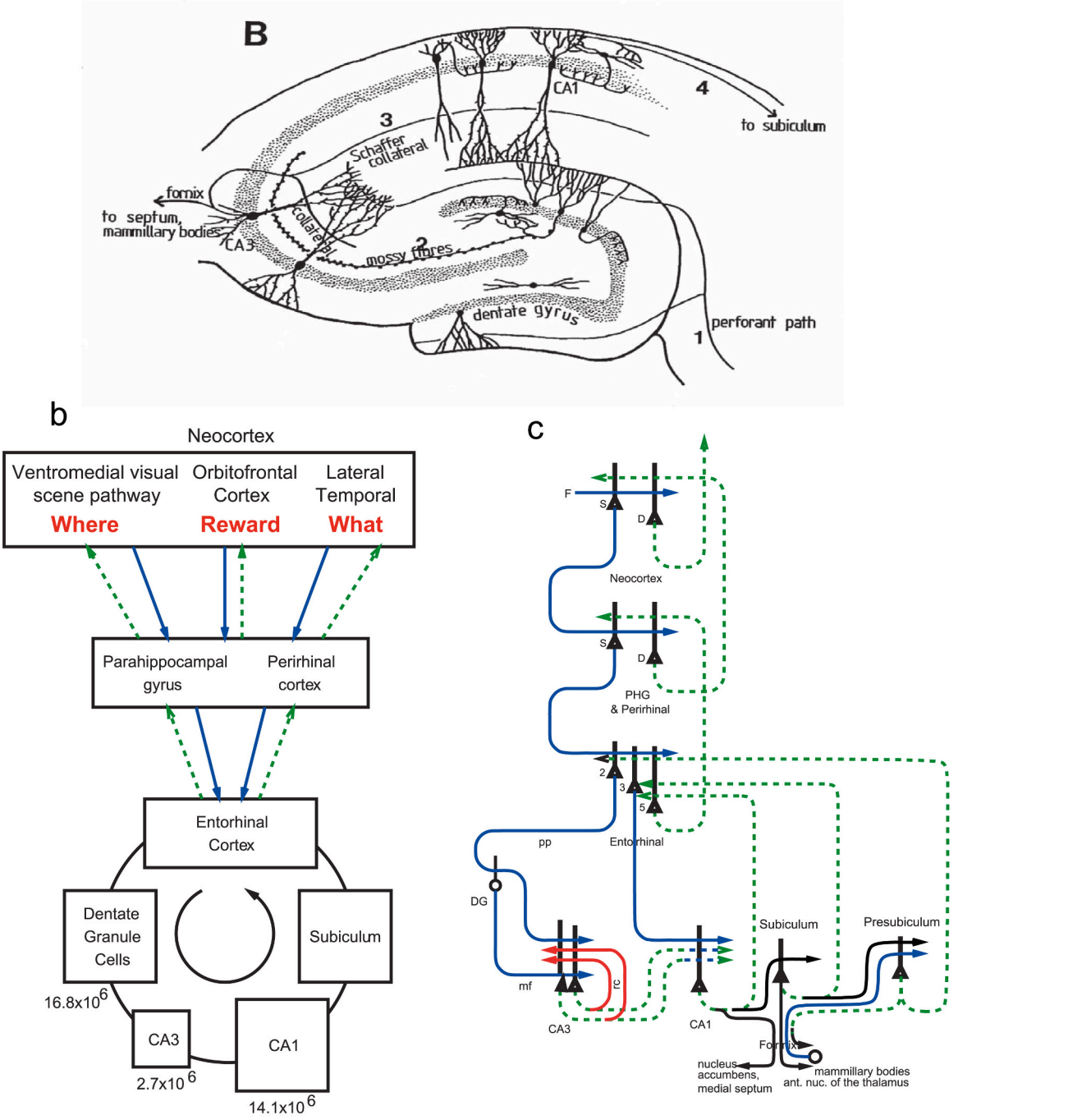

Fig. 7. a. Connections within the hippocampus. Inputs reach the hippocampus through the perforant path (1) which makes synapses with the dendrites of the dentate granule cells and also with the apical dendrites of the CA3 pyramidal cells. The dentate granule cells project via the mossy fibres (2) to the CA3 pyramidal cells. The well-developed recurrent collateral system of the CA3 cells is indicated. The CA3 pyramidal cells project via the Schaffer collaterals (3) to the CA1 pyramidal cells, which in turn have connections (4) to the subiculum. b-c. The human/ primate hippocampus receives neocortical input connections (blue) not only from the 'what' lateral temporal lobe and 'where' ventromedial visual cortical scene pathway, but also from the 'reward' prefrontal cortex areas (orbitofrontal cortex, vmPFC, and anterior cingulate cortex) for episodic memory storage; and has return backprojections (green) to the same neocortical areas for memory recall. There is great convergence via the parahippocampal gyrus, perirhinal cortex, and dentate gyrus in the forward connections down to the single network implemented in the CA3 pyramidal cells, which have a highly developed recurrent collateral system (red) to implement an attractor episodic memory by associating the what, where and reward components of an episodic memory. b: Block diagram. c: Some of the principal excitatory neurons and their connections in the pathways. Time and temporal order are also important in episodic memory, and may be computed in the entorhinal-hippocampal circuitry (Rolls and Mills, 2019). Abbreviations - D: Deep pyramidal cells. DG: Dentate Granule cells. F: Forward inputs to areas of the association cortex from preceding cortical areas in the hierarchy. mf: mossy fibres. PHG: parahippocampal gyrus and perirhinal cortex. pp: perforant path. rc: recurrent collateral of the CA3 hippocampal pyramidal cells. S: Superficial pyramidal cells. 2: pyramidal cells in layer 2 of the entorhinal cortex. 3: pyramidal cells in layer 3 of the entorhinal cortex. The thick lines above the cell bodies represent the dendrites. The numbers of neurons in different parts of the hippocampal trisynaptic circuit in humans (Rogers Flattery et al., 2020) are shown in (b), and indicate very many dentate granule cells, consistent with expansion encoding and the production of sparse uncorrelated representations prior to CA3 (Rolls, 2016a, 2021a).

hippocampus to the neocortex (Rolls, 1989, 2023b; Rolls and Treves, 1994, 2024; Treves and Rolls, 1994; Rolls et al., 2024c). In this theory, the backprojections to the neocortex (Fig. 7) are associatively modifiable at the time of learning, so that the backprojection synapses in (at least one stage of (McClelland et al., 1995)) the multistage backprojection pathway show associative modification to associate the output of the hippocampus with whatever neocortical neurons are active during the learning. When later a partial recall cue for an episodic memory is applied as the input to the hippocampus, there is completion in CA3, and via CA1 the multistage backprojection pathways to the neocortex recall using pattern association at each stage the memory back to all three potential neocortical regions, for 'where', 'what', and reward.

The question arose about how many backprojection synapses are needed onto each neocortical neuron in the backprojection pathways for as many memories to be recalled back to the neocortex as could be stored in CA3. The answer emerged when we realised that the multistage backprojection pattern association pathway from the hippocampus to the neocortex (Fig. 7) could be considered as successive recall loops in an autoassociation network, resulting in an estimate that there should be as many synapses on each neuron in the backprojection pathways for recall as on each CA3 neuron (for that number sets the number of memories that can be stored in CA3 (with appropriate weighting by the sparseness of the representation) (Treves and Rolls, 1994). Given that there are approximately 17,500 CA3 to CA3 synapses on each CA3 neuron in humans (Watson et al., 2025), the number of synapses on each neuron in the backprojection pathways should be of the same order (at least more than 10,000), and this is the only quantitative theory for why there are approximately as many backprojection synapses on each neocortical neuron as forward or recurrent connection synapses (Treves and Rolls, 1994; Rolls, 2021d, 2023b; Rolls and Treves, 2024).

This whole neocortical-hippocampal computational system thus is well set up for episodic memory (Rolls and Treves, 2024; Rolls, 2025c). How well would the computational architecture work if it were purely a spatial map, like a cognitive map? The original capacity estimates for CA3 (or any other recurrent associative network) for storing place cell information as charts or maps in a continuous attractor network were relatively high, with over one hundred charts estimated as possible (Battaglia and Treves, 1998). But more recently, it has been shown that the storage capacity is considerably reduced if each neuron is randomly assigned more than one place field and the place fields are of different sizes (Schonsberg et al., 2024) (which is a good model for bats in a long runway for CA1 though not CA3 cells which have close to 1 place field (Eliav et al., 2021) and for rodents too (Panikkassery and Treves, 2025)). The implication is that using hippocampal CA3 as a purely spatial, map or chart, continuous attractor is inefficient, as disorder reduces its storage capacity well below what it could be in an optimally engineered network (Rolls and Treves, 2024). On the other and, if the CA3 network stores both continuous spatial and associated discrete object information (with a random set of neurons with binary rates representing each object) (Rolls et al., 2002) (Fig. 8), then the whole CA3 system might operate well to associate viewed spatial locations with objects and rewards, which is what is needed for episodic memory.

The implication is that use of the primate including human hippocampus to store associations between viewed locations, and objects and rewards for episodic memory seems to be a computationally attractive use of the computational architecture provided by the hippocampus, rather than it being a primarily spatial map or chart.

