Received: 8 February 2024 | Revised: 7 June 2024 | Accepted: 19 August 2024
DOI: 10.1002/hipo.23636

RESEARCH ARTICLE

WILEY

Hippocampal storage and recall of neocortical "What"–"Where" representations

Edmund T. Rolls[1,2,3] | **Chenfei Zhang**[3] | **Jianfeng Feng**[2,3]

[1]Oxford Centre for Computational Neuroscience, Oxford, UK
[2]Department of Computer Science, University of Warwick, Coventry, UK
[3]Institute of Science and Technology for Brain Inspired Intelligence, Fudan University, Shanghai, China

Correspondence
Edmund T. Rolls, Department of Computer Science, University of Warwick, Coventry CV4 7AL, UK.
Email: edmund.rolls@oxcns.org

Funding information
National Key R&D Program of China, Grant/Award Numbers: 2019YFA0709502, 2018YFC1312904; 111 Project, Grant/Award Number: B18015; Shanghai Municipal Science and Technology Major Project, Grant/Award Number: 2018SHZDZX01; Shanghai Center for Brain Science and Brain-Inspired Technology

Abstract

A key question for understanding the function of the hippocampus in memory is how information is recalled from the hippocampus to the neocortex. This was investigated in a neuronal network model of the hippocampal system in which "What" and "Where" neuronal firing rate vectors were applied to separate neocortical modules, which then activated entorhinal cortex "What" and "Where" modules, then the dentate gyrus, then CA3, then CA1, then the entorhinal cortex, and then the backprojections to the neocortex. A rate model showed that the whole system could be trained to recall "Where" in the neocortex from "What" applied as a retrieval cue to the neocortex, and could in principle be trained up towards the theoretical capacity determined largely by the number of synapses onto any one neuron divided by the sparseness of the representation. The trained synaptic weights were then imported into an integrate-and-fire simulation of the same architecture, which showed that the time from presenting a retrieval cue to a neocortex module to recall the whole memory in the neocortex is approximately 100 ms. This is sufficiently fast for the backprojection synapses to be trained onto the still active neocortical neurons during storage of the episodic memory, and this is needed for recall to operate correctly to the neocortex. These simulations also showed that the long loop neocortex–hippocampus–neocortex that operates continuously in time may contribute to complete recall in the neocortex; but that this positive feedback long loop makes the whole dynamical system inherently liable to a pathological increase in neuronal activity. Important factors that contributed to stability included increased inhibition in CA3 and CA1 to keep the firing rates low; and temporal adaptation of the neuronal firing and of active synapses, which are proposed to make an important contribution to stabilizing runaway excitation in cortical circuits in the brain.

KEYWORDS
attractor network, competitive network, hippocampal episodic memory, integrate-and-fire model of the hippocampus, memory recall, stability of cortical excitatory networks, temporal adaptation

1 | INTRODUCTION

The aim of this research is to advance understanding of the storage of information from the neocortex to the hippocampus, and the recall of information back to the neocortex. Key issues investigated are (1) how recall to the neocortex from the hippocampus operates, to recall for example a neocortical "Where" representation from a neocortical "What" recall cue; (2) the capacity of this storage and recall operation in terms of the number of memories that can be stored and later recalled; (3) the effect of continuous interaction between the neocortex and hippocampus in retrieving a complete memory; and (4) the roles of strong inhibition in hippocampal CA3 and CA1, and of temporal adaptation of neuronal firing and of active synapses, in maintaining stability in the long loop with the excitatory connections from the neocortex to the hippocampus and back to the neocortex when it operates in continuous time.

The model and simulations described build on a foundation of the only quantitative computational theory of the storage of information from the neocortex in the hippocampus, and the recall of information from the hippocampus back to the neocortex (Kesner & Rolls, 2015; Rolls, 1995, 2018, 2021c, 2023b; Rolls et al., 2002; Rolls & Treves, 1994, 2024; Treves & Rolls, 1992, 1994). (One previous model did not include the neocortex, did not have an analytic theory for the memory capacity of the whole model, and did not measure the memory capacity of the whole network, that is the number of memories that can be stored and successfully recalled (Hasselmo & Wyble, 1997). Another model did not have an analytic theory for the memory capacity of the whole model, and did not measure the memory capacity of the whole network (Norman & O'Reilly, 2003).) The model described here enables key aspects of the memory storage and recall computations to be tested; and provides a brain system that can become part of a larger simulation of how different brain systems link together. Such a larger simulation could include a model of the "What" cortical system for object and face representations (Rolls, 2021d, 2023b); a model of the ventromedial "Where" cortical stream for the representation of locations in spatial scenes (Rolls, 2024b, 2024c; Rolls & Stringer, 2005; Rolls & Treves, 2024; Stringer et al., 2005); and a model of the type described here of how for episodic memory the hippocampus is involved in associating "What" with "Where" neocortical inputs, and later recalling them back to neocortex to remember what was seen, and where it was seen, on a particular occasion (Kesner & Rolls, 2015; Rolls, 2023b, 2024c; Rolls & Treves, 2024).

A key feature of the research described here is that it includes an integrate-and-fire implementation of the neocortical–hippocampal system for memory recall, to enable an estimate of the time it takes for a memory retrieval cue applied to one part of the neocortex to recall the whole of the episodic memory to relevant other parts of the neocortex by accessing the hippocampus, and activating the return pathways to the neocortex. This is important, for the theory of how the correct neocortical neurons are activated by the hippocampal backprojections requires that the backprojections are active during learning and are sufficiently fast in reaching the neocortex for a pattern association to be learned between the active backprojection axons (green in Figures 1 and 2) to the still active neocortical pyramidal cells (Rolls, 1989a; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994). That time is currently unknown, and this is as far as we know the first full integrate-and-fire neuron model of the neocortical–hippocampal–neocortical system as illustrated in Figure 1. An integrate-and-fire implementation is an appropriate way to test this time of processing, for integrate-and-fire implementations take into account realistic time constants for the different synapses involved, and the time that it takes for a biologically plausible attractor network such as hippocampal CA3 to fall into its basin of attraction (Battaglia & Treves, 1998; Panzeri et al., 2001; Rolls, 2023b; Rolls & Webb, 2012; Treves et al., 1997; Webb et al., 2011).

The architecture of the hippocampo–neocortical system to be investigated is illustrated in Figures 1 and 2 (Rolls, 2023c). The overall concept is that the hippocampus in its CA3 attractor network can associate representations about objects or faces, so-called "What" representations, with spatial or "Where" representations, to provide an episodic memory for where a particular face or object has been seen on a particular previous occasion (Rolls, 2023b; Rolls & Treves, 2024; Treves & Rolls, 1994). In primates including humans the neocortical "What" object and face information is in the inferior temporal visual cortical regions, and the "Where" information is about the spatial view, in regions such as the medial temporal lobe parahippocampal scene (sometimes called place) area, and perhaps other neocortical regions (Epstein & Baker, 2019; Rolls, 2021d, 2023b; Rolls, Deco, et al., 2023a; Rolls, Feng, & Zhang, 2024; Rolls & Turova, 2024; Rolls, Yan, et al., 2024). The backprojection pathways for memory recall are shown in Figures 1 and 2 in dashed green lines, and in red the CA3 recurrent collaterals via which "what" and "where" representations present at the same time can be associated during episodic memory storage, and via which completion of a whole memory from a part can occur during recall. In rodents the neocortical representations are less well understood, and the main spatial representations are in the hippocampus about the place where the individual is located (Burgess & O'Keefe, 1996; Hartley et al., 2014; O'Keefe, 1979), and in the entorhinal cortex again about places where the individual is located using grid cells (Moser et al., 2017).

Quantitative details of the architecture that was simulated are shown in Figure 2 (Rolls, 2023c). All synapses are associatively modifiable except for the Dentate Gyrus (DG) mossy fiber (mf) synapses on the CA3 pyramidal cells. The dentate granule cells, the CA1 cells, and the entorhinal cortex inputs from the neocortex operate as competitive networks (Rolls, 2023b). The CA3 cells operate as an autoassociation (Huang et al., 2021) attractor network to implement completion (Rolls, 2023b). The backprojection connections shown in green operate as pattern association networks (Rolls, 2023b).

Recent research on the pathways involved in this hippocampal processing in the human brain, and on the implications for understanding hippocampal episodic memory, and memory consolidation, include the following: (Huang et al., 2021; Ma et al., 2022; Rolls, 2018, 2020, 2021b, 2021c, 2022, 2023a, 2023b, 2023c, 2024a, 2024c; Rolls et al., 2022a, 2022b; Rolls, Deco, et al., 2023a, 2023b; Rolls, Feng, &

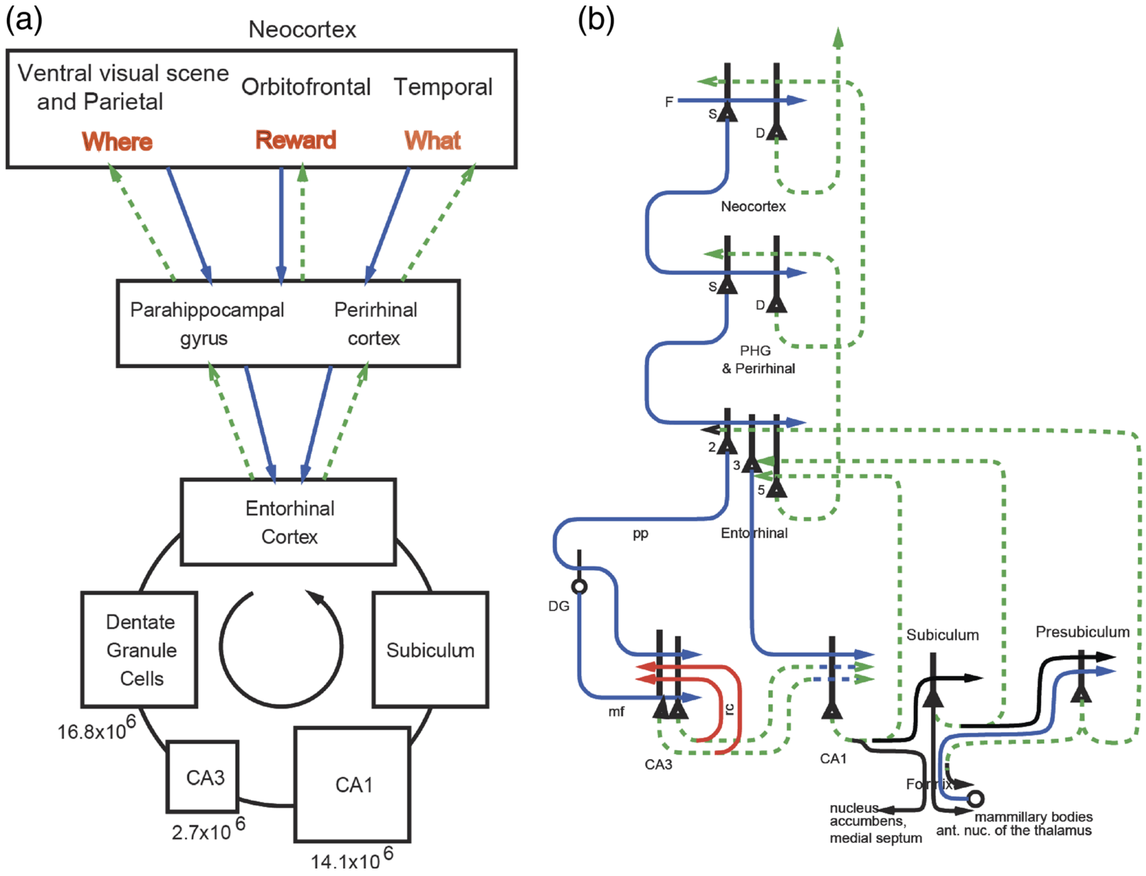

FIGURE 1 The human/primate hippocampus receives neocortical input connections (blue) not only from the "what" temporal lobe and "where" parietal and ventral visual scene areas but also from the "reward" prefrontal cortex areas (orbitofrontal cortex, vmPFC, and anterior cingulate cortex) for episodic 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. (a) Block diagram. (b) 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 & Mills, 2019). 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 fibers; 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 (a), and indicate very many dentate granule cells, consistent with expansion encoding and the production of sparse uncorrelated representations prior to CA3 (Rolls, 2016b, 2021a).

