

A theory of hippocampal function: New developments

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ABSTRACT

We develop further here the only quantitative theory of the storage of information in the hippocampal episodic memory system and its recall back to the neocortex. The theory is upgraded to account for a revolution in understanding of spatial representations in the primate, including human, hippocampus, that go beyond the place where the individual is located, to the location being viewed in a scene. This is fundamental to much primate episodic memory and navigation: functions supported in humans by pathways that build 'where' spatial view representations by feature combinations in a ventromedial visual cortical stream, separate from those for 'what' object and face information to the inferior temporal visual cortex, and for reward information from the orbitofrontal cortex. Key new computational developments include the capacity of the CA3 attractor network for storing whole charts of space; how the correlations inherent in self-organizing continuous spatial representations impact the storage capacity; how the CA3 network can combine continuous spatial and discrete object and reward representations; the roles of the rewards that reach the hippocampus in the later consolidation into long-term memory in part via cholinergic pathways from the orbitofrontal cortex; and new ways of analysing neocortical information storage using Potts networks.

Key points:

- A theory of the capacity of the hippocampal CA3 attractor network for associating what, where and reward representations for episodic memory incorporating sparse representations, diluted connectivity, and graded firing rates
- How correlations inherent in self-organising continuous spatial representations reduce the capacity of the hippocampal CA3 attractor network
- Mechanisms for the recall of information from the hippocampus to the neocortex that quantify the capacity in terms of the number of backprojection synapses onto a neocortical neuron
- A revolution in understanding hippocampal spatial representations in primates including humans that are for locations in scenes by spatial view cells that are fundamental for much memory and navigation
- A ventromedial visual cortical stream in primates including humans that builds 'Where' spatial view representations using

feature combination learning and a continuous attractor network

- How reward value information reaches the primate including human hippocampus from the orbitofrontal cortex and contributes to memory consolidation in part via cholinergic pathways

1. Introduction

The hippocampus is a key brain system involved in episodic memory and spatial function (O'Keefe and Nadel, 1978; Squire and Zola-Morgan, 1991; Takeuchi et al., 2014; Kesner and Rolls, 2015; Moscovitch et al., 2016; Moser et al., 2017; Rolls, 2023c). A theory of the operation of the hippocampal memory system that included pattern separation in the dentate gyrus, an attractor network for pattern completion in the CA3 cells, and of how the memory could later be recalled to activate neocortical neurons was developed (Rolls, 1987, 1989b). This was

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developed into a quantitative theory of the hippocampal storage, and later recall of information back to the neocortex (Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994). This remains the only quantitative theory of hippocampal memory and recall back to the neocortex, with the memory capacity, the number of memories that can be stored and recalled, described analytically in terms of the key factors that influence the memory capacity.

A key aim of this paper is to describe the many advances made since then (Treves and Rolls, 1994) in understanding better the computational neuroscience of the hippocampal memory system, taking into account quantitative aspects of its neuronal network architecture as in two previous approaches (Marr, 1971; Treves and Rolls, 1994). These advances include developments that are fundamental to understanding the operation of memory systems in humans which is a key aim and contribution of the research described here. In this paper in Sections 2–7 we summarize some of the key points in the original quantitative theory (Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994), and update the theory and the evidence relevant to it to produce an up-to-date quantitative theory of hippocampal function. Then in Sections 8–12 we extend the analysis to consider wider systems-level developments in our understanding of hippocampal and neocortical function, including the types of spatial representation found in the primate including human hippocampus, and the connectivity in humans that enables different types of input to reach the hippocampus from the neocortex, and the connectivity back to the neocortex used for memory recall. (Key types of neuronal network in the hippocampal system include autoassociation (attractor) networks, pattern association networks, and competitive networks, and a description of their architecture, operation, and quantitative properties is provided by Rolls 2023c in an Open Access publication that is accompanied by Matlab (Octave-compatible) and Python demonstration programs. Brief descriptions of these networks are provided in the Supplementary Material of this paper, and the Supplementary Material also includes a Glossary of some of the terms and concepts referred to in this paper.)

An overview of the computations performed by different parts of the hippocampal system in the theory is provided next with reference to the schematic connectivity for primates including humans shown in Fig. 1. Spatial inputs from ‘where’ neocortical systems, object and person inputs from ‘what’ neocortical systems, and reward inputs from the orbitofrontal cortex reach the hippocampal system via the parahippocampal and perirhinal cortex, and medial and lateral entorhinal cortex. The dentate granule cells operate by competitive learning to implement pattern separation and sparse representations to reduce the correlations between inputs presented at different times as that is important for the CA3 stage that follows. The low number of mossy fibre contacts from the dentate granule cells to the CA3 cells enables a new random set of CA3 cells to be selected for each new episodic memory, to reduce interference between different episodic memories. The CA3 network operates as a single autoassociation or attractor network to associate together ‘what’, ‘where’ and reward inputs present at any one time by utilising the associative synaptic modifiability of the CA3 to CA3 recurrent collateral synapses. The recurrent collaterals extend throughout the CA3 cells to form a single attractor network, and this enables any ‘what’, ‘where’ and reward inputs that are simultaneously present, and all of which are components of episodic memory, to be associated together for the particular event / episodic memory. Later during recall any component of the episodic memory (for example ‘where’) can recall the other components (for example ‘what’ and reward) by the completion property of the CA3 attractor network. This recall in CA3 is triggered by the associatively modifiable perforant path inputs from the entorhinal cortex to the CA3, as there is a relatively large number of these inputs onto any one CA3 neuron (Treves and Rolls, 1992). The outputs of CA3 then reach the CA1 network, where competitive learning enables them to be compressed into an efficient retrieval cue for the recall process back to the neocortex. The retrieval cue provided by CA1 can be efficient in that the separate components in CA3 need no longer be kept separate, and

can be combined into a single efficient cue for retrieval back to the neocortex. Some episodic memories have a sequence of single events, and time cells in the hippocampus (Eichenbaum, 2014) potentially enable the sequence of events to be associated with different time cells, which may contribute to sequential memories of places, objects, and odors (Kesner and Rolls, 2015; Eichenbaum, 2017).

The theory of the recall process back to neocortex (via the back-projection connectivity shown in green in Fig. 1) is that during the learning of the episodic memory, the backprojection pathways are active and by pattern association learning become associated with the neocortical neuronal activity present during the learning. Then later, perhaps days later, when neocortical activity in one neocortical region triggers completion in the CA3 network, the memory retrieval cue generated in CA1 works by pattern association to retrieve the neocortical activity that was present during the original learning of the episodic memory. The different stages of this processing have been treated analytically as described below, and the operation of the whole system as described has been confirmed