8. New vistas: how the hippocampus may contribute to learning new semantic representations and the consolidation of memories

A key feature of the human brain is that semantic representations are found in the anterior temporal lobe (Patterson et al., 2007; Peelen and Caramazza, 2012; Bonner and Price, 2013; Hickok and Poeppel, 2015; Kemmerer, 2015; Milton et al., 2021; Rolls et al., 2022a; Rolls, 2023b).

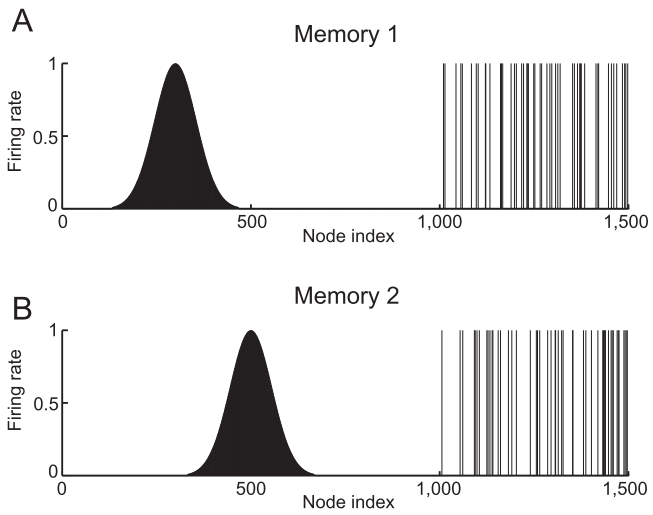

Fig. 8. Autoassociation attractor networks such as hippocampal CA3 can store association between continuous spatial representations (neurons 1–1000) and discrete object and face representations (neurons 1001–1500). The types of firing patterns stored in continuous attractor networks are illustrated for the patterns present on neurons 1–1000 for Memory 1 (panel A, when the firing is that produced when the spatial state represented is that for location 300), and for Memory 2 (panel B, when the firing is that produced when the spatial state represented is that for location 500). The continuous nature of the spatial representation results from the fact that each neuron has a Gaussian firing rate that peaks at its optimal location. This mixed network also contains representations that consist of discrete subsets of active binary firing rate neurons in the range 1001–1500 with a random set of neurons representing each object or face. During learning, Memory 1 is stored in the synaptic weights, then Memory 2, etc, and each memory contains part that is continuously distributed to represent physical space, and part that represents a discrete event or object. The spatial and object representations are bound together by being simultaneously present when the event is stored. (From Rolls, Stringer and Trappenberg, 2002, where further details can be found).

These semantic representations are of knowledge about the world, for example about categories such as vehicles, animals, trees, humans, lakes, rivers, fruit, food, and oranges. This semantic information is quite distinct from an episodic memory, which might describe what happened where, who was present, the pleasantness or unpleasantness, and when it happened (Squire and Wixted, 2011; Bennett and Stark, 2016; Moscovitch et al., 2016; Rolls and Treves, 2024; Rolls et al., 2024d). Although previously learned semantic representations are unimpaired by hippocampal damage that produces an episodic memory deficit, the learning of new semantic information may be impaired after hippocampal damage (Duff et al., 2019).

To develop an understanding of how the hippocampus may be involved in learning new semantic representations, we investigated the connectivity of the hippocampus with semantic cortical regions (Rolls et al., 2022a, 2025), with some of the results shown in Fig. 9. This reveals very much connectivity between the hippocampus and anterior temporal lobe semantic regions. We then hypothesized that if related episodic memories were recalled while thinking about them, slow learning over the time course of the recall might help what was in common between the related episodic memories to be incorporated into anterior temporal lobe memories for the category of objects that was present in the recalled memories, and this was demonstrated to be possible in a neuronal network model and simulation (Rolls et al., 2025). More specifically, I propose that the hippocampal memory system uses temporal and/or spatial contiguity to bind together components into episodic memories, and that subsequent recall of these bound components of related episodic memories to the neocortex (by mechanisms that we have described (Treves and Rolls, 1994; Rolls and Treves, 2024)) helps the neocortex to build semantic memories using these already

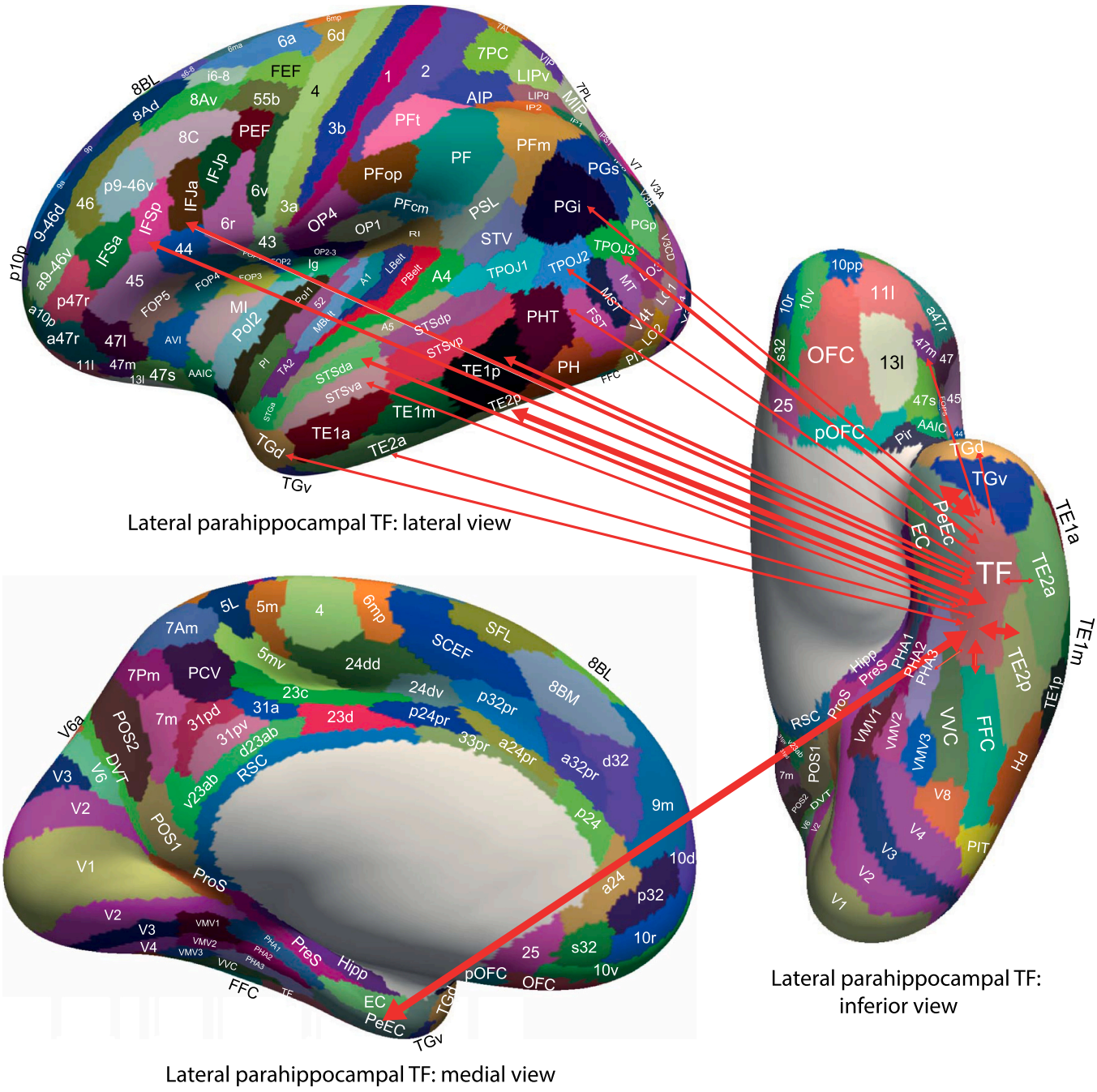

Fig. 9. Connectivity of the hippocampal episodic memory system includes connectivity with many cortical regions in and connected to anterior temporal lobe semantic memory systems. The connectivity of the lateral parahippocampal cortex region TF which includes connectivity to semantic systems related to 'What' representations is shown (see text). The effective connectivity between cortical regions in the Human Connectome Project Multimodal Parcellation atlas (HCP-MMP) (Glasser et al., 2016a; Huang et al., 2022) is shown. A list of the cortical regions in the HCP-MMP atlas is shown in the Supplementary Material. The width of the arrows represents the magnitude of the effective connectivity, and the size of the arrowheads the magnitude in each direction. The data are from effective connectivity matrices computed from resting state timeseries in 171 HCP participants imaged at 7 T (Rolls et al., 2022a, 2022c, 2023a). (After (Rolls et al., 2025)).

bound components, and slow neocortical learning using for example a memory trace learning rule with a time period of several seconds (Rolls et al., 2025; Rolls, 2026b).