Zhang, 2024; Rolls & Turova, 2024; Rolls, Wirth, et al., 2023; Rolls, Yan, et al., 2024).

2 | METHODS

The theory of operation of the hippocampo–neocortical system (Rolls & Treves, 2024; Treves & Rolls, 1994) referred to in the Introduction provides a foundation for the model simulated here and shown in Figure 2. The model was implemented as follows, first as a Rate model, and then to measure the recall time, as an integrate-and-fire model, with full details provided in the Appendix S1.

2.1 | Rate model of the neocortical–hippocampal system

The model utilized diluted connectivity, for this is a feature of neocortical and hippocampal design (Rolls, 2016a, 2018, 2023b; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994), and was indeed incorporated in an earlier model (Rolls, 1995), which is extended here by adding neocortical "What" and "Where" layers, and by correspondingly adding separate entorhinal cortex lateral "What" and medial "Where" parts, as in Figure 2. The dilution of connectivity (the proportion of synapses on a neuron compared to the number of neurons in the network (Rolls, 2023b)) utilized in the model was in general 5, with for example 200 synapses on each neuron in a network with 1000

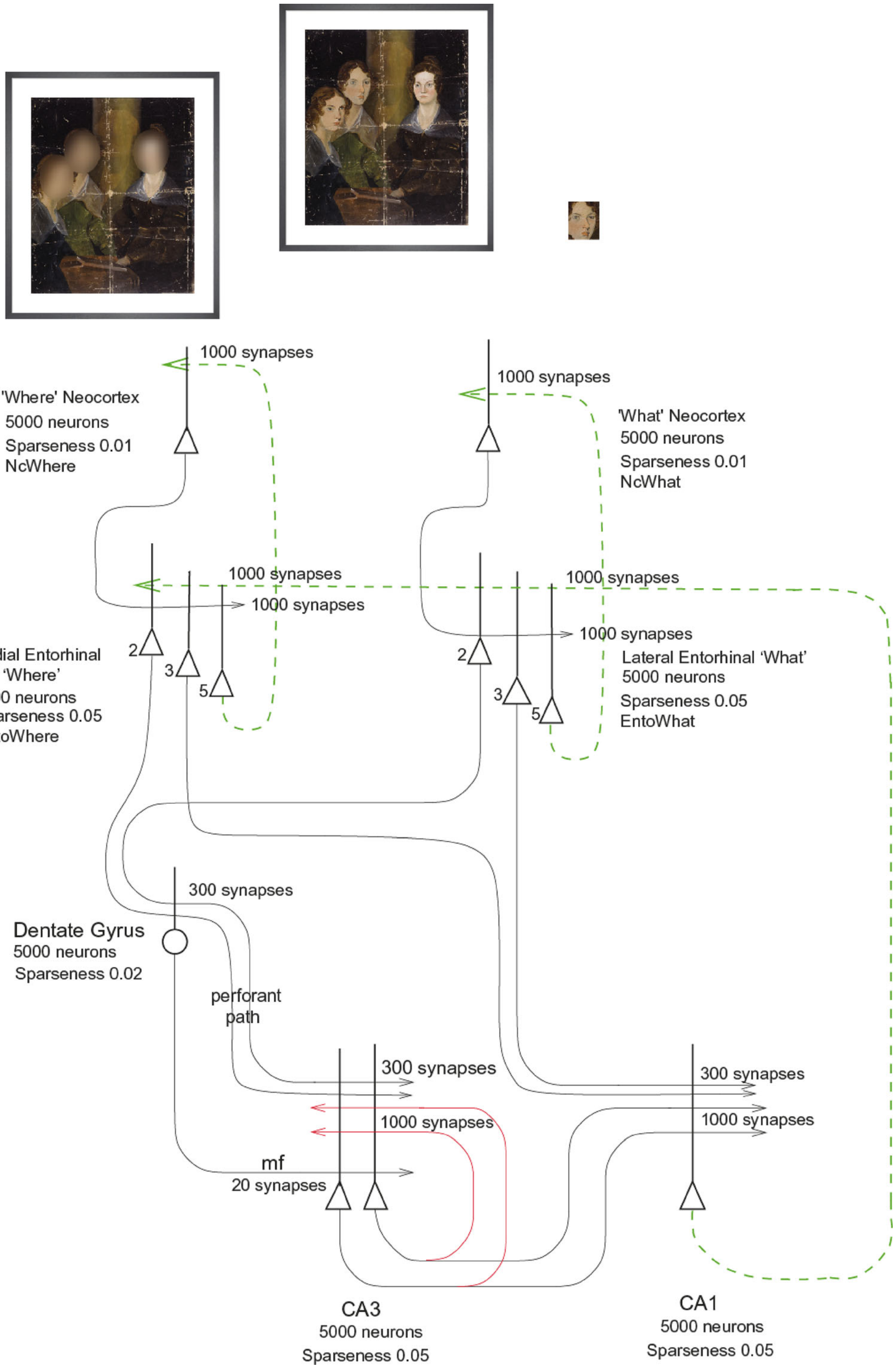

FIGURE 2 Simulation of neocortical "what" and "where" inputs to the hippocampus for the storage of episodic memory, and for the recall of "what" (object or face) and "where" (spatial view) information back to the "what" and "where" neocortex. The pyramidal cell bodies are shown as triangles, the dendrites as the thick lines above the cell bodies, and the axons as thin lines terminated with an arrow. The numbers of synapses shown are the numbers on any one neuron. The backprojection pathways for memory recall are shown in dashed green lines and in red the CA3 recurrent collaterals via which "what" and "where" representations present at the same time can be associated during episodic memory storage, and via which completion of a whole memory from a part can occur during recall. All synapses are associatively modifiable except for the Dentate Gyrus (DG) mossy fiber (mf) synapses on the CA3 pyramidal cells. The dentate granule cells, the CA1 cells, and the entorhinal cortex inputs from the neocortex operate as competitive networks. The CA3 cells operate as an autoassociation attractor network to implement completion. The backprojection connections shown in green operate as pattern association networks (Rolls, 2021c). At the top, the central image shows what might be stored; the right image shows the recall cue, and the network then recalls in the Where neocortex where that face was in the scene shown on the left. This is what the network performs, and is typical of episodic memory in which the locations of faces or objects in a scene are remembered (after Rolls (2023c)).

neurons. Although the dilution in the neocortex is probably close to 10 (Rolls, 2016a, 2023b), the value of 5 enables the effects of dilution to be examined in a network that is not too large. Sparse binary patterns are used throughout, as the capacity of this system is easier to analyze than a system with graded firing rates for each pattern to be stored and recalled (Rolls & Treves, 1990; Treves, 1990, 1991b; Treves & Rolls, 1991). To achieve this, threshold-binary neurons were implemented, with the sparseness set to achieve the sparseness shown in Figure 2 for each brain region, and a rate implementation was used. The rate implementation of the pattern association, attractor, and competitive networks was as described by Rolls (2016a, 2023b), where sample Matlab code for each of these classes of network is made available (see Code Availability statement). Code of that general type was used in the rate simulations described here, and the equations are provided in Appendix S1.

2.1.1 | Neocortex

This receives the inputs to the whole system. The neocortical inputs are defined as sparse binary random patterns. Each pattern, for example pattern 1, consisted of a vector of binary firing rates with values of 0 or 1, with the elements set to 1 being chosen randomly for each pattern, and to achieve a sparseness of the representation with the values shown in Figure 2. As these are binary representations, the sparseness is simply the proportion of 1s in the whole vector (Rolls, 2023b). Separate “what” and “where” inputs are provided. The model learns to associate each pair of “what” and “where” inputs. When tested by presenting only a “what” input pattern, the network recalls the neocortical “where” pattern that was associated with it.

During storage, the neocortex neurons pass on their activity to the entorhinal cortex; but also learn to associate whatever backprojected input to the neocortex is being provided from the entorhinal cortex using pattern association learning.

During recall, the backprojections to the neocortex from the entorhinal cortex enable, by pattern association, recall of the correct memory pattern to be recalled in the neocortex. For simplicity, the principles involved are illustrated without including in this simulation the parahippocampal / perirhinal stages of processing shown in Figure 1.

2.1.2 | Entorhinal cortex

Each entorhinal cortex network learns representations of neocortical what and where representations based on previous experience using competitive learning (Rolls, 2023b). [This learning does not produce the place cells found in the rodent medial entorhinal cortex (Fyhn et al., 2004; Kraus et al., 2015; Moser et al., 2014, 2015, 2017), but is a key part of the feature combination learning process by which the spatial view cells found in the primate “Where” system could be learned (Rolls & Treves, 2024). This process involves a series of competitive networks like those found in a model of the “What” ventral visual system VisNet (Rolls, 2021d, 2023b), but with little convergence from stage to stage to enable the spatial representations to be maintained through the hierarchy (Rolls, 2024b). The spatial feature combination neurons learned by this system (cf. De Araujo et al., 2001) are bound together by the use of a continuous attractor network as in previous research (Stringer et al., 2005).] During the learning of a new episodic memory, these representations are passed forward to the dentate and CA3. Also during learning/storage, the backprojection input is received from CA1, and this is associated using pattern association learning with whatever firing in present in the entorhinal cortex.

During recall, the backprojected input from CA1 retrieves the correct set of firing in the Entorhinal cortex “What” and “Where” neurons, due to the previous pattern association learning.

2.1.3 | Dentate granule cells

These learn sparse representations of neocortical what and where representations based on previous experience using competitive learning (Marr, 1971; McNaughton & Morris, 1987; Rolls, 1987, 2016b; Rolls & Treves, 2024). During storage of a new episodic memory, the dentate granule cells receive inputs from both entorhinal cortex networks, and apply competition to produce a sparse representation in the dentate granule cell population for each memory pattern to pass on to CA3 via the mossy fibers.