The main point here is that in humans it appears possible to take forward our understanding of hippocampal function and how this may relate to something as cognitive as forming new semantic categories by recalling previous related episodic memories, and this appears to be another difference beyond research in rodents focussing on place cells and maps, for semantic memories become highly developed in humans and are part of the language system, and involve the anterior temporal lobe, which is very highly developed in humans (Rolls et al., 2022a; Rolls, 2023b). Semantic systems are not a feature of research in rodents.

A difference between rodent and human semantic representations is that humans have 'concept cells' which are multimodal, responding for example to the sight of a person (with one example Jennifer Anniston), but also to the sound of the person's voice, the written name of the person or object, to places in which they have been seen, and even to their friends (Quian Quiroga et al., 2005; Quian Quiroga, 2012, 2013; Ison et al., 2015; Rey et al., 2015; De Falco et al., 2016; Bausch et al., 2021; Mackay et al., 2024). There is some evidence for multimodal cells

in macaques that have some properties of concept cells (Rolls, 2023d), but clearly there is no similar extension to word-based descriptors. In this context, it is very likely that word-based descriptors are important in helping separate out semantic categories, as the words themselves are relatively orthogonal to each other (Rolls, 2026b). Once semantic representations have been built in the anterior temporal lobe (Rolls et al., 2025; Rolls, 2026b), they will of course have access to the hippocampal memory system as shown by the connectivity in humans (Rolls et al., 2025) (Fig. 9), so that the full concept of a person as represented by concept cells can be part of an episodic memory, such as that one saw a particular person at a particular meeting in a particular place.

There is previous research on memory consolidation, though that does not typically deal with what has just been described which is the mechanism by which new semantic memories are built using inputs from the hippocampal episodic memory system (Rolls et al., 2025; Rolls, 2026b). One previous approach has been to note that there are complementary learning systems, a hippocampal episodic and a neocortical long-term memory system (McClelland et al., 1995), with ideas now developing about possible mechanisms (McClelland et al., 2020). Another approach has been to invoke hippocampal-neocortical dialogue / replay during sharp-wave ripples and sleep (Wilson and McNaughton, 1994; Buzsaki, 2015; Chen and Wilson, 2017, 2023; Foster, 2017; Skelin et al., 2019; Yang et al., 2024). However these approaches do not address the key issues involved, such as how the correct neocortical neurons are brought into activity when an episodic memory is retrieved, what the capacity of the retrieval process is in terms of the number of memories that can be recalled to neocortex, how the capacity depends on the number of synapses on each neuron in the backprojection pathway, why the backprojection pathways have to be multistage, and why there are as many backprojections as forward connections between every adjacent neocortical stage in a hierarchy, which are all addressed quantitatively by our computational theory of the hippocampus (Rolls, 1989, 2026b; Rolls and Treves, 1994, 2024; Treves and Rolls, 1994; Rolls et al., 2024c).

A more recent approach to memory consolidation has been based on the connectivity of the human brain, showing that the ventromedial prefrontal cortex provides a route for orbitofrontal cortex reward value information to reach the hippocampal memory system providing a route for reward value and affect to be incorporated into episodic memory (Rolls et al., 2022b). It is proposed that when reward-related or aversive memories are recalled from the hippocampal memory system, the affective component which implies importance of the memory leads to more and deeper processing of those affective memories, which promotes greater memory consolidation in the neocortex (Rolls, 2022).

Further, it was found that the human medial orbitofrontal cortex (pOFC region) has effective connectivity directed to the basal forebrain magnocellular nucleus of Meynert (yellow in Fig. 6 (Rolls et al., 2022b)), which contains cholinergic neurons that project to the neocortex in humans (Mesulam, 1990; Zaborszky et al., 2008, 2018). Moreover, it has been shown that different magnocellular neurons in the basal nucleus which are probably cholinergic respond to reinforcing (rewarding, or punishing), or novel, stimuli (Wilson and Rolls, 1990a, b, c), all represented in the orbitofrontal cortex (Rolls et al., 2005a; Rolls, 2019b, a). It is therefore proposed (Rolls, 2022) that cholinergic activation by these types of 'salient' stimuli can be utilised to enhance memory storage and consolidation in the neocortex when these rewarding, punishing, or novel stimuli are encountered or are recalled from the hippocampus, which is evolutionarily adaptive by facilitating memory storage when rewarding, punishing, or novel environmental situations are encountered or remembered (Rolls and Deco, 2015; Rolls, 2021c, 2026b).

It was also found that the human pregenual anterior cingulate cortex (regions subgenual 25 and 10r) has effective connectivity directed to the septal nuclei (yellow in Fig. 6 (Rolls et al., 2022b)), which contains cholinergic neurons that project to the hippocampus in humans (Mesulam, 1990; Zaborszky et al., 2008, 2018). It is also proposed that this may in a similar way enhance the storage of episodic memories in the hippocampus when rewarding or aversive stimuli are present (Rolls, 2022, 2026b).

In summary, in this section it has been shown how hippocampal binding of components into episodes may help in the formation of new semantic memories in the neocortex (Rolls et al., 2025); and how reward value processing may be a factor in memory consolidation by increased processing of recalled episodic memories with affective value, and by reward, aversive and novelty-related influences from the orbitofrontal cortex, vmPFC and anterior cingulate cortex via cholinergic pathways on memory storage in the neocortex and hippocampus (Rolls, 2022).

9. Concluding remarks

A number of revolutions, turning round of concepts, in our understanding of hippocampal functions in primates including humans have been described, which go beyond place cells and cognitive maps in rodents. A point being made is that although the research on the rodent hippocampus is extremely interesting, we are now in a position where we can build on and go beyond that to understand how the hippocampal system operates in primates including humans.

First, research in rodents has emphasised hippocampal place cells and medial entorhinal cortex grid cells for places, but in primates including humans, and in some birds, hippocampal system neurons respond to spatial view, to where the individual looks in space.

Second, research in rodents has emphasised navigation as moving from hippocampal encoded place to place using self-motion, which is almost 'blind' navigation, with a path integration place system that when it drifts can be reset by for example allocentric boundary vector cells. In primates including humans, the highly developed foveal visual system and hippocampal spatial view cells allow use of visual landmarks, which leads to completely different strategies for navigation.

Third, research in primates including humans emphasises the role of the hippocampus in episodic memory, in which objects including faces, viewed spatial locations, and rewards are associated together to form a unique episodic memory, which can later be recalled from any of its components, using associations made in hippocampal CA3.

Fourth, in primates including humans the pathways to the hippocampus are now becoming understood, with a ventromedial cortical visual pathway for scenes using spatial view cells; with the ventrolateral cortical visual pathway for visually fixated faces and objects; and with reward inputs from the highly developed orbitofrontal cortex reaching the hippocampus via the ventromedial prefrontal cortex and anterior cingulate cortex. Similar equivalent and highly developed cortical pathways in rodents are not described or are much less clear. The extensive connectivity of the human hippocampal system with the orbitofrontal cortex reward and emotion system is important not only in episode memory by providing reward / emotion inputs to the hippocampal episodic memory system, and for providing the goals for navigation, but also it is proposed for memory consolidation.

Fifth, all of this fits well in primates including humans with the quantitative theory of hippocampal CA3 circuitry as being useful for episodic memory, and with the highly developed pathways from the hippocampus to the neocortex being appropriate to recall the same number of episodic memories as can be stored in the hippocampus.

Sixth, in humans, the major connectivity from the hippocampal episodic memory system to the anterior temporal lobe semantic cortical regions is now becoming understood, and is stimulating new approaches to how the hippocampus may help semantic cortical regions build semantic memories (Rolls et al., 2025), with no clear equivalent yet understood in rodents.

Seventh, in humans reward value processing may be a factor in memory consolidation by increased processing of recalled episodic memories with affective value; and by reward, aversive and novelty-related influences from the orbitofrontal cortex, vmPFC, and anterior cingulate cortex via cholinergic pathways on memory storage in the neocortex and hippocampus (Rolls, 2022).

In this paper I have thus built on the evidence on hippocampal function in rodents, but have gone beyond that by showing that key revolutions in our understanding of the primate including human hippocampal system and its connected cortical regions are taking place that are very important in understanding what the primate including human hippocampus does, that is, what and how it computes (Rolls, 2026b). This understanding is important, for it helps in the understanding of the episodic memory, memory consolidation, and other problems that can follow medial temporal lobe damage and damage to related systems such as the ventromedial prefrontal cortex in humans (Scoville and Milner, 1957; Smith and Milner, 1981; Zola-Morgan et al., 1986; Feigenbaum and Morris, 2004; Squire and Wixted, 2011; Dede et al., 2016; Moscovitch et al., 2016; Bonnici and Maguire, 2018; McCormick et al., 2018; De Luca et al., 2019; Renoult et al., 2019; Rolls, 2022, 2026b).

Author contributions

The author wrote the paper.

Ethical permissions

No data were collected as part of the research described here.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Generative AI and AI-assisted technologies in the writing process

None were used.

Declaration of Competing Interest

The author declares no competing interests.

Acknowledgements

Many wonderful colleagues have participated in the research described here, and their collaboration and important contributions are gratefully acknowledged, and are evident in the papers cited. The author warmly acknowledges helpful discussions with Dr. Sylvia Wirth (CNRS Marc Jeannerod, Lyon, France). The author also acknowledges use of data from the Human Connectome Project (Van Essen et al., 2012; Barch et al., 2013; Glasser et al., 2016b) in some of the research described here, and of the Human Connectome Project Multimodal Parcellation of the human cerebral cortex (Glasser et al., 2016a), which is also available in an extended version with 66 subcortical regions added (Huang et al., 2022).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2025.106492.

Data availability

The implementation of the pattern association, attractor, and competitive networks that are part of some of the computational research described here was as described by Rolls (2016b), (2021c), (2023b), and sample Matlab code for each of these classes of network as described there is made available at https://www.oxcns.org/NeuronalNetworkSimulationSoftware.html, as are .pdfs of many of the papers referred to, and a .pdf of *Brain Computations and Connectivity* (Rolls, 2023b), which is Open Access.

References

Abramson, S., Kraus, B.J., White, J.A., Hasselmo, M.E., Derdikman, D., Morris, G., 2023. Flexible coding of time or distance in hippocampal cells. Elife 12.
Aggelopoulos, N.C., Rolls, E.T., 2005. Natural scene perception: inferior temporal cortex neurons encode the positions of different objects in the scene. Eur. J. Neurosci. 22, 2903–2916.
Alexander, A.S., Carstensen, L.C., Hinman, J.R., Raudies, F., Chapman, G.W., Hasselmo, M.E., 2020. Egocentric boundary vector tuning of the retrosplenial cortex. Sci. Adv. 6, eaaz2322.
Andersen, P., Morris, R.G.M., Amaral, D.G., Bliss, T.V.P., O'Keefe, J., 2007. The Hippocampus Book. Oxford University Press, Oxford and New York.
Baraduc, P., Duhamel, J.R., Wirth, S., 2019. Schema cells in the macaque hippocampus. Science 363, 635–639.
Barch, D.M., Burgess, G.C., Harms, M.P., Petersen, S.E., Schlaggar, B.L., Corbetta, M., Glasser, M.F., Curtiss, S., Dixit, S., Feldt, C., Nolan, D., Bryant, E., Hartley, T., Footer, O., Bjork, J.M., Poldrack, R., Smith, S., Johansen-Berg, H., Snyder, A.Z., Van Essen, D.C., Consortium, W.U.-M.H., 2013. Function in the human connectome: task-fMRI and individual differences in behavior. Neuroimage 80, 169–189.
Battaglia, F.P., Treves, A., 1998. Attractor neural networks storing multiple space representations: a model for hippocampal place fields. Phys. Rev. E 58, 7738–7753.
Bausch, M., Niediek, J., Reber, T.P., Mackay, S., Bostrom, J., Elger, C.E., Mormann, F., 2021. Concept neurons in the human medial temporal lobe flexibly represent abstract relations between concepts. Nat. Commun. 12, 6164.
Baxter, M.G., Murray, E.A., 2001. Impairments in visual discrimination learning and recognition memory produced by neurotoxic lesions of rhinal cortex in rhesus monkeys. Eur. J. Neurosci. 13, 1228–1238.
Bennett, I.J., Stark, C.E., 2016. Mnemonic discrimination relates to perforant path integrity: An ultra-high resolution diffusion tensor imaging study. Neurobiol. Learn. Mem. 129, 107–112.
Bonner, M.F., Price, A.R., 2013. Where is the anterior temporal lobe and what does it do? J. Neurosci. 33, 4213–4215.
Bonnici, H.M., Maguire, E.A., 2018. Two years later - Revisiting autobiographical memory representations in vmPFC and hippocampus. Neuropsychologia 110, 159–169.
Booth, M.C.A., Rolls, E.T., 1998. View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. Cereb. Cortex 8, 510–523.
Borzello, M., Ramirez, S., Treves, A., Lee, I., Scharfman, H., Stark, C., Knierim, J.J., Rangel, L.M., 2023. Assessments of dentate gyrus function: discoveries and debates. Nat. Rev. Neurosci. 24, 502–517.
Brown, T.I., Carr, V.A., LaRocque, K.F., Favila, S.E., Gordon, A.M., Bowles, B., Bailenson, J.N., Wagner, A.D., 2016. Prospective representation of navigational goals in the human hippocampus. Science 352, 1323–1326.
Buckley, M.J., 2005. The role of the perirhinal cortex and hippocampus in learning, memory, and perception. Q. J. Exp. Psychol. B 58, 246–268.
Buckley, M.J., Gaffan, D., 2000. The hippocampus, perirhinal cortex, and memory in the monkey. In: Bolhuis, J.J. (Ed.), Brain, Perception, and Memory: Advances in Cognitive Neuroscience. Oxford University Press, Oxford, pp. 279–298.
Buffalo, E.A., 2025. Visual exploration and the primate hippocampal formation. Hippocampus 35, e23673.
Burgess, N., 2008. Spatial cognition and the brain. Ann. N. Y. Acad. Sci. 1124, 77–97.
Burgess, N., Jackson, A., Hartley, T., O'Keefe, J., 2000. Predictions derived from modelling the hippocampal role in navigation. Biol. Cyber 83, 301–312.
Burgess, N., O'Keefe, J., 1996. Neuronal computations underlying the firing of place cells and their role in navigation. Hippocampus 6, 749–762.
Butler, W.N., Smith, K.S., van der Meer, M.A.A., Taube, J.S., 2017. The head-direction signal plays a functional role as a neural compass during navigation. Curr. Biol. 27, 1259–1267.
Buzsaki, G., 2015. Hippocampal sharp wave-ripple: a cognitive biomarker for episodic memory and planning. Hippocampus 25, 1073–1188.
Cahusac, P.M.B., Miyashita, Y., Rolls, E.T., 1989. Responses of hippocampal formation neurons in the monkey related to delayed spatial response and object-place memory tasks. Behav. Brain Res. 33, 229–240.
Chadwick, M.J., Hassabis, D., Weiskopf, N., Maguire, E.A., 2010. Decoding individual episodic memory traces in the human hippocampus. Curr. Biol. 20, 544–547.
Chadwick, M.J., Mullally, S.L., Maguire, E.A., 2013. The hippocampus extrapolates beyond the view in scenes: an fMRI study of boundary extension. Cortex 49, 2067–2079.
Chen, Z., Wilson, M.A., 2017. Deciphering neural codes of memory during sleep. Trends Neurosci. 40, 260–275.
Chen, Z.S., Wilson, M.A., 2023. How our understanding of memory replay evolves. J. Neurophysiol. 129, 552–580.
Chettih, S.N., Mackevicius, E.L., Hale, S., Aronov, D., 2024. Barcoding of episodic memories in the hippocampus of a food-caching bird. Cell 187, 1922–1935 e1920.
Clark, B.J., LaChance, P.A., Winter, S.S., Mehlman, M.L., Butler, W., LaCour, A., Taube, J. S., 2024. Comparison of head direction cell firing characteristics across thalamo-parahippocampal circuitry. Hippocampus 34, 168–196.
Corkin, S., 2002. What's new with the amnesic patient H.M.? Nat. Rev. Neurosci. 3, 153–160.
Cullen, K.E., Taube, J.S., 2017. Our sense of direction: progress, controversies and challenges. Nat. Neurosci. 20, 1465–1473.
De Araujo, I.E.T., Rolls, E.T., Stringer, S.M., 2001. A view model which accounts for the spatial fields of hippocampal primate spatial view cells and rat place cells. Hippocampus 11, 699–706.