2.1.4 | CA3 network

This operates in the theory (Hasselmo et al., 1995; McClelland et al., 1995; McNaughton & Morris, 1987; Rolls, 1987, 1989b; Rolls & Treves, 2024; Treves & Rolls, 1992, 1994) as an attractor network to enable a whole memory to be completed during recall from any part.

During storage, the strong non-modifiable very sparse mossy fiber synapses connecting the Dentate Granule cells to the CA3 network force a new random set of CA3 neurons to be activated during learning. The entorhinal cortex inputs, which will be for a new memory, do not activate CA3 neurons during the storage of an episodic memory. The mossy fiber inputs are not used during recall (see Treves & Rolls, 1992) when the parameter *dg* is set to 0. The possible roles of acetylcholine in this modulation of the efficacy of the mossy fibers inputs to CA3 compared to the entorhinal inputs are discussed elsewhere (Hasselmo et al., 1995; Hasselmo & McGaughy, 2004; Vogt & Regehr, 2001; Zaborszky et al., 2018). During storage, the recurrent collateral synapses in the attractor network are learned by standard Hebbian associative learning, to set up the attractor network connections. Also during storage, a pattern association is learned between the entorhinal cortex inputs and the CA3 cells that are firing. This will be used later for recall (Treves & Rolls, 1992). Because there are “what” and “where” entorhinal connections with the CA3 network, this is effectively how the “what” and “where” components of an episodic memory become associated with the firing of CA3 neurons that represent “what” and “where.” It is likely, because of the diluted connectivity in the system, that somewhat different CA3 neurons become linked with "what" and others with "where," enabling CA3 pattern completion to be useful.

During retrieval, the entorhinal cortex inputs to the CA3 neurons using pattern association retrieval start the recall process in CA3, which continues to completion using the CA3–CA3 recurrent collateral autoassociation attractor property.

2.1.5 | CA1 network

This operates as a competitive network to categorize the firing received from CA3. Although the separate components of episodic memory (e.g., "What" and "Where") must be separately represented in CA3 implicitly to enable completion, the separate components need no longer be kept separate for the recall process back to the neocortex, so can be recategorized as a sparse and more compressed recall cue (Rolls & Treves, 1994, 2024; Treves & Rolls, 1994). During storage, competitive network learning takes place.

During retrieval, the CA1 network provides the sparse and categorized representation produced in it via its CA3 inputs, and passes this categorized output to be used by the entorhinal cortex to recall the entorhinal cortex firing that was present during storage. After that, the entorhinal cortex backprojections to the neocortex recall the correct set of firing in the neocortex by pattern association backprojection recall.

In the brain, there is a great expansion of cell numbers from CA1 back to the neocortex, and the multiple-stage recall process from CA1 back to the neocortex allows the number of neurons to increase at each stage, while at the same time allowing the number of backprojection synapses to each neocortical neuron to be kept limited at approximately 10,000 synapses onto each neuron (Rolls, 2016a, 2023b; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994). The expansion of neuron numbers is not included in this simulation as it is not essential to the storage and recalls processes themselves, but may be useful to enhance the memory capacity provided for by the CA1 to entorhinal connections (Rolls & Treves, 2024).

For the purposes of these simulations, the entorhinal cortex to CA1 connections which are smaller in number than the CA3 connections to CA1 was not modeled, partly because there is evidence that they are relatively weak and are unlikely to be the key driver of CA1 activity as discussed elsewhere (Rolls & Treves, 2024). [Although the evidence suggests that the entorhinal to CA1 connections are weak compared to the CA3 inputs to the CA1 neurons (Rolls & Treves, 2024; Zhao et al., 2020), there is a treatment of them as a competitive network (Hasselmo & Wyble, 1997).]

2.2 | Integrate-and-fire model of the neocortical–hippocampal system

The aims of these simulations are to estimate the time from presenting a recall cue to, for example, "What" neocortex, to produce completion in CA3 and recall of the rest of the episodic memory in, for example, "Where" neocortex; and to investigate the stability of the dynamics in this whole system shown in Figure 2.

The integrate-and-fire model was set up using synaptic channels for AMPA, NMDA, and GABA_A receptors which was developed for attractor networks (Brunel & Wang, 2001), and has been used and developed considerably (Deco et al., 2009, 2013; Deco & Rolls, 2006; Loh et al., 2007; Rolls, 2023b; Rolls et al., 2010a, 2010b, 2012; Rolls & Deco, 2010, 2015a, 2015b, 2016; Wang, 2002). The details of the biophysical implementation are provided in Appendix S1.

The whole network that was implemented with integrate-and-fire neurons was the same as that shown in Figure 2 for the rate model with the same parameters. Because this was a large network with 7 modules, each with 5000 excitatory neurons and 1250 inhibitory neurons (43,750 neurons, more than 288,750,000 synapses) it was implemented on a GPU with Pytorch. It is noted that a relatively large-scale simulation of this type is needed with integrate-and-fire neurons with the low firing rates typical of hippocampal neurons, as otherwise the stochastic almost Poisson firing times of individual neurons and the sparseness of the representations would mean stochasticity in the readout of the results produced. (The close to Poisson distribution of spike times for a given mean rate is helped in simulations of this type (Brunel & Wang, 2001) by the Poisson background input to each neuron described in the Methods.) The connectivity from the excitatory to the inhibitory neurons and vice versa within a module was complete, and the dilution of the connectivity between modules was as shown in Figure 2, simulating the diluted connectivity in the cortex.

The implementation of the attractor network for CA3 in the integrate-and-fire simulation was relatively straightforward, at least for testing after the synaptic weights had been learned, in view of the research cited above.

The implementation of competitive networks (key parts of the medial and lateral entorhinal cortex, the dentate, and CA1) during learning was more difficult because of the need to control the sparseness of the representation, and because of the stochastic nature of the incoming spikes to each synapse, which required at least 100–250 ms of firing each time that input was being received to estimate the mean presynaptic and postsynaptic firing rates necessary for the associative synaptic update using a Hebb rule. (It is suggested that in the brain, the long time constant of NMDA synapses, 100 ms, might be relevant to this process.) These constraints made the training using integrate-and-fire neurons produce stochastic estimates for the synaptic weight changes, and was prohibitively slow. There is therefore a great difficulty in integrate-and-fire network simulations without the very large-scale neuron and synapse numbers found in the brain that relate to the effects of the stochasticity which is introduced into the synaptic weights unless the implementation is very large. We therefore adopted the method, which we now propose is very useful, of training the synaptic weights with rate neurons (as described in Section 2.1), and then importing these synaptic weights into an integrate-and-fire version of the same architecture. It was found that this worked well, with considerable work then still required to set up stable dynamics of the whole network, as described next.

A key issue of the network simulated in Figure 2 arises as follows. When a recall cue is applied for example to the "What" neocortex, the firing proceeds to CA3 where completion occurs in the attractor network, and then via the return backprojection pathways (green in Figure 2), firing via CA1 and the entorhinal cortices reaches the neocortical "Where" module, and the neocortical "What" module. But because this is a whole dynamical system with continuous dynamics, the signal then returns back from the neocortex to the hippocampus, and then returns to the neocortex, continuously. It is proposed that this is a long-loop system (Rolls, 2023b) that contributes to the generation of the whole memory being recalled well to the neocortex. This is an important concept and complements what can be implemented by CA3 to potentially over a short period of time produce even better recall by the "long-loop" positive feedback.

But the issue then arises that the "long excitatory loop" from the neocortex to the hippocampus and back can result in runaway positive feedback which results in very high firing rates throughout the circuit. It was found to be possible to control this by a combination of a number of methods, as follows.

One method was to introduce neuronal adaptation into the neurons in the circuit. Adaptation is a known property of neocortical and hippocampal neurons (Liu & Wang, 2001; Rolls, 2023b; Rolls & Deco, 2015b). The method adopted was the spike-frequency adaptation mechanism using Ca^{2+}-activated K^+ hyper-polarizing currents (Liu & Wang, 2001), and is described in Appendix S1, and has been used before in a number of applications (Hasselmo et al., 1995; Rolls & Deco, 2015a, 2015b). Its parameters were chosen to produce moderate to strong spike frequency adaptation, with $[Ca^{2+}]$ initially set to be 0 μM, $\tau_{Ca} = 300$ ms, $\alpha = 0.002$, $V_K = -80$ mV, and $g_{AHP} = 0$–150 nS (where 0 nS produces no adaptation). As a result of these investigations, it is proposed that adaptation, whether neuronal (Liu & Wang, 2001) or synaptic (Kern & Chao, 2023; Mongillo et al., 2008; Rolls et al., 2013; Tsodyks & Markram, 1997), is a major contributor to the stability of cortical circuitry, which necessarily with the local excitatory recurrent connectivity between pyramidal cells and the long-loop excitatory connectivity (Rolls, 2016a, 2023b) is liable to runaway excitation.

A second method is to increase local inhibition. In the model attractor network (Brunel & Wang, 2001; Rolls & Deco, 2010, 2015b; Wang, 2002), the default value for the excitatory to inhibitory (E to I) neuron connectivity, and for the inhibitory to excitatory connectivity, is 1.0. This Excitatory to Excitatory value can be increased between a population of excitatory neurons to for example 2.1 to form an attractor population (Brunel & Wang, 2001; Rolls & Deco, 2010, 2015b; Wang, 2002). It was found in this investigation that increasing the E to I connectivity to, for example, 9 in some modules could help to stabilize the whole network, and was especially important in CA3 and CA1. Indeed, it is proposed here that inhibition may be especially high in CA3 and CA1 in the hippocampus to keep the firing rates low, thereby helping to minimize the risk of runaway excitation. The exact values for all the parameters are provided in Appendix S1. Inhibitory feedback to control the level of excitatory neuron firing was used in an attractor network in a rate simulation previously (Hasselmo et al., 1995), and its use is essential in integrate-and-fire networks of the type used here, with the new point made here that it may need to be especially strong in the hippocampal CA3 and CA1 networks to help control runaway excitation produced by the long loop (neocortex–hippocampus–neocortex) dynamics described here.

A third method to control the firing rates of the excitatory neurons in this cortical–hippocampal–cortical system and to prevent runaway excitation was to use presynaptic adaptation or depression in which each spike in a presynaptic terminal depletes the amount of transmitter, leaving less to be released by the next spike (Mongillo et al., 2008). The amount of transmitter left is represented by x, which starts with a value of 1 and has a minimum value of 0. x modulates the corresponding synaptic weight to model the reduction in the amount of transmitter released. x recovers with a time constant τ_D of 200 ms, with the mechanism and implementation described in Appendix S1 and elsewhere (Mongillo et al., 2008). Presynaptic adaptation was found to be very useful in the integrate-and-fire simulations in minimizing runaway excitation in this system, in enabling the other parameters such as the connection strengths between the different networks to be found, and to enable the rather low firing rates typical of hippocampal neurons (typically < 20 spikes/s for the maximal response (Georges-François et al., 1999; Robertson et al., 1998; Rolls et al., 1997; Rolls et al., 1998)) to be modeled. Presynaptic adaptation or depression may help in part by mimicking the top, flatter, part of a sigmoid activation function.

A fourth method was to apply the recall stimulus, for example the "What" neocortex module, for only a short time period, with 50 ms found suitable. A short period of high firing could be produced in the cortex by the adaptation mechanisms described above.