De Falco, E., Ison, M.J., Fried, I., Quian Quiroga, R., 2016. Long-term coding of personal and universal associations underlying the memory web in the human brain. Nat. Commun. 7, 13408.
De Luca, F., McCormick, C., Ciaramelli, E., Maguire, E.A., 2019. Scene processing following damage to the ventromedial prefrontal cortex. Neuroreport 30, 828–833.
Dede, A.J., Frascino, J.C., Wixted, J.T., Squire, L.R., 2016. Learning and remembering real-world events after medial temporal lobe damage. Proc. Natl. Acad. Sci. U. S. A. 113, 13480–13485.
Deng, W., Aimone, J.B., Gage, F.H., 2010. New neurons and new memories: how does adult hippocampal neurogenesis affect learning and memory? Nat. Rev. Neurosci. 11, 339–350.
Derdikman, D., Whitlock, J.R., Tsao, A., Fyhn, M., Hafting, T., Moser, M.B., Moser, E.I., 2009. Fragmentation of grid cell maps in a multicompartment environment. Nat. Neurosci. 12, 1325–1332.
Duff, M.C., Covington, N.V., Hilverman, C., Cohen, N.J., 2019. Semantic memory and the hippocampus: revisiting, reaffirming, and extending the reach of their critical relationship. Front. Hum. Neurosci. 13, 471.
Edvardsen, V., Bicanski, A., Burgess, N., 2020. Navigating with grid and place cells in cluttered environments. Hippocampus 30, 220–232.
Eichenbaum, H., 2014. Time cells in the hippocampus: a new dimension for mapping memories. Nat. Rev. Neurosci. 15, 732–744.
Eichenbaum, H., 2017. On the integration of space, time, and memory. Neuron 95, 1007–1018.
Eichenbaum, H., Cohen, N.J., 2014. Can we reconcile the declarative memory and spatial navigation views on hippocampal function? Neuron 83, 764–770.
Ekstrom, A.D., Kahana, M.J., Caplan, J.B., Fields, T.A., Isham, E.A., Newman, E.L., Fried, I., 2003. Cellular networks underlying human spatial navigation. Nature 425, 184–188.
Eliav, T., Maimon, S.R., Aljadeff, J., Tsodyks, M., Ginosar, G., Las, L., Ulanovsky, N., 2021. Multiscale representation of very large environments in the hippocampus of flying bats. Science 372, eabg4020.
Epstein, R.A., Baker, C.I., 2019. Scene perception in the human brain. Annu Rev. Vis. Sci. 5, 373–397.
Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. Nature 392, 598–601.
Feigenbaum, J.D., Morris, R.G., 2004. Allocentric versus egocentric spatial memory after unilateral temporal lobectomy in humans. Neuropsychology 18, 462–472.
Feigenbaum, J.D., Rolls, E.T., 1991. Allocentric and egocentric spatial information processing in the hippocampal formation of the behaving primate. Psychobiology 19, 21–40.
Foster, D.J., 2017. Replay comes of age. Annu. Rev. Neurosci. 40, 581–602.
Fyhn, M., Molden, S., Witter, M.P., Moser, E.I., Moser, M.B., 2004. Spatial representation in the entorhinal cortex. Science 305, 1258–1264.
Gaffan, D., 1994. Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. J. Cogn. Neurosci. 6, 305–320.
Gaffan, D., Parker, A., 1996. Interaction of perirhinal cortex with the fornix-fimbria: memory for objects and "object-in-place" memory. J. Neurosci. 16, 5864–5869.
Gaffan, D., Saunders, R.C., 1985. Running recognition of configural stimuli by fornix-transected monkeys. Q. J. Exp. Psychol. B 37, 61–71.
Gage, F.H., 2025. Adult neurogenesis in the human dentate gyrus. Hippocampus 35, e23655.
Georges-François, P., Rolls, E.T., Robertson, R.G., 1999. Spatial view cells in the primate hippocampus: allocentric view not head direction or eye position or place. Cereb. Cortex 9, 197–212.
Giocomo, L.M., Moser, M.B., Moser, E.I., 2011. Computational models of grid cells. Neuron 71, 589–603.
Glasser, M.F., Coalson, T.S., Robinson, E.C., Hacker, C.D., Harwell, J., Yacoub, E., Ugurbil, K., Andersson, J., Beckmann, C.F., Jenkinson, M., Smith, S.M., Van Essen, D. C., 2016a. A multi-modal parcellation of human cerebral cortex. Nature 536, 171–178.
Glasser, M.F., Smith, S.M., Marcus, D.S., Andersson, J.L., Auerbach, E.J., Behrens, T.E., Coalson, T.S., Harms, M.P., Jenkinson, M., Moeller, S., Robinson, E.C., Sotiropoulos, S.N., Xu, J., Yacoub, E., Ugurbil, K., Van Essen, D.C., 2016b. The Human Connectome Project's neuroimaging approach. Nat. Neurosci. 19, 1175–1187.
Graham, J.A., Dumont, J.R., Winter, S.S., Brown, J.E., LaChance, P.A., Amon, C.C., Farnes, K.B., Morris, A.J., Streltzov, N.A., Taube, J.S., 2023. Angular head velocity cells within brainstem nuclei projecting to the head direction circuit. J. Neurosci. 43, 8403–8424.
Hampton, R.R., Hampstead, B.M., Murray, E.A., 2004. Selective hippocampal damage in rhesus monkeys impairs spatial memory in an open-field test. Hippocampus 14, 808–818.
Hartley, T., Burgess, N., Lever, C., Cacucci, F., O'Keefe, J., 2000. Modeling place fields in terms of the cortical inputs to the hippocampus. Hippocampus 10, 369–379.
Hartley, T., Lever, C., Burgess, N., O'Keefe, J., 2014. Space in the brain: how the hippocampal formation supports spatial cognition. Philos. Trans. R. Soc. Lond. B Biol. Sci. 369, 20120510.
Hassabis, D., Chu, C., Rees, G., Weiskopf, N., Molyneux, P.D., Maguire, E.A., 2009. Decoding neuronal ensembles in the human hippocampus. Curr. Biol. 19, 546–554.
Hassabis, D., Kumaran, D., Maguire, E.A., 2007. Using imagination to understand the neural basis of episodic memory. J. Neurosci. 27, 14365–14374.
Hassabis, D., Maguire, E.A., 2007. Deconstructing episodic memory with construction. Trends Cogn. Sci. 11, 299–306.
Hickok, G., Poeppel, D., 2015. Neural basis of speech perception. Handb. Clin. Neurol. 129, 149–160.
Howard, M.W., Eichenbaum, H., 2015. Time and space in the hippocampus. Brain Res 1621, 345–354.
Hoydal, O.A., Skytoen, E.R., Andersson, S.O., Moser, M.B., Moser, E.I., 2019. Object-vector coding in the medial entorhinal cortex. Nature 568, 400–404.
Huang, C.C., Rolls, E.T., Feng, J., Lin, C.P., 2022. An extended Human Connectome Project multimodal parcellation atlas of the human cortex and subcortical areas. Brain Struct. Funct. 227, 763–778.
Huang, C.-C., Rolls, E.T., Hsu, C.-C.H., Feng, J., Lin, C.-P., 2021. Extensive cortical connectivity of the human hippocampal memory system: beyond the "what" and "where" dual-stream model. Cereb. Cortex 31, 4652–4669.
Ison, M.J., Quian Quiroga, R., Fried, I., 2015. Rapid encoding of new memories by individual neurons in the human brain. Neuron 87, 220–230.
Israel, I., Chapuis, N., Glasauer, S., Charade, O., Berthoz, A., 1993. Estimation of passive horizontal linear whole-body displacement in humans. J. Neurophysiol. 70, 1270–1273.
Israel, I., Grasso, R., Georges-Francois, P., Tsuzuku, T., Berthoz, A., 1997. Spatial memory and path integration studied by self-driven passive linear displacement. I. Basic properties. J. Neurophysiol. 77, 3180–3192.
Itskov, P.M., Vinnik, E., Diamond, M.E., 2011. Hippocampal representation of touch-guided behavior in rats: persistent and independent traces of stimulus and reward location. PLoS One 6, e16462.
Izquierdo, A., 2017. Functional heterogeneity within rat orbitofrontal cortex in reward learning and decision making. J. Neurosci. 37, 10529–10540.
Kemmerer, D., 2015. Cognitive Neuroscience of Language. Psychology Press, New York.
Kesner, R.P., Rolls, E.T., 2015. A computational theory of hippocampal function, and tests of the theory: new developments. Neurosci. Biobehav. Rev. 48, 92–147.
Khazali, M.F., Brandt, A., Reinacher, P.C., Kahana, M., Jacobs, J., Schulze-Bonhage, A., Kunz, L., 2024. A preserved neural code for temporal order between memory formation and recall in the human medial temporal lobe. bioRxiv.
Kolibius, L.D., Roux, F., Parish, G., Ter Wal, M., Van Der Plas, M., Chelvarajah, R., Sawlani, V., Rollings, D.T., Lang, J.D., Gollwitzer, S., Walther, K., Hopfengartner, R., Kreiselmeyer, G., Hamer, H., Staresina, B.P., Wimber, M., Bowman, H., Hanslmayr, S., 2023. Hippocampal neurons code individual episodic memories in humans. Nat. Hum. Behav. 7, 1968–1979.
Kondo, H., Lavenex, P., Amaral, D.G., 2009. Intrinsic connections of the macaque monkey hippocampal formation: II. CA3 connections. J. Comp. Neurol. 515, 349–377.
Kringelbach, M.L., Rolls, E.T., 2003. Neural correlates of rapid reversal learning in a simple model of human social interaction. Neuroimage 20, 1371–1383.
Kropff, E., Carmichael, J.E., Moser, M.B., Moser, E.I., 2015. Speed cells in the medial entorhinal cortex. Nature 523, 419–424.
Kropff, E., Treves, A., 2008. The emergence of grid cells: Intelligent design or just adaptation? Hippocampus 18, 1256–1269.
Kunz, L., Brandt, A., Reinacher, P.C., Staresina, B.P., Reifenstein, E.T., Weidemann, C.T., Herweg, N.A., Patel, A., Tsitsiklis, M., Kempter, R., Kahana, M.J., Schulze-Bonhage, A., Jacobs, J., 2021. A neural code for egocentric spatial maps in the human medial temporal lobe. Neuron 109, 2781–2796 e2710.
Leutgeb, S., Leutgeb, J.K., Barnes, C.A., Moser, E.I., McNaughton, B.L., Moser, M.B., 2005. Independent codes for spatial and episodic memory in hippocampal neuronal ensembles. Science 309, 619–623.
Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., Burgess, N., 2009. Boundary vector cells in the subiculum of the hippocampal formation. J. Neurosci. 29, 9771–9777.
Mackay, S., Reber, T.P., Bausch, M., Bostrom, J., Elger, C.E., Mormann, F., 2024. Concept and location neurons in the human brain provide the 'what' and 'where' in memory formation. Nat. Commun. 15, 7926.
Maguire, E.A., 2014. Memory consolidation in humans: new evidence and opportunities. Exp. Physiol. 99, 471–486.
Mao, D., 2023. Neural correlates of spatial navigation in primate hippocampus. Neurosci. Bull. 39, 315–327.
Mao, D., Avila, E., Caziot, B., Laurens, J., Dickman, J.D., Angelaki, D.E., 2021. Spatial modulation of hippocampal activity in freely moving macaques. Neuron 109, 3521–3534 e3526.
McClelland, J.L., McNaughton, B.L., Lampinen, A.K., 2020. Integration of new information in memory: new insights from a complementary learning systems perspective. Philos. Trans. R. Soc. Lond. B Biol. Sci. 375, 20190637.
McClelland, J.L., McNaughton, B.L., O'Reilly, R.C., 1995. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. Psychol. Rev. 102, 419–457.
McCormick, C., Ciaramelli, E., De Luca, F., Maguire, E.A., 2018. Comparing and contrasting the cognitive effects of hippocampal and ventromedial prefrontal cortex damage: a review of human lesion studies. Neuroscience 374, 295–318.
McNaughton, B.L., Barnes, C.A., O'Keefe, J., 1983. The contributions of position, direction, and velocity to single unit activity in the hippocampus of freely-moving rats. Exp. Brain Res. 52, 41–49.
McNaughton, B.L., Barnes, C.A., Gerrard, J.L., Gothard, K., Jung, M.W., Knierim, J.J., Kudrimoti, H., Qin, Y., Skaggs, W.E., Suster, M., Weaver, K.L., 1996. Deciphering the hippocampal polyglot: the hippocampus as a path integration system. J. Exp. Biol. 199, 173–185.
McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., Moser, M.B., 2006. Path integration and the neural basis of the 'cognitive map. Nat. Rev. Neurosci. 7, 663–678.
McNaughton, B.L., Chen, L.L., Markus, E.J., 1991. "Dead reckoning", landmark learning, and the sense of direction: a neurophysiological and computational hypothesis. J. Cogn. Neurosci. 3, 190–202.
Mesulam, M.M., 1990. Human brain cholinergic pathways. Prog. Brain Res. 84, 231–241.