The simulation protocol was to simulate 200 ms of spontaneous activity, and to follow this with a recall cue presented for time = 200 to time = 250 ms to the NcWhat neurons with a rate of an extra 6 Hz above the Poisson spontaneous input to each neuron of 3 Hz produced through the 800 synapses for these inputs on each neuron, following the general approach of Brunel and Wang (2001). The actual values for the spontaneous rates etc are evident in Figures 4 and 5, and we ensured that there was some spontaneous firing before any recall cue was applied as some spontaneous firing is important in the rapid recall that occurs in biologically realistic attractor neuronal networks (Battaglia & Treves, 1998; Panzeri et al., 2001; Rolls, 2023b). The simulation was then allowed to run until 1 s had elapsed by which time a firing rate typical of those in the hippocampus had been achieved, and a decrease back to lower rates had started, due in part to the adaptation that was implemented as described above. The measure of performance was whether the correct neurons, identified by their indices from the Rate simulation, had increased firing in the NcWhere module. A low rate for the recall firing was considered satisfactory, for this could trigger a local recurrent attractor network in the neocortex (NcWhere) module. The rate network was trained with randomly chosen populations of binary neurons for each memory, one population in neocortical What and the other in neocortical Where. The figures show the firing of the neurons trained for memory pair 1 (called pattern 1) when pattern 1 is applied as a recall cue only to the NcWhat module. The figures show as a control the firing of the neurons that had been trained for memory pattern 2, to illustrate that the firing is much greater when pattern 1 is applied than for the neurons trained with pattern 2. As the whole network is symmetric, it can be tested with memory pattern 2 as an input to, for example, NcWhere, and the correct firing is produced appropriate for pattern 2 in NcWhat.

3 | RESULTS

3.1 | Rate simulation of the neocortical–hippocampal architecture shown in Figure 2 for memory storage and recall

One aim was to investigate key parameters that influence the number of memory sets or patterns of neocortical neuronal firing that can be stored in the hippocampus and later recalled back to the neocortex. The architecture is shown in Figure 2, which reflects approximately the relative numbers of neurons and synapses per neuron in different parts of the neocortical–hippocampal circuitry. The paradigm was to train the network with randomly generated pairs of binary input patterns presented simultaneously to the What and Where neocortical modules, and then later to present only a What neocortical retrieval cue, and measure whether utilizing completion in CA3 and the modified backprojection synapses shown in green in Figure 2, the other part of the memory could be correctly recalled to the neocortical Where module. The second aim was to train synaptic weights in the matrices in each of the modules in Figure 2 so that these synaptic weights could be transferred to an integrate-and-fire simulation. Then in the integrate-and-fire simulation the time could be measured for the recall of information to the neocortical Where module after a retrieval cue was applied to the neocortical What module.

The architecture with the parameters shown in Figure 2 scaled down by 5 (with thus $C = 200$ synapses per neuron for most of the networks shown in Figure 2, except for the entorhinal to CA3 projection which was 60 with this scaling down by 5) was able to store "What" – "Where" associated random binary patterns of neuronal activity with perfect recall of "Where" components to NcWhere when provided only with the "What" component as an input to the neocortex with 50 patterns. With 100 patterns the neocortex 'Where' information was recalled with a mean correlation across the patterns of 0.895.

Although the capacity of the CA3 autoassociation network is known analytically (Treves & Rolls, 1991), and of the pattern association networks (Rolls & Treves, 1990) used in recall (from the entorhinal cortex to CA3, from CA1 to the entorhinal cortex, and from the entorhinal cortex to the neocortex), the capacity of the whole neocortex–hippocampus–neocortex system has not been tested before. To measure the capacity of the whole neocortex–hippocampus–neocortex system, the whole network shown in Figure 2 scaled down by 5 was trained with paired combinations of neocortex "What" and "Where" random binary patterns, and then the network was tested with only the neocortex "What" pattern used as a recall cue, and recall was measured in the neocortex "Where" network (see Figure 2). It was found that one limitation on the memory capacity of the whole network was the number of synapses from the entorhinal cortex to the CA3 neurons (estimated to be in the order of 3600 in the rat (Amaral et al., 1990; Rolls & Treves, 1998; Treves & Rolls, 1992)), set at 60 for these simulations scaled down by 5 from what is shown in Figure 2 to reflect what is found in the hippocampus (Rolls & Treves, 1994; Treves & Rolls, 1994). This was shown by increasing the number of synapses from the entorhinal cortex to each CA3 neuron to 200, for which the NcWhere retrieval pattern correlation was now 0.990 with 50 pattern pairs. This connectivity from the entorhinal cortex to CA3 operates as a pattern association network (Rolls, 2023b; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994), and the capacity found here is consistent with the analysis of the storage capacity of a pattern association network with sparse coding shown in Equation 1 (Rolls, 2023b; Rolls & Treves, 1990). The maximum number of patterns, $p_{\max}$, that can be stored and correctly retrieved in a pattern association network is approximately

$$p_{\max} = \frac{C}{\left[a_o \log\left(\frac{1}{a_o}\right)\right]} \tag{1}$$

where C is the number of synaptic connections onto each neuron and a_o is the sparseness of the output representation (Rolls & Treves, 1990).

To examine more fully the effect of loading on the retrieval of memories to the Where neocortex from the What neocortex via the hippocampus, Figure 3 (blue, o) shows the NcWhere recall correlation as a function of the number of patterns stored during training in the whole network as just described. It can be seen that the recall, measured by how high the correlation is of the recalled memory with what was stored, starts to degrade when the number of patterns increases beyond 200. This is exactly what is expected, for the storage capacity estimated using the analytically derived Equations 1 and 2 is approximately 250 memory patterns with 200 synapses per neuron and the sparseness of the representations used. (These simulations were run with the architecture shown in Figure 2 scaled down by 5 in terms of the number of neurons and the number of synapses per neuron, except that for these simulations the number of synaptic connections from the entorhinal cortex to CA3 was also set to 200, to test whether given this, the whole system could be trained up to a theoretical capacity.)

To gain further insight into the operation of the whole neocortex–hippocampus–neocortex system, Figure 3 also shows the correlations of the dentate gyrus firing rates (green, x) when only the neocortex "What" input was applied compared to the firing after training when both the neocortex What and Where inputs were applied. Because the dentate granule cells are modeled as a competitive network, applying just half the inputs from the entorhinal cortex (entorhinal What) produces firing in the dentate that is only correlated

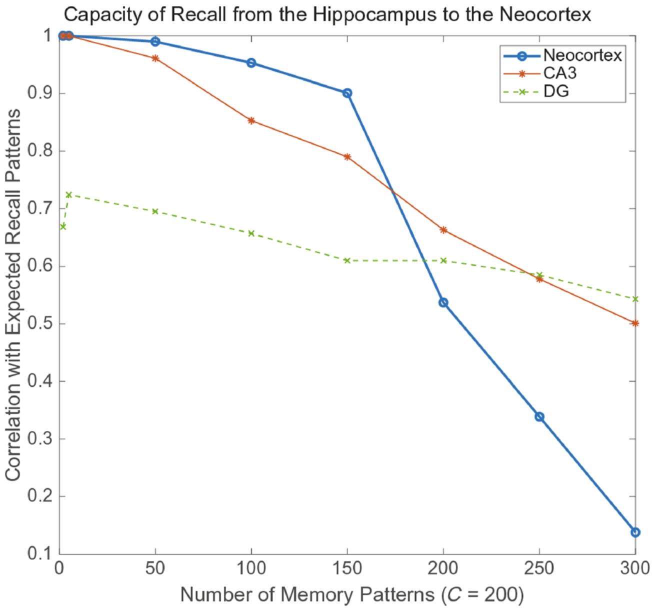

FIGURE 3 Capacity of the neocortex–hippocampus–neocortex network. After training with paired combinations of neocortex "What" and "Where" random binary patterns, the network was tested with only the neocortex "What" pattern used as a recall cue, and recall was measured in the neocortex "Where" network (see Figure 2). The capacity was measured with the network shown in Figure 2 scaled down by 5 to have $C = 200$ synapses per neuron and with $N = 1000$ neurons in each network. The abscissa shows the number of random binary patterns presented to NcWhat with which the whole network was trained. The ordinate neocortex plot (o, blue) shows the mean correlation of the memory patterns recalled in NcWhere with what was expected for both NcWhat and NcWhere as the recall cue. The ordinate CA3 plot (*, red) shows the mean correlation of the memory patterns recalled in the CA3 cells with what was expected. The ordinate DG plot (x, green) shows the mean correlation of the memory patterns recalled in the dentate granule cells with what was expected. The critical capacity of each network alone is calculated to be close to 250 with $C = 200$ synapses per neuron and the sparseness $a = 0.05$ (see Equations 1 and 2).

about 0.5–0.7 with what was expected when both the neocortex What and Where inputs are applied.

Figure 3 shows that CA3 does operate as an attractor network, in that when only the neocortex What input is used as a recall cue, for loading up to approximately 150, the correlation of CA3 firing with what is expected was high (0.79–1 depending on the loading). This was confirmed by disabling the CA3 to CA3 recurrent collateral connectivity that implements the attractor network. When the loading was 200 or more, the performance of CA3 as an attractor network then failed, and recall correlated only 0.5–0.66 with what was expected. This is consistent with the analytic approach, which shows that the memory capacity of an attractor network in terms of p the maximum number of patterns that can be stored and correctly retrieved is approximately

$$p = \frac{Ck}{\left[a \log\left(\frac{1}{a}\right)\right]} \tag{2}$$

where C is the number of recurrent collateral synaptic connections onto each neuron, a is the sparseness of the representation, and k is a factor that depends weakly on the detailed structure of the firing rate distribution, on the connectivity, and so on, but is roughly in the order of 0.2–0.3 (Rolls, 2023b; Treves, 1991a, 1991b; Treves & Rolls, 1991). For 200 synapses per neuron, Equation (2) evaluates to approximately 270, so that the fall in the CA3 recall correlations when the number of patterns stored is about 200 (Figure 3) and above is consistent with the analysis.

Figure 3 also shows that the pattern association implemented by the backprojections from CA1 to entorhinal cortex, and from entorhinal cortex to the neocortex, can improve the final recall in the neocortex (blue, o) above what is found in CA3 alone, as expected because these backprojections are modeled as pattern association networks, and the capacity is as shown in Equation (1).

In summary, the simulations illustrated in Figure 3 show that the capacity of the whole neocortex–hippocampus–neocortex system is high and what is expected analytically given the capacity limits of each of the separate networks in the system illustrated in Figure 3. That is, the capacity of the whole neocortex–hippocampus–neocortex system is very similar to the capacity of any single network in the system. In this context, the number of synapses from the entorhinal cortex to any one neuron in CA3 may be the limiting capacity of the whole system, and further research on the number of these synapses on any one CA3 neuron in different species will be of great interest.

3.2 | Integrate-and-fire simulation of the neocortical–hippocampal architecture shown in Figure 2 for memory storage and recall

One aim of these investigations is to measure the time from applying a retrieval cue to the neocortex (e.g., the What module NcWhat in Figure 2), to retrieving the rest of the memory in another part of the neocortex (e.g., NcWhere in Figure 2). Further aims are to investigate factors that may enable the whole dynamical system to operate stably given that once some recall has occurred back to the neocortex, the neocortical signals are fed back into the hippocampus, and can return then back to the neocortex. This may be advantageous for what we will term "long-loop recall," but has major risks of the positive feedback in the long loop leading to runaway excitation that could contribute to temporal lobe epilepsy due to excessive neuronal firing.

The operation of the integrate-and-fire simulation of the neocortical–hippocampal–neocortical circuitry for recall is shown in Figures 4 and 5. To illustrate the time course, the whole network was trained in the Rate model with pairs of random binary patterns applied to the neocortex What and Where modules. Then in the integrate and fire model, one of the patterns was applied to the neocortex What module, and recall was measured after passage through the hippocampal CA3 and CA1 system back to the neocortex Where Module (see Figure 2). Figure 4a shows the effects of the 6 Hz recall cue applied from time = 200 until time = 250 ms to the NcWhat neurons for memory pattern 1. The mean rate of the NcWhat neurons

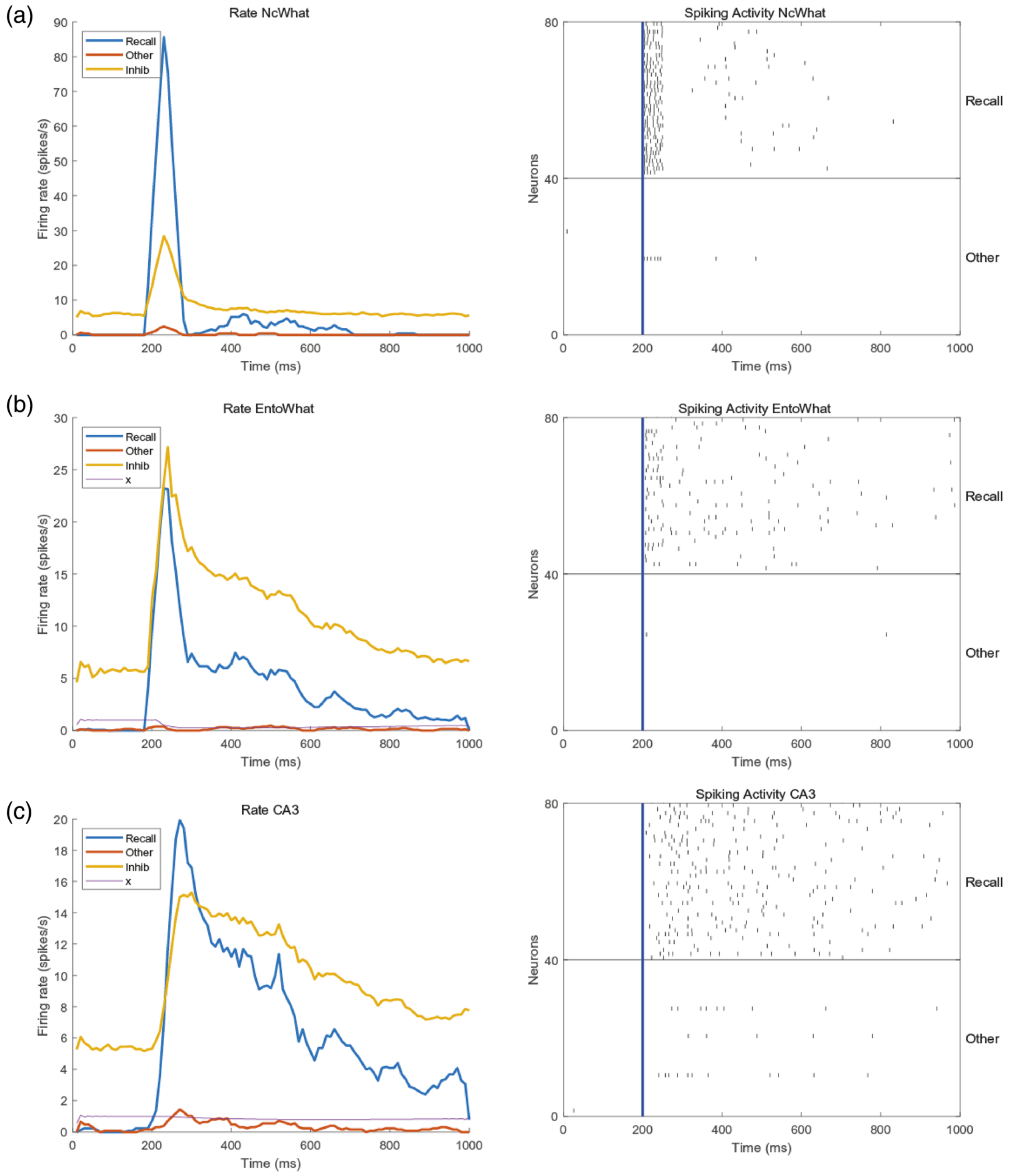

FIGURE 4 Integrate-and-fire simulation of the dynamics of the neocortical–hippocampal system illustrated in Figure 2. Left panels: The firing rates are shown for the neurons trained for pattern 1 (blue), pattern 2 (red), and the inhibitory neurons (yellow) for the "What" neocortical module (NcWhat) to which pattern stimulus 1 was applied at time = 200 ms, and for the lateral "What" entorhinal cortex module, and for the CA3 module. Rastergrams for 40 neurons chosen at random from the population trained for pattern 1 ("Recall"), and for the population trained to pattern 2 ("Other") are shown. Because pattern 1 was applied to NcWhat, the firing rates are higher for all the neurons that should be activated by memory pattern 1 (blue), than for the neurons that were trained for pattern 2, indicating correct operation. For the integrate-and-fire simulations, similar results were obtained with 2 or 20 memory pattern pairs ("what" and "where") stored in the network. The plot of "x" for some networks shows the extent of any presynaptic adaptation, where a value of 1 indicates no adaptation, and the maximal adaptation occurs as x approaches 0. The firing rate plots were smoothed with a 5-point filter, and the recall cue actually started at 200 ms.

allocated to recall pattern 1 (blue in Figure 4a, labeled "Recall") increased within ms to approximately 80 spikes/s, and then decreased when the stimulus was removed. The firing rate would have decreased to the mean firing rate of approximately 1 spike/s without the feedback effects coming back to NcWhat from the hippocampal circuitry. The neurons allocated to memory pattern 2 (red in

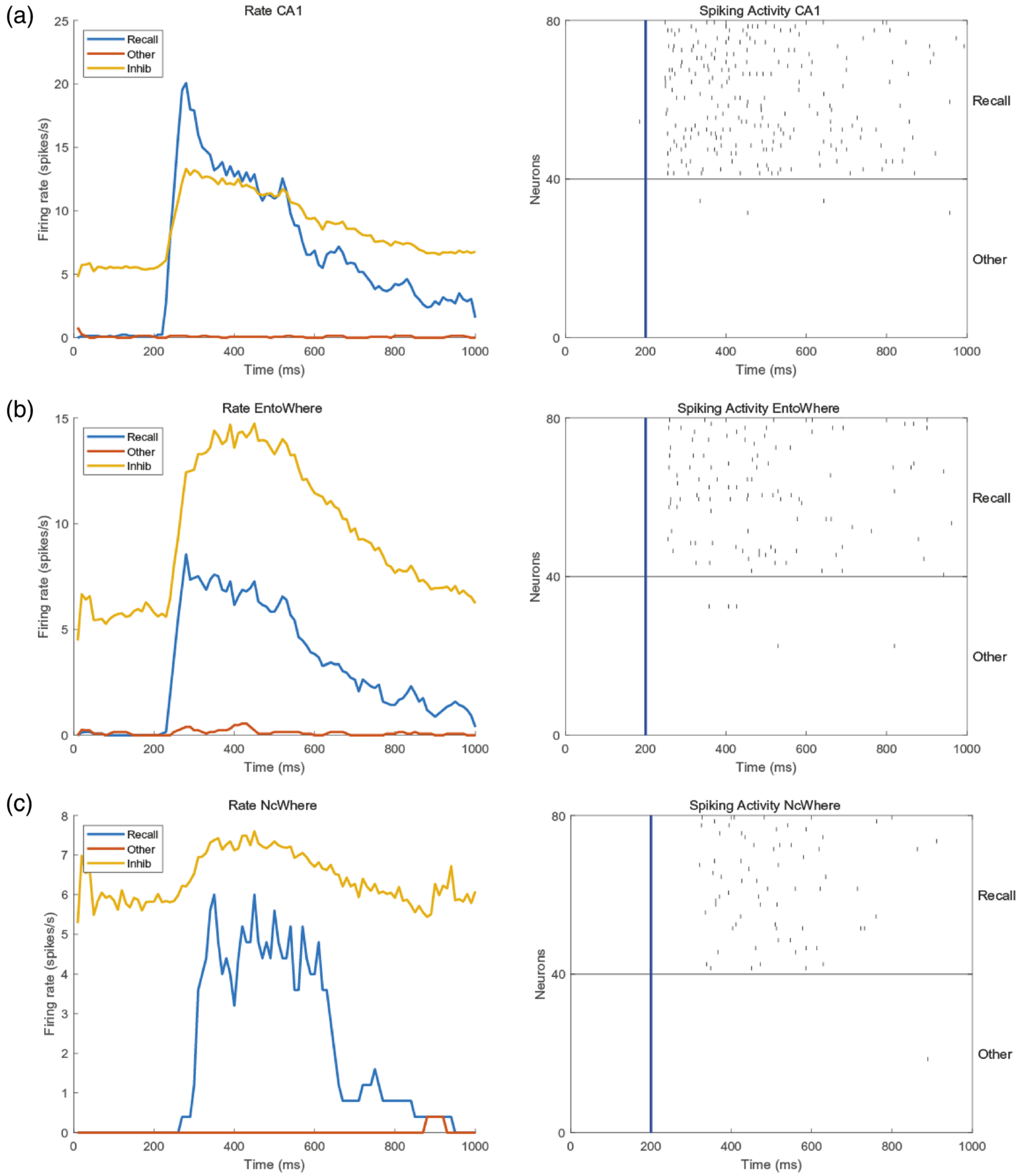

FIGURE 5 Integrate-and-fire simulation of the dynamics of the neocortical–hippocampal system illustrated in Figure 2. Left panels: The firing rates are shown for the neurons trained for pattern 1 (blue), pattern 2 (red), and the inhibitory neurons (yellow) for the CA3 module, for the medial entorhinal cortex "Where" module, and for the neocortical "Where" module (NcWhere). Conventions as in Figure 4. Because pattern 1 was applied to NcWhat, the firing rates are higher for all the neurons that should be activated by memory pattern 1 (blue), than for the neurons that were trained for pattern 2, indicating correct operation right through CA1, EntoWhere to NcWhere (see text).

Figure 4a, labeled "Other") hardly increased their firing, showing that the effects were selective as expected for the neurons trained to memory pattern 1. In all cases in this and subsequent Figures, the other excitatory neurons hardly altered their rates during the memory recall, again showing that the effects were selective to the training patterns. Because the timing and selectivity can be measured with just two training memory patterns, that was the number used in the integrate-and-fire simulations, though the rate model itself could be tested up towards the theoretical capacity as described above.