Miller, J.F., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, I., Hefft, S., Merkow, M., Polyn, S.M., Jacobs, J., Kahana, M.J., Schulze-Bonhage, A., 2013. Neural activity in human hippocampal formation reveals the spatial context of retrieved memories. Science 342, 1111–1114.
Milton, C.K., Dhanaraj, V., Young, I.M., Taylor, H.M., Nicholas, P.J., Briggs, R.G., Bai, M. Y., Fonseka, R.D., Hormovas, J., Lin, Y.H., Tanglay, O., Conner, A.K., Glenn, C.A., Teo, C., Doyen, S., Sughrue, M.E., 2021. Parcellation-based anatomic model of the semantic network. Brain Behav. 11, e02065.
Morris, R.G.M., 2025. Episodic aspects of a path navigated through hippocampal neurobiology. Hippocampus 35, e23672.
Morris, R., Amaral, D.G., Bliss, T., Duff, K., O'Keefe, J., 2025. The Hippocampus Book, 2 ed. Oxford University Press, Oxford.
Morris, R.G., Garrud, P., Rawlins, J.N., O'Keefe, J., 1982. Place navigation impaired in rats with hippocampal lesions. Nature 297, 681–683.
Moscovitch, M., Cabeza, R., Winocur, G., Nadel, L., 2016. Episodic memory and beyond: the hippocampus and neocortex in transformation. Annu. Rev. Psychol. 67, 105–134.
Moser, E.I., Moser, M.B., McNaughton, B.L., 2017. Spatial representation in the hippocampal formation: a history. Nat. Neurosci. 20, 1448–1464.
Moser, E.I., Moser, M.B., Roudi, Y., 2014. Network mechanisms of grid cells. Philos. Trans. R. Soc. Lond. B Biol. Sci. 369, 20120511.
Moser, M.B., Rowland, D.C., Moser, E.I., 2015. Place cells, grid cells, and memory. Cold Spring Harb. Perspect. Biol. 7, a021808.
Muller, R.U., Bostock, E., Taube, J.S., Kubie, J.L., 1994. On the directional firing properties of hippocampal place cells. J. Neurosci. 14, 7235–7251.
Muller, R.U., Kubie, J.L., 1987. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. J. Neurosci. 7, 1951–1968.
Murray, E.A., Baxter, M.G., Gaffan, D., 1998. Monkeys with rhinal cortex damage or neurotoxic hippocampal lesions are impaired on spatial scene learning and object reversals. Behav. Neurosci. 112, 1291–1303.
Murray, E.A., Mishkin, M., 1998. Object recognition and location memory in monkeys with excitotoxic lesions of the amygdala and hippocampus. J. Neurosci. 18, 6568–6582.
O'Doherty, J., Kringelbach, M.L., Rolls, E.T., Hornak, J., Andrews, C., 2001. Abstract reward and punishment representations in the human orbitofrontal cortex. Nat. Neurosci. 4, 95–102.
O'Keefe, J., 1979. A review of the hippocampal place cells. Prog. Neurobiol. 13, 419–439.
O'Keefe, J., 1990. A computational theory of the hippocampal cognitive map. Prog. Brain Res. 83, 301–312.
O'Keefe, J., Burgess, N., 1996. Geometric determinants of the place fields of hippocampal neurons. Nature 381, 425–428.
O'Keefe, J., Burgess, N., Donnett, J.G., Jeffery, K.J., Maguire, E.A., 1998. Place cells, navigational accuracy, and the human hippocampus. Philos. Trans. R. Soc. Lond. B Biol. Sci. 353, 1333–1340.
O'Keefe, J., Dostrovsky, J., 1971. The hippocampus as a spatial map: preliminary evidence from unit activity in the freely moving rat. Brain Res 34, 171–175.
O'Keefe, J., Krupic, J., 2021. Do hippocampal pyramidal cells respond to nonspatial stimuli? Physiol. Rev. 101, 1427–1456.
O'Keefe, J., Nadel, L., 1978. The Hippocampus as a Cognitive Map. Clarendon Press, Oxford.
O'Mara, S.M., Rolls, E.T., Berthoz, A., Kesner, R.P., 1994. Neurons responding to whole-body motion in the primate hippocampus. J. Neurosci. 14, 6511–6523.
Omer, D.B., Maimon, S.R., Las, L., Ulanovsky, N., 2018. Social place-cells in the bat hippocampus. Science 359, 218–224.
Panikkassery, A., Treves, A., 2025. Place cells full of sound and fury, signifying nothing. Neuron 113, 971–973.
Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. Nat. Rev. Neurosci. 8, 976–987.
Peelen, M.V., Caramazza, A., 2012. Conceptual object representations in human anterior temporal cortex. J. Neurosci. 32, 15728–15736.
Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurons responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47, 329–342.
Piza, D.B., Corrigan, B.W., Gulli, R.A., Do Carmo, S., Cuello, A.C., Muller, L., Martinez-Trujillo, J., 2024. Primacy of vision shapes behavioral strategies and neural substrates of spatial navigation in marmoset hippocampus. Nat. Commun. 15, 4053.
Purandare, C.S., Dhingra, S., Rios, R., Vuong, C., To, T., Hachisuka, A., Choudhary, K., Mehta, M.R., 2022. Moving bar of light evokes vectorial spatial selectivity in the immobile rat hippocampus. Nature 602, 461–467.
Quian Quiroga, R., 2012. Concept cells: the building blocks of declarative memory functions. Nat. Rev. Neurosci. 13, 587–597.
Quian Quiroga, R., 2013. Gnostic cells in the 21st century. Acta Neurobiol. Exp. (Wars.) 73, 463–471.
Quian Quiroga, R., Reddy, L., Kreiman, G., Koch, C., Fried, I., 2005. Invariant visual representation by single neurons in the human brain. Nature 435, 1102–1107.
Renoult, L., Irish, M., Moscovitch, M., Rugg, M.D., 2019. From knowing to remembering: the semantic-episodic distinction. Trends Cogn. Sci. 23, 1041–1057.
Rey, H.G., Ison, M.J., Pedreira, C., Valentin, A., Alarcon, G., Selway, R., Richardson, M. P., Quian Quiroga, R., 2015. Single-cell recordings in the human medial temporal lobe. J. Anat. 227, 394–408.
Robertson, R.G., Rolls, E.T., Georges-François, P., 1998. Spatial view cells in the primate hippocampus: Effects of removal of view details. J. Neurophysiol. 79, 1145–1156.
Robertson, R.G., Rolls, E.T., Georges-François, P., Panzeri, S., 1999. Head direction cells in the primate pre-subiculum. Hippocampus 9, 206–219.
Rogers Flattery, C.N., Rosen, R.F., Farberg, A.S., Dooyema, J.M., Hof, P.R., Sherwood, C. C., Walker, L.C., Preuss, T.M., 2020. Quantification of neurons in the hippocampal formation of chimpanzees: comparison to rhesus monkeys and humans. Brain Struct. Funct. 225, 2521–2531.
Rolls, E.T., 1984. Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. Hum. Neurobiol. 3, 209–222.
Rolls, E.T., 1989. Functions of neuronal networks in the hippocampus and neocortex in memory. In: Byrne, J.H., Berry, W.O. (Eds.), Neural Models of Plasticity: Experimental and Theoretical Approaches. Academic Press, San Diego, pp. 240–265.
Rolls, E.T., 2016a. Pattern separation, completion, and categorisation in the hippocampus and neocortex. Neurobiol. Learn. Mem. 129, 4–28.
Rolls, E.T., 2016b. Cerebral Cortex: Principles of Operation. Oxford University Press, Oxford.
Rolls, E.T., 2019b. The orbitofrontal cortex and emotion in health and disease, including depression. Neuropsychologia 128, 14–43.
Rolls, E.T., 2019a. The Orbitofrontal Cortex. Oxford University Press, Oxford.
Rolls, E.T., 2020. Spatial coordinate transforms linking the allocentric hippocampal and egocentric parietal primate brain systems for memory, action in space, and navigation. Hippocampus 30, 332–353.
Rolls, E.T., 2021b. Neurons including hippocampal spatial view cells, and navigation in primates including humans. Hippocampus 31, 593–611.
Rolls, E.T., 2021d. The connections of neocortical pyramidal cells can implement the learning of new categories, attractor memory, and top-down recall and attention. Brain Struct. Funct. 226, 2523–2536.
Rolls, E.T., 2021e. Learning invariant object and spatial view representations in the brain using slow unsupervised learning. Front. Comput. Neurosci. 15, 686239.
Rolls, E.T., 2021a. On pattern separation in the primate including human hippocampus. Trends Cogn. Sci. 25, 920–922.
Rolls, E.T., 2021c. Brain Computations: What and How. Oxford University Press, Oxford.
Rolls, E.T., 2022. The hippocampus, ventromedial prefrontal cortex, and episodic and semantic memory. Prog. Neurobiol. 217, 102334.
Rolls, E.T., 2023d. Hippocampal spatial view cells, place cells, and concept cells: View representations. Hippocampus 33, 667–687.
Rolls, E.T., 2023b. Brain Computations and Connectivity. Oxford University Press, Open Access, Oxford.
Rolls, E.T., 2023a. Emotion, motivation, decision-making, the orbitofrontal cortex, anterior cingulate cortex, and the amygdala. Brain Struct. Funct. 228, 1201–1257.
Rolls, E.T., 2023c. Hippocampal spatial view cells for memory and navigation, and their underlying connectivity in humans. Hippocampus 33, 533–572.
Rolls, E.T., 2024. Two what, two where, visual cortical streams in humans. Neurosci. Biobehav. Rev. 160, 105650.
Rolls, E.T., 2025a. A theory and model of scene representations with hippocampal spatial view cells. Hippocampus 35, e70013.
Rolls, E.T., 2025c. Hippocampal Discoveries: spatial view cells, connectivity, and computations for memory and navigation, in primates including humans. Hippocampus 35, e23666.
Rolls, E.T., 2025b. Primate hippocampal speed cells and navigation. In: Berthoz, A., Gretty, M. (Eds.), Breaking Frontiers to understand the brain. Odile Jacob, Paris.
Rolls, E.T., 2025d. The Orbitofrontal Cortex, Oxford Research Encyclopedia of Neuroscience. Oxford University Press, New York and Oxford. https://doi.org/10.1093/acrefore/9780190264086.9780190264013.9780190264560.
Rolls, E.T., 2026a. Neuroscience Discoveries. MIT Press, Cambridge, MA.
Rolls, E.T., 2026b. Brain Computations and their Principles; and AI. Oxford University Press, Oxford.
Rolls, E.T., Aggelopoulos, N.C., Zheng, F., 2003. The receptive fields of inferior temporal cortex neurons in natural scenes. J. Neurosci. 23, 339–348.
Rolls, E.T., Browning, A.S., Inoue, K., Hernadi, I., 2005a. Novel visual stimuli activate a population of neurons in the primate orbitofrontal cortex. Neurobiol. Learn. Mem. 84, 111–123.
Rolls, E.T., Cowey, A., 1970. Topography of the retina and striate cortex and its relationship to visual acuity in rhesus monkeys and squirrel monkeys. Exp. Brain Res. 10, 298–310.
Rolls, E.T., Critchley, H.D., Browning, A.S., Inoue, K., 2006a. Face-selective and auditory neurons in the primate orbitofrontal cortex. Exp. Brain Res. 170, 74–87.
Rolls, E.T., Deco, G., 2015. Stochastic cortical neurodynamics underlying the memory and cognitive changes in aging. Neurobiol. Learn. Mem. 118, 150–161.
Rolls, E.T., Deco, G., Huang, C.-C., Feng, J., 2022a. The human language effective connectome. Neuroimage 258, 119352.
Rolls, E.T., Deco, G., Huang, C.C., Feng, J., 2022b. The human orbitofrontal cortex, vmPFC, and anterior cingulate cortex effective connectome: emotion, memory, and action. Cereb. Cortex 33, 330–356.
Rolls, E.T., Deco, G., Huang, C.C., Feng, J., 2022c. The effective connectivity of the human hippocampal memory system. Cereb. Cortex 32, 3706–3725.
Rolls, E.T., Deco, G., Huang, C.-C., Feng, J., 2023a. Multiple cortical visual streams in humans. Cereb. Cortex 33, 3319–3349.
Rolls, E.T., Deco, G., Zhang, Y., Feng, J., 2023b. Hierarchical organization of the human ventral visual streams revealed with magnetoencephalography. Cereb. Cortex 33, 10686–10701.
Rolls, E.T., Feng, J., Zhang, R., 2024a. Selective activations and functional connectivities to the sight of faces, scenes, body parts and tools in visual and non-visual cortical regions leading to the human hippocampus. Brain Struct. Funct. 229, 1471–1493.
Rolls, E.T., Mills, P., 2019. The generation of time in the hippocampal memory system. Cell Rep. 28, 1649–1658 e1646.
Rolls, E.T., Miyashita, Y., Cahusac, P.M.B., Kesner, R.P., Niki, H., Feigenbaum, J., Bach, L., 1989. Hippocampal neurons in the monkey with activity related to the place in which a stimulus is shown. J. Neurosci. 9, 1835–1845.
Rolls, E.T., O'Mara, S.M., 1995. View-responsive neurons in the primate hippocampal complex. Hippocampus 5, 409–424.