The next stage of the circuitry is the lateral entorhinal cortex What module, and as it had been trained as a competitive network (Rolls, 2023b), the Recall neurons responded rapidly, within approximately 20 ms, to the input from NcWhat (Figure 4b). The sparseness of the representation here is 0.05, and with that greater proportion of neurons responding to the input, an increase in the firing of the inhibitory neurons is also clear. The neurons that are related to memory pattern 2 had a small increase in firing (red) due to feedback effects round the hippocampal circuit, but the firing was still selective for the memory pattern 1 neurons (blue).

The next stage of the circuitry during recall is via the lateral entorhinal What module associatively modified synapses to the CA3 neurons, which operate as an autoassociation attractor network. They fall into their basin of attraction quickly, within approximately a further 20 ms (Figure 4c), in line with the theory that an integrate-and-fire attractor network can retrieve the whole memory from one part within perhaps 2 or a few time constants of the synapses (Battaglia & Treves, 1998; Panzeri et al., 2001; Rolls, 2023b; Rolls & Webb, 2012; Treves et al., 1997; Webb et al., 2011). The latency (measuring from the firing when it has reached approximately 1/3 of its maximum and from the response in the NcWhat module) is approximately 40 ms.

The next stage of circuitry is from CA3 to CA1, and because this is implemented as a competitive network, the recall is within approximately 20 ms (Figure 5a), and the elapsed time since the NcWhat response was now approximately 60 ms.

The next stage of circuitry is from CA1 to the medial entorhinal “Where” cortex, and because this is implemented as a competitive network, the recall is within approximately 15–20 ms (Figure 5b), and the elapsed time since the NcWhat response was now approximately 90 ms.

The final stage of the circuitry is from the medial entorhinal “Where” cortex to the “Where” neocortex (NcWhere), and because this is implemented as a competitive network, this recall is potentially fast, but because the firing rates were kept low, the recall took a little longer (Figure 5c), and the elapsed time since the NcWhat response to the early part of a NcWhere response was now approximately 100 ms. The firing rate in this module was relatively low because the synaptic backprojection connection strengths to the neocortex were set relatively low, to minimize the effects of the positive excitatory feedback to produce runaway excitation, and because forward inputs must always dominate cortical firing. In more detail, the backprojection connections needed for memory recall and top-down attention need to be much smaller than the forward connections, so that the forward inputs, when present dominate the firing (Deco & Rolls, 2004, 2005a, 2005b; Rolls, 2023b; Rolls et al., 2012; Rolls & Deco, 2010, 2015a). The concept is that this low firing rate for the recall from the hippocampus to the neocortex is sufficient to then trigger a neocortical attractor network response to add to the recall process.

The key finding is that the time for the neocortical–hippocampal–neocortical loop to recall memory to the neocortex is approximately 100 ms. This is sufficiently fast that the backprojection-firing is sufficiently rapid during the learning of the episodic memory for the backprojections to reach the neocortex from the hippocampal system sufficiently fast so that the neocortical neurons are still active in response to their input, allowing the backprojection synapses to be modified by pattern association learning to implement memory recall from the hippocampus to the neocortex, as in the Rolls and Treves theory of the hippocampus (Rolls, 1987, 1989a; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994).

Another feature of what is shown in Figures 4 and 5 is the late activity at approximately 310 ms after the NcWhat module has started to respond. Although the CA3 continuing firing in its attractor state contributes to this, this later firing after the recall has been produced is partly due to positive feedback from the hippocampus to the neocortex by the synapses from CA1 to the entorhinal cortex, and from the entorhinal cortex to the neocortex. This was shown by disabling the CA1 to entoWhat, and entoWhat to NCWhat, backprojection synapses, which left the recall to entoWhere intact, but abolished the high firing rates that tended to develop after approximately 100 ms. It is proposed that the effects of these backprojection synapses contribute to a long-loop recall effect maximizing the completion of what is recalled in the neocortex, and complementing the completion provided by CA3. However, what was found in the integrate-and-fire simulations is that the backprojection effects must be carefully controlled, to prevent runaway excitation in the neocortex–hippocampus–neocortex circuit. The requirement became very clear as a result of these integrate-and-fire simulations.

The integrate-and-fire simulations also enabled the investigation of how the long-loop positive feedback could be controlled. One way was to have high inhibition in CA3 and CA1, and this was implemented by increasing the E to I neuron connection strength ratio from its default value of 1 to 9 for CA3, and to 7 for CA1. This helped to keep the firing rates of these CA3 and CA1 hippocampal neurons low (Figures 4 and 5), just as they are in the brain, and, it is proposed, to help prevent runaway long-loop excitation. It was also found useful to increase the E to I connection value to 15 for the entorhinal cortex.

A second way to control the long-loop positive feedback that was found to be important in the integrate-and-fire simulations was to introduce temporal adaptation into the circuit. This was implemented with neuronal adaptation using the g_{AHP} mechanism for excitatory neurons, which was set to quite a high value of g_{AHP} (150 nS by default and 450 ns for the entorhinal cortex, and to facilitate continuing firing to 0 nS for CA3) to show clearly the adaptation in the figures.

A third way to control the long-loop positive feedback was to limit the duration of the recall cue applied to NcWhat, in this case to 50 ms. This may be implemented in part by the neocortical adaptation described above.

A fourth way to control the long-loop positive feedback that was found to be useful in the integrate-and-fire simulations was to keep the recall cue applied to NcWhat to be relatively low, 6 Hz extra firing for the NCWhat neurons in memory pattern 1 to act as the recall cue.

4 | DISCUSSION

4.1 | Integrate-and-fire simulations of neocortical–hippocampal–neocortical recall

Key findings with the integrate-and-fire simulations of neocortical–hippocampal–neocortical recall were as follows.

First, the time for recall to reach the neocortex round the neocortex–hippocampus–neocortex loop was sufficiently fast, approximately 100 ms, for the backprojections from the hippocampal system to the neocortex (green in Figure 2) to be firing while the neocortical pyramidal cells are still being driven by the to-be-remembered input, allowing pattern association to be learned between the backprojections and the neocortical pyramidal cells.

Second, it was found in the integrate and fire simulation of recall from the hippocampus that a long-loop attractor was also set up by the neocortical–hippocampal–neocortical loop. This has the potential advantage of feeding back information into the hippocampal system to produce better completion in all relevant neocortical regions (e.g., what, where, and reward, see Figure 1), and complementing the completion implemented in CA3. Of course these two types of completion are different and complementary, in that because there is a single attractor network in CA3 given the extensive range of the CA3 recurrent collaterals (McNaughton & Morris, 1987; Rolls, 1987, 1989a; Rolls & Treves, 1994, 2024; Treves & Rolls, 1994) (also modeled by others (Hasselmo et al., 1995; Hasselmo & Wyble, 1997)) that is clearly evident in primates (Kondo et al., 2009), the CA3 network can associate any of its inputs with any others of its inputs, which is required for "what," "where," and "reward" combination episodic memory.

The role of the backprojection pathways from CA3 via CA1 to the neocortex in improving recall is demonstrated by the model. When the system is heavily loaded with many "What"–"Where" patterns to be associated, recall may not be perfect in CA3, but can become better by the time that the neocortex is reached (e.g., Figure 3 for loadings less than 200). This can be understood very clearly computationally, because the backprojection connectivity from CA1 to the entorhinal cortex, and from the entorhinal cortex to the neocortex, both act as pattern associators, which have exactly this property (Rolls, 2023b).

Third, it was found in the integrate and fire simulation of recall from the hippocampus that the long-loop attractor was potentially a major problem for the operation of the neocortex–hippocampal–neocortex system, because it made runaway excitation due to the positive feedback between the excitatory neurons in the different modules in this circuit a danger. We were able to show in the integrate-and-fire simulations that several mechanisms may contribute to maintaining the whole system stable. One is high inhibition in e.g. the CA3 and CA1 parts of the hippocampus (and during learning probably in the dentate gyrus too), implemented by strong connectivity from excitatory to inhibitory neurons (E to I connections within each module). This need may help to account for why the firing rates of CA3 and CA1 pyramidal neurons are relatively low, typically less than 15 spikes/s in primates (Georges-François et al., 1999; Robertson et al., 1998; Rolls et al., 1997, 1998). A second mechanism is temporal adaptation (see also Hasselmo et al., 1995), which was found to be very important in controlling runaway excitation in the neocortex–hippocampus–neocortex system. Indeed, it is proposed that temporal adaptation, including neuronal and presynaptic adaptation, is a key property of cortical including hippocampal neurons, because it helps to maintain stability in local and long-loop intermodule networks that are inherently unstable because of the excitatory-to-excitatory connections (Rolls, 2023b). A third approach that contributed to the stability of the whole neocortex–hippocampus–neocortex system was keeping the application time for the recall cue to be relatively short, which could be implemented in part by temporal adaptation, whether neuronal (Liu & Wang, 2001) or synaptic (Kern & Chao, 2023; Mongillo et al., 2008; Rolls et al., 2013; Tsodyks & Markram, 1997) or both. A fourth approach was to allow the recall stimulus applied to the neocortex to be not too strong so that the firing rates were kept down to reasonable levels for the neocortex, as shown in Figure 4a.

Fourth, it was difficult to train the whole network in the integrate-and-fire implementation because the almost Poisson spike times and relatively low firing rates meant that any estimate of the presynaptic and postsynaptic terms needed to associatively modify a synaptic weight tended to be noisy, so introducing stochastic noise into the synaptic weights that were learned. Another problem of training in the integrate-and-fire implementation was that it therefore took a long time, at least 250 ms, every time that a stimulus was presented, to estimate the presynaptic and postsynaptic terms, and given the considerable training that was needed, the computational time for the simulations would have been enormously long. The solution that was adopted was to train the synaptic weights with the rate model, and then import the synaptic weights into the integrate-and-fire model. That was a good solution to the issue. It is noted that although much training was needed in the Rate simulation for the network, once the weights had been learned, it would be easy to add a new episodic memory to the system in one training trial, provided that it consisted of components, for example, a location and an object, that had already been trained into the system. That is close to the distinction between slow semantic learning, and fast learning of new associations in the hippocampal system of the semantic components are already present (McClelland et al., 1995, 2020).

4.2 | Rate simulations of neocortical–hippocampal–neocortical memory storage and recall

Key findings with the Rate simulations of neocortical–hippocampal–neocortical recall were about how the dilution of connectivity in the cortex affects the operation of this cortical circuitry, and about the capacity of the whole system.

Diluted connectivity is a feature of cortical connections, and was implemented in the investigations described here (Rolls, 2016a, 2023b). Diluted connectivity can have advantages in competitive networks, for it helps to break the symmetry between the neurons, and helps the competitive network to stably allocate different input patterns to be categorized by different neurons (Rolls, 2016b). Sparse representations of the output neurons in the competitive network can also help different categories to be learned to different input patterns (Rolls, 2015, 2016a, 2023b).