Rolls, E.T., Robertson, R.G., Georges-François, P., 1997. Spatial view cells in the primate hippocampus. Eur. J. Neurosci. 9, 1789–1794.
Rolls, E.T., Stringer, S.M., Elliot, T., 2006b. Entorhinal cortex grid cells can map to hippocampal place cells by competitive learning. Netw. Comput. Neural Syst. 17, 447–465.
Rolls, E.T., Stringer, S.M., Trappenberg, T.P., 2002. A unified model of spatial and episodic memory. Proc. R. Soc. B 269, 1087–1093.
Rolls, E.T., Treves, A., Robertson, R.G., Georges-François, P., Panzeri, S., 1998. Information about spatial view in an ensemble of primate hippocampal cells. J. Neurophysiol. 79, 1797–1813.
Rolls, E.T., Treves, A., 1994. Neural networks in the brain involved in memory and recall. Prog. Brain Res. 102, 335–341.
Rolls, E.T., Treves, A., 2024. A theory of hippocampal function: New developments. Prog. Neurobiol. 238, 102636.
Rolls, E.T., Turova, T.S., 2025. Visual cortical networks for 'What' and 'Where' to the human hippocampus revealed with dynamical graphs. Cereb. Cortex 35, bhaf106.
Rolls, E.T., Vatansever, D., Li, Y., Cheng, W., Feng, J., 2020. Rapid rule-based reward reversal and the lateral orbitofrontal cortex. Cereb. Cortex Commun. 1, tgaa087 doi: 010.1093/texcom/tgaa1087.
Rolls, E.T., Xiang, J.-Z., Franco, L., 2005b. Object, space and object-space representations in the primate hippocampus. J. Neurophysiol. 94, 833–844.
Rolls, E.T., Xiang, J.-Z., 2004. Reward-place neurons in the primate anterior hippocampus. Soc. Neurosci. Abstr.
Rolls, E.T., Xiang, J.-Z., 2005. Reward-spatial view representations and learning in the hippocampus. J. Neurosci. 25, 6167–6174.
Rolls, E.T., Xiang, J.-Z., 2006. Spatial view cells in the primate hippocampus, and memory recall. Rev. Neurosci. 17, 175–200.
Rolls, E.T., Yan, X., Deco, G., Zhang, Y., Jousmaki, V., Feng, J., 2024b. A ventromedial visual cortical 'Where' stream to the human hippocampus for spatial scenes revealed with magnetoencephalography. Commun. Biol. 7, 1047.
Rolls, E.T., Zhang, C., Feng, J., 2024c. Hippocampal storage and recall of neocortical 'What' - 'Where' representations. Hippocampus 34, 608–624.
Rolls, E.T., Zhang, C., Feng, J., 2025. Slow semantic learning in the cerebral cortex, and its relation to the hippocampal episodic memory system. Cereb. Cortex 35, bhah107.
Rolls, E.T., Zhang, R., Deco, G., Vatansever, D., Feng, J., 2024d. Selective brain activations and connectivities related to the storage and recall of human object-location, reward-location, and word-pair episodic memories. Hum. Brain Mapp. 45, e70056.
Salz, D.M., Tiganj, Z., Khasnabish, S., Kohley, A., Sheehan, D., Howard, M.W., Eichenbaum, H., 2016. Time cells in hippocampal area CA3. J. Neurosci. 36, 7476–7484.
Schonsberg, F., Monasson, R., Treves, A., 2024. Continuous Quasi-Attractors dissolve with too much - or too little - variability. PNAS Nexus 3, pgae525.
Scoville, W.B., Milner, B., 1957. Loss of recent memory after bilateral hippocampal lesions. J. Neurol. Neurosurg. Psychiatry 20, 11–21.
Sharpe, M.J., Wikenheiser, A.M., Niv, Y., Schoenbaum, G., 2015. The state of the orbitofrontal cortex. Neuron 88, 1075–1077.
Shine, J.P., Valdes-Herrera, J.P., Tempelmann, C., Wolbers, T., 2019. Evidence for allocentric boundary and goal direction information in the human entorhinal cortex and subiculum. Nat. Commun. 10, 4004.
Skelin, I., Kilianski, S., McNaughton, B.L., 2019. Hippocampal coupling with cortical and subcortical structures in the context of memory consolidation. Neurobiol. Learn. Mem. 160, 21–31.
Smith, M.L., Milner, B., 1981. The role of the right hippocampus in the recall of spatial location. Neuropsychologia 19, 781–793.
Solstad, T., Moser, E.I., Einevoll, G.T., 2006. From grid cells to place cells: a mathematical model. Hippocampus 16, 1026–1031.
Spalla, D., Treves, A., Boccara, C.N., 2022. Angular and linear speed cells in the parahippocampal circuits. Nat. Commun. 13, 1907.
Squire, L.R., Wixted, J.T., 2011. The cognitive neuroscience of human memory since H. M. Annu. Rev. Neurosci. 34, 259–288.
Stringer, S.M., Rolls, E.T., Trappenberg, T.P., 2005. Self-organizing continuous attractor network models of hippocampal spatial view cells. Neurobiol. Learn. Mem. 83, 79–92.
Sugar, J., Moser, M.B., 2019. Episodic memory: Neuronal codes for what, where, and when. Hippocampus 29, 1190–1205.
Takeuchi, T., Duszkiewicz, A.J., Morris, R.G., 2014. The synaptic plasticity and memory hypothesis: encoding, storage and persistence. Philos. Trans. R. Soc. Lond. B Biol. Sci. 369, 20130288.
Taube, J.S., 2017. New building blocks for navigation. Nat. Neurosci. 20, 131–133.
Taube, J.S., Muller, R.U., Ranck Jr., J.B., 1990. Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. J. Neurosci. 10, 420–435.
Thorpe, S.J., Rolls, E.T., Maddison, S., 1983. The orbitofrontal cortex: neuronal activity in the behaving monkey. Exp. Brain Res. 49, 93–115.
Treves, A., Rolls, E.T., 1992. Computational constraints suggest the need for two distinct input systems to the hippocampal CA3 network. Hippocampus 2, 189–199.
Treves, A., Rolls, E.T., 1994. A computational analysis of the role of the hippocampus in memory. Hippocampus 4, 374–391.
Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J.J., Moser, M.B., Moser, E.I., 2018. Integrating time from experience in the lateral entorhinal cortex. Nature 561, 57–62.
Tsitsiklis, M., Miller, J., Qasim, S.E., Inman, C.S., Gross, R.E., Willie, J.T., Smith, E.H., Sheth, S.A., Schevon, C.A., Sperling, M.R., Sharan, A., Stein, J.M., Jacobs, J., 2020. Single-neuron representations of spatial targets in humans. Curr. Biol. 30, 245–253 e244.
Umbach, G., Kantak, P., Jacobs, J., Kahana, M., Pfeiffer, B.E., Sperling, M., Lega, B., 2020. Time cells in the human hippocampus and entorhinal cortex support episodic memory. Proc. Natl. Acad. Sci. U. S. A. 117, 28463-28474.
Van Essen, D.C., Ugurbil, K., Auerbach, E., Barch, D., Behrens, T.E., Bucholz, R., Chang, A., Chen, L., Corbetta, M., Curtiss, S.W., Della Penna, S., Feinberg, D., Glasser, M.F., Harel, N., Heath, A.C., Larson-Prior, L., Marcus, D., Michalareas, G., Moeller, S., Oostenveld, R., Petersen, S.E., Prior, F., Schlaggar, B.L., Smith, S.M., Snyder, A.Z., Xu, J., Yacoub, E., Consortium, W.U.-M.H., 2012. The Human Connectome Project: a data acquisition perspective. Neuroimage 62, 2222–2231.
Vericel, M.E., Baraduc, P., Duhamel, J.R., Wirth, S., 2024. Organizing space through saccades and fixations between primate posterior parietal cortex and hippocampus. Nat. Commun. 15, 10448.
Vijayabaskaran, S., Zeng, X., Ghazinouri, B., Wiskott, L., Cheng, S., 2025. A taxonomy of spatial navigation in mammals: Insights from computational modeling. Neurosci. Biobehav. Rev. 176, 106282.
Waters, S.J., Basile, B.M., Murray, E.A., 2023. Reevaluating the role of the hippocampus in memory: A meta-analysis of neurotoxic lesion studies in nonhuman primates. Hippocampus 33, 787–807.
Watson, J.F., Vargas-Barroso, V., Morse-Mora, R.J., Navas-Olive, A., Tavakoli, M.R., Danzl, J.G., Tomschik, M., Rossler, K., Jonas, P., 2025. Human hippocampal CA3 uses specific functional connectivity rules for efficient associative memory. Cell 188, 501–514 e518.
Wiener, J.M., Berthoz, A., Wolbers, T., 2011. Dissociable cognitive mechanisms underlying human path integration. Exp. Brain Res. 208, 61–71.
Wiener, S.I., Paul, C.A., Eichenbaum, H., 1989. Spatial and behavioral correlates of hippocampal neuronal activity. J. Neurosci. 9, 2737–2763.
Wilson, M.A., McNaughton, B.L., 1994. Reactivation of hippocampal ensemble memories during sleep. Science 265, 676–679.
Wilson, F.A.W., Rolls, E.T., 1990b. Neuronal responses related to reinforcement in the primate basal forebrain. Brain Res 509, 213–231.
Wilson, F.A.W., Rolls, E.T., 1990a. Learning and memory are reflected in the responses of reinforcement-related neurons in the primate basal forebrain. J. Neurosci. 10, 1254–1267.
Wilson, F.A.W., Rolls, E.T., 1990c. Neuronal responses related to the novelty and familiarity of visual stimuli in the substantia innominata, diagonal band of Broca and periventricular region of the primate. Exp. Brain Res. 80, 104–120.
Wilson, R.C., Takahashi, Y.K., Schoenbaum, G., Niv, Y., 2014. Orbitofrontal cortex as a cognitive map of task space. Neuron 81, 267–279.
Wirth, S., Baraduc, P., Plante, A., Pinede, S., Duhamel, J.R., 2017. Gaze-informed, task-situated representation of space in primate hippocampus during virtual navigation. PLoS Biol. 15, e2001045.
Wise, S.P., 2008. Forward frontal fields: phylogeny and fundamental function. Trends Neurosci. 31, 599–608.
Yan, W., Mao, D., 2024. Disrupted spatial selectivity in the primate hippocampal-orbitofrontal circuit during navigation in virtual reality. Society for Neuroscience Abstracts. PSTR, 140.122.
Yang, W., Sun, C., Huszar, R., Hainmueller, T., Kiselev, K., Buzsaki, G., 2024. Selection of experience for memory by hippocampal sharp wave ripples. Science 383, 1478–1483.
Zaborszky, L., Gombkoto, P., Varsanyi, P., Gielow, M.R., Poe, G., Role, L.W., Ananth, M., Rajebhosale, P., Talmage, D.A., Hasselmo, M.E., Dannenberg, H., Minces, V.H., Chiba, A.A., 2018. Specific basal forebrain-cortical cholinergic circuits coordinate cognitive operations. J. Neurosci. 38, 9446–9458.
Zaborszky, L., Hoemke, L., Mohlberg, H., Schleicher, A., Amunts, K., Zilles, K., 2008. Stereotaxic probabilistic maps of the magnocellular cell groups in human basal forebrain. Neuroimage 42, 1127–1141.
Zeidman, P., Maguire, E.A., 2016. Anterior hippocampus: the anatomy of perception, imagination and episodic memory. Nat. Rev. Neurosci. 17, 173–182.
Zola-Morgan, S., Squire, L.R., Amaral, D.G., 1986. Human amnesia and the medial temporal region: enduring memory impairment following a bilateral lesion limiited to field CA1 of the hippocampus. J. Neurosci. 6, 2950–2957.