On the other hand, although pattern association networks can operate reasonably well with diluted connectivity (Rolls, 2015; Rolls & Treves, 1990), in part by reducing the probability of more than one synapse between an input and output neuron (Rolls, 2015), the simulations described here showed that if the representations in the pattern association networks used for recall using backprojections (e.g., CA1 to entorhinal and entorhinal to neocortex) had not only diluted connectivity but also utilized sparse representations (e.g., 0.01), then recall became poor. This was because the combination of missing synapses and sparse input patterns to the pattern association network could result in poor activation of some output neurons that should have been active in the recalled pattern.

We have then something of a conflict between the desired properties for competitive and pattern association networks. With diluted connectivity, it can be advantageous to have sparse input patterns to be categorized by competitive networks, but for pattern association networks with diluted connectivity, the input patterns should not be too sparse. This leads to an interesting and potentially important implication for understanding the design and operation of the neocortex. For the forward connectivity in a hierarchically organized system such as sensory neocortical systems (Rolls, 2016a) in which learning of new representations is required, perhaps using competitive learning, it may be advantageous to have sparse representations. The superficial layers of the neocortex fit this computational function of learning new representations up through the neocortical hierarchy (Rolls, 2016a, 2023b). It is therefore proposed that for this reason the superficial layers (2 and 3) of the neocortex should utilize sparse representations. For the top-down backprojections in a cortical hierarchy, it is likely for the reasons just described, that to recall patterns of firing in earlier neocortical regions as part of memory recall (Rolls, 2016a), not very sparse representations could be advantageous in the deep layers of the neocortex that provide the backprojections to the preceding neocortical region used for recall. Thus it is proposed that representations in the deep layers of the neocortex (5 and 6) should be less sparse than in the superficial layers. It is indeed proposed that this is a design principle for the neocortex, and provides one key reason why the neocortex uses superficial and deep layers. The same argument applies to the entorhinal cortex: it is proposed that the representations in the superficial layer (especially 2) should be relatively sparse, whereas the representation in the deep layer involved in backprojections used for recall (in this case layer 5) should be less sparse, more distributed. This approach to understanding why the neocortex has superficial and deep layers complements earlier hypotheses (Rolls, 2023b; Rolls & Mills, 2017).

The rate simulations also showed that the bottleneck in terms of storage capacity, the number of episodic memories that can be stored and correctly retrieved, was in the entorhinal to CA3 connections used to initiate recall firing in the CA3 network (Treves & Rolls, 1992). This is in line with theoretical estimates for pattern association and attractor networks, with the number of synapses per CA3 neuron from the entorhinal cortex at 3600 in rodents, less than in other parts of the system (e.g., 12,000 for the CA3-CA3 recurrent collaterals; Rolls, 2023b; Rolls & Treves, 2024; Treves & Rolls, 1994). It is suggested that in light of this, it would be important to obtain further estimates of the number of synaptic connections from entorhinal cortex neurons onto each CA3 neuron, especially in primates, as this sets the limit of this pattern association recall capacity (Rolls, 2023b; Rolls & Treves, 1990).

4.3 | Conclusions and synthesis

This research elaborates and makes more specific the theory that recall of memories from the hippocampus to the neocortex can be implemented by backprojection synapses that are modifiable at one or more stages back to the neocortex that act as a pattern associator trained by the conjunctive activity in the backprojection synapses and the neocortical neurons firing to the memory that is being stored (Rolls, 1989a, 1995; Rolls & Treves, 2024; Treves & Rolls, 1994). In a sense, this mechanism provides a pointer to which neocortical neurons should be activated during memory recall. It had been recognized before this theory that a pointer was needed even though no theory of its implementation was available (Teyler & DiScenna, 1986). The finding emphasized here that the hippocampus can maintain activity for at least a short time after stimuli are removed in two or several more distant cortical systems (here "What" and "Where") because of continuing backprojection activity to them leads to the proposal that this pointer-like binding or coupling computation could be a way in which the hippocampus is involved in helping to form new neocortical semantic memories, by holding online continuing activity in distant neocortical areas for particular representations, thereby helping the neocortex to reorganize its semantic representations.

The research also shows with the integrate-and-fire simulations that the feedback from the hippocampus is sufficiently fast, within 100 ms, for the learning required for this theory of hippocampal recall to the neocortex (Rolls, 1989a, 1995; Treves & Rolls, 1994) to be biologically plausible.

The research also shows with the integrate-and-fire simulations that the whole circuit from neocortex to hippocampal CA3 and back to neocortex when operating in continuous time allows not just CA3, but the whole neocortex–hippocampus–neocortex system to settle into a systems-level, long-loop, attractor that potentially enhances memory recall to the neocortex.

The research also shows that this long loop attractor in inherently unstable, and that stability may be promoted by high inhibition in CA3 and CA1, and by utilizing the temporal adaptation of firing rates that is a strong feature of hippocampal neuronal activity, as well as typically of neocortical neuronal activity.

The research also shows how the whole circuit can operate with diluted connectivity, which is a key feature of cortical including hippocampal connectivity, and which can indeed be computationally useful in competitive networks such as those in the dentate granule cells and CA1 by helping their learning to categorize their inputs.

The research here complements other approaches to how "What" cortical representations of objects and faces are built (Rolls, 2021d, 2023b), and of how cortical "Where" representations are built (Rolls, 2024b), by showing how representations in these systems can be associated together for episodic memory and then recalled later from a partial recall cue (see also Rolls & Treves, 2024). The model being developed (Rolls, 2024b) of the ventromedial "Where" cortical stream for the representation of locations in spatial scenes involves binding together visual features at a particular location in a scene complemented by a continuous attractor network that links these features based on how far apart they are in a scene to build a map or chart of the locations of features in a whole scene (De Araujo et al., 2001; Rolls, 2024b, 2024c; Rolls & Stringer, 2005; Rolls & Treves, 2024; Stringer et al., 2005).

FUNDING INFORMATION

The work was supported by the following grants. Professor J. Feng: National Key R&D Program of China (No. 2019YFA0709502); 111 Project (No. B18015); Shanghai Municipal Science and Technology Major Project (No. 2018SHZDZX01), ZJLab, and Shanghai Center for Brain Science and Brain-Inspired Technology; and National Key R&D Program of China (No. 2018YFC1312904). The funding sources had no role in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the article for publication.

CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

DATA AVAILABILITY STATEMENT

The implementation of the pattern association, attractor, and competitive networks was as described by Rolls (2016a, 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. Additional code used in the simulations is available from the senior author.

ORCID

Edmund T. Rolls https://orcid.org/0000-0003-3025-1292
Chenfei Zhang https://orcid.org/0000-0001-5548-0521

REFERENCES

Amaral, D. G., Ishizuka, N., & Claiborne, B. (1990). Neurons, numbers and the hippocampal network. *Progress in Brain Research*, *83*, 1–11.

Battaglia, F. P., & Treves, A. (1998). Stable and rapid recurrent processing in realistic auto-associative memories. *Neural Computation*, *10*, 431–450.

Brunel, N., & Wang, X. J. (2001). Effects of neuromodulation in a cortical network model of object working memory dominated by recurrent inhibition. *Journal of Computational Neuroscience*, *11*, 63–85.

Burgess, N., & O'Keefe, J. (1996). Neuronal computations underlying the firing of place cells and their role in navigation. *Hippocampus*, *6*, 749–762.

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.

Deco, G., & Rolls, E. T. (2004). A neurodynamical cortical model of visual attention and invariant object recognition. *Vision Research*, *44*, 621–642.

Deco, G., & Rolls, E. T. (2005a). Attention, short-term memory, and action selection: A unifying theory. *Progress in Neurobiology*, *76*, 236–256.

Deco, G., & Rolls, E. T. (2005b). Neurodynamics of biased competition and co-operation for attention: A model with spiking neurons. *Journal of Neurophysiology*, *94*, 295–313.

Deco, G., & Rolls, E. T. (2006). Decision-making and Weber's Law: A neurophysiological model. *European Journal of Neuroscience*, *24*, 901–916.

Deco, G., Rolls, E. T., Albantakis, L., & Romo, R. (2013). Brain mechanisms for perceptual and reward-related decision-making. *Progress in Neurobiology*, *103*, 194–213.

Deco, G., Rolls, E. T., & Romo, R. (2009). Stochastic dynamics as a principle of brain function. *Progress in Neurobiology*, *88*, 1–16.

Epstein, R. A., & Baker, C. I. (2019). Scene perception in the human brain. *Annual Review of Vision Science*, *5*, 373–397.

Fyhn, M., Molden, S., Witter, M. P., Moser, E. I., & Moser, M. B. (2004). Spatial representation in the entorhinal cortex. *Science*, *305*, 1258–1264.

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. *Cerebral Cortex*, *9*, 197–212.

Hartley, T., Lever, C., Burgess, N., & O'Keefe, J. (2014). Space in the brain: How the hippocampal formation supports spatial cognition. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *369*, 20120510.

Hasselmo, M. E., & McGaughy, J. (2004). High acetylcholine levels set circuit dynamics for attention and encoding and low acetylcholine levels set dynamics for consolidation. *Progress in Brain Research*, *145*, 207–231.

Hasselmo, M. E., Schnell, E., & Barkai, E. (1995). Dynamics of learning and recall at excitatory recurrent synapses and cholinergic modulation in rat hippocampal region CA3. *Journal of Neuroscience*, *15*, 5249–5262.

Hasselmo, M. E., & Wyble, B. P. (1997). Free recall and recognition in a network model of the hippocampus: Simulating effects of scopolamine on human memory function. *Behavioural Brain Research*, *89*, 1–34.

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. *Cerebral Cortex*, *31*, 4652–4669.

Kern, F. B., & Chao, Z. C. (2023). Short-term neuronal and synaptic plasticity act in synergy for deviance detection in spiking networks. *PLoS Computational Biology*, *19*, e1011554.

Kesner, R. P., & Rolls, E. T. (2015). A computational theory of hippocampal function, and tests of the theory: New developments. *Neuroscience and Biobehavioral Reviews*, *48*, 92–147.

Kondo, H., Lavenex, P., & Amaral, D. G. (2009). Intrinsic connections of the macaque monkey hippocampal formation: II. CA3 connections. *Journal of Comparative Neurology*, *515*, 349–377.

Kraus, B. J., Brandon, M. P., Robinson, R. J., Connerney, M. A., Hasselmo, M. E., & Eichenbaum, H. (2015). During running in place, grid cells integrate elapsed time and distance run. *Neuron*, *88*, 578–589.

Liu, Y. H., & Wang, X. J. (2001). Spike-frequency adaptation of a generalized leaky integrate-and-fire model neuron. *Journal of Computational Neuroscience*, *10*, 25–45.

Loh, M., Rolls, E. T., & Deco, G. (2007). A dynamical systems hypothesis of schizophrenia. *PLoS Computational Biology*, *3*, e228.

Ma, Q., Rolls, E. T., Huang, C.-C., Cheng, W., & Feng, J. (2022). Extensive cortical functional connectivity of the human hippocampal memory system. *Cortex*, *147*, 83–101.

Marr, D. (1971). Simple memory: A theory for archicortex. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *262*, 23–81.

McClelland, J. L., McNaughton, B. L., & Lampinen, A. K. (2020). Integration of new information in memory: New insights from a complementary learning systems perspective. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *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. *Psychological Review*, *102*, 419–457.

McNaughton, B. L., & Morris, R. G. M. (1987). Hippocampal synaptic enhancement and information storage within a distributed memory system. *Trends in Neurosciences*, *10*, 408–415.

Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. *Science*, *319*, 1543–1546.

Moser, E. I., Moser, M. B., & McNaughton, B. L. (2017). Spatial representation in the hippocampal formation: A history. *Nature Neuroscience*, *20*, 1448–1464.

Moser, E. I., Roudi, Y., Witter, M. P., Kentros, C., Bonhoeffer, T., & Moser, M. B. (2014). Grid cells and cortical representation. *Nature Reviews: Neuroscience*, *15*, 466–481.

Moser, M. B., Rowland, D. C., & Moser, E. I. (2015). Place cells, grid cells, and memory. *Cold Spring Harbor Perspectives in Biology*, *7*, a021808.

Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, *110*, 611–646.

O'Keefe, J. (1979). A review of the hippocampal place cells. *Progress in Neurobiology*, *13*, 419–439.

Panzeri, S., Rolls, E. T., Battaglia, F., & Lavis, R. (2001). Speed of feedforward and recurrent processing in multilayer networks of integrate-and-fire neurons. *Network*, *12*, 423–440.

Robertson, R. G., Rolls, E. T., & Georges-François, P. (1998). Spatial view cells in the primate hippocampus: Effects of removal of view details. *Journal of Neurophysiology*, *79*, 1145–1156.

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 Structure & Function*, *225*, 2521–2531.

Rolls, E. T. (1987). Information representation, processing and storage in the brain: Analysis at the single neuron level. In J.-P. Changeux & M. Konishi (Eds.), *The neural and molecular bases of learning* (pp. 503–540). Wiley.

Rolls, E. T. (1989a). Functions of neuronal networks in the hippocampus and neocortex in memory. In J. H. Byrne & W. O. Berry (Eds.), *Neural models of plasticity: Experimental and theoretical approaches* (pp. 240–265). Academic Press.

Rolls, E. T. (1989b). Parallel distributed processing in the brain: Implications of the functional architecture of neuronal networks in the hippocampus. In R. G. M. Morris (Ed.), *Parallel distributed processing: Implications for psychology and neurobiology* (pp. 286–308). Oxford University Press.

Rolls, E. T. (1995). A model of the operation of the hippocampus and entorhinal cortex in memory. *International Journal of Neural Systems*, *6*, 51–70.

Rolls, E. T. (2015). Diluted connectivity in pattern association networks facilitates the recall of information from the hippocampus to the neocortex. *Progress in Brain Research*, *219*, 21–43.

Rolls, E. T. (2016a). *Cerebral cortex: Principles of operation*. Oxford University Press.

Rolls, E. T. (2016b). Pattern separation, completion, and categorisation in the hippocampus and neocortex. *Neurobiology of Learning and Memory*, *129*, 4–28.

Rolls, E. T. (2018). The storage and recall of memories in the hippocampo-cortical system. *Cell and Tissue Research*, *373*, 577–604.

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. (2021a). On pattern separation in the primate including human hippocampus. *Trends in Cognitive Sciences*, *25*, 920–922.

Rolls, E. T. (2021b). Neurons including hippocampal spatial view cells, and navigation in primates including humans. *Hippocampus*, *31*, 593–611.

Rolls, E. T. (2021c). *Brain computations: What and how*. Oxford University Press.

Rolls, E. T. (2021d). Learning invariant object and spatial view representations in the brain using slow unsupervised learning. *Frontiers in Computational Neuroscience*, *15*, 686239.

Rolls, E. T. (2022). The hippocampus, ventromedial prefrontal cortex, and episodic and semantic memory. *Progress in Neurobiology*, *217*, 102334.

Rolls, E. T. (2023a). 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.

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. (2024a). The memory systems of the human brain and generative artificial intelligence. *Heliyon*, *10*, e31965.

Rolls, E. T. (2024b). *A theory and model of scene representations with hippocampal spatial view cells*.

Rolls, E. T. (2024c). Two what, two where, visual cortical streams in humans. *Neuroscience and Biobehavioral Reviews*, *160*, 105650.

Rolls, E. T., & Deco, G. (2010). *The Noisy brain: Stochastic dynamics as a principle of brain function*. Oxford University Press.

Rolls, E. T., & Deco, G. (2015a). Networks for memory, perception, and decision-making, and beyond to how the syntax for language might be implemented in the brain. *Brain Research*, *1621*, 316–334.

Rolls, E. T., & Deco, G. (2015b). Stochastic cortical neurodynamics underlying the memory and cognitive changes in aging. *Neurobiology of Learning and Memory*, *118*, 150–161.

Rolls, E. T., & Deco, G. (2016). Non-reward neural mechanisms in the orbitofrontal cortex. *Cortex*, *83*, 27–38.

Rolls, E. T., Deco, G., Huang, C. C., & Feng, J. (2022a). The human orbitofrontal cortex, vmPFC, and anterior cingulate cortex effective connectome: Emotion, memory, and action. *Cerebral Cortex*, *33*, 330–356.

Rolls, E. T., Deco, G., Huang, C. C., & Feng, J. (2022b). The effective connectivity of the human hippocampal memory system. *Cerebral Cortex*, *32*, 3706–3725.

Rolls, E. T., Deco, G., Huang, C. C., & Feng, J. (2023a). Multiple cortical visual streams in humans. *Cerebral Cortex*, *33*, 3319–3349.

Rolls, E. T., Deco, G., Huang, C. C., & Feng, J. (2023b). The human posterior parietal cortex: Effective connectome, and its relation to function. *Cerebral Cortex*, *33*, 3142–3170.

Rolls, E. T., Dempere-Marco, L., & Deco, G. (2013). Holding multiple items in short term memory: A neural mechanism. *PLoS One*, *8*, e61078.

Rolls, E. T., Feng, J., & Zhang, R. (2024). 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 Structure & Function*, *229*, 1471–1493.

Rolls, E. T., Grabenhorst, F., & Deco, G. (2010a). Choice, difficulty, and confidence in the brain. *NeuroImage*, *53*, 694–706.

Rolls, E. T., Grabenhorst, F., & Deco, G. (2010b). Decision-making, errors, and confidence in the brain. *Journal of Neurophysiology*, *104*, 2359–2374.

Rolls, E. T., & Mills, P. (2019). The generation of time in the hippocampal memory system. *Cell Reports*, *28*, 1649–1658.e6.

Rolls, E. T., & Mills, W. P. C. (2017). Computations in the deep vs superficial layers of the cerebral cortex. *Neurobiology of Learning and Memory*, *145*, 205–221.

Rolls, E. T., Robertson, R. G., & Georges-François, P. (1997). Spatial view cells in the primate hippocampus. *European Journal of Neuroscience*, *9*, 1789–1794.

Rolls, E. T., & Stringer, S. M. (2005). Spatial view cells in the hippocampus, and their idiothetic update based on place and head direction. *Neural Networks*, *18*, 1229–1241.

Rolls, E. T., Stringer, S. M., & Trappenberg, T. P. (2002). A unified model of spatial and episodic memory. *Proceedings of the Royal Society B: Biological Sciences*, *269*, 1087–1093.

Rolls, E. T., & Treves, A. (1990). The relative advantages of sparse versus distributed encoding for associative neuronal networks in the brain. *Network*, *1*, 407–421.

Rolls, E. T., & Treves, A. (1994). Neural networks in the brain involved in memory and recall. *Progress in Brain Research*, *102*, 335–341.

Rolls, E. T., & Treves, A. (1998). *Neural networks and brain function*. Oxford University Press.

Rolls, E. T., & Treves, A. (2024). A theory of hippocampal function: New developments. *Progress in Neurobiology*, *238*, 102636.

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. *Journal of Neurophysiology*, *79*, 1797–1813.

Rolls, E. T., & Turova, T. S. (2024). *Visual cortical networks for 'What' and 'Where' to the human hippocampus revealed with dynamical graphs*.

Rolls, E. T., & Webb, T. J. (2012). Cortical attractor network dynamics with diluted connectivity. *Brain Research*, *1434*, 212–225.

Rolls, E. T., Webb, T. J., & Deco, G. (2012). Communication before coherence. *European Journal of Neuroscience*, *36*, 2689–2709.

Rolls, E. T., Wirth, S., Deco, G., Huang, C.-C., & Feng, J. (2023). The human posterior cingulate, retrosplenial and medial parietal cortex effective connectome, and implications for memory and navigation. *Human Brain Mapping*, *44*, 629–655.

Rolls, E. T., Yan, X., Deco, G., Zhang, Y., Jousmaki, V., & Feng, J. (2024). A ventromedial visual cortical 'Where' stream to the human hippocampus for spatial scenes revealed with magnetoencephalography. *Communications Biology*, *7*, 1047.

Stringer, S. M., Rolls, E. T., & Trappenberg, T. P. (2005). Self-organizing continuous attractor network models of hippocampal spatial view cells. *Neurobiology of Learning and Memory*, *83*, 79–92.

Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral Neuroscience*, *100*, 147–154.

Treves, A. (1990). Graded-response neurons and information encodings in autoassociative memories. *Physical Review A*, *42*, 2418–2430.

Treves, A. (1991a). Are spin-glass effects relevant to understanding realistic auto-associative networks. *Journal of Physics A*, *24*, 2645–2654.

Treves, A. (1991b). Dilution and sparse coding in threshold-linear nets. *Journal of Physics A*, *24*, 327–335.

Treves, A., & Rolls, E. T. (1991). What determines the capacity of autoassociative memories in the brain? *Network*, *2*, 371–397.

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.

Treves, A., Rolls, E. T., & Simmen, M. (1997). Time for retrieval in recurrent associative memories. *Physica D*, *107*, 392–400.

Tsodyks, M. V., & Markram, H. (1997). The neural code between neocortical pyramidal neurons depends on neurotransmitter release probability. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 719–723.

Vogt, K. E., & Regehr, W. G. (2001). Cholinergic modulation of excitatory synaptic transmission in the CA3 area of the hippocampus. *Journal of Neuroscience*, *21*, 75–83.

Wang, X. J. (2002). Probabilistic decision making by slow reverberation in cortical circuits. *Neuron*, *36*, 955–968.

Webb, T. J., Rolls, E. T., Deco, G., & Feng, J. (2011). Noise in attractor networks in the brain produced by graded firing rate representations. *PLoS One*, *6*, e23630.

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. *Journal of Neuroscience*, *38*, 9446–9458.

Zhao, X., Wang, Y., Spruston, N., & Magee, J. C. (2020). Membrane potential dynamics underlying context-dependent sensory responses in the hippocampus. *Nature Neuroscience*, *23*, 881–891.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Rolls, E. T., Zhang, C., & Feng, J. (2024). Hippocampal storage and recall of neocortical "What"–"Where" representations. *Hippocampus*, *34*(11), 608–624. https://doi.org/10.1002/hipo.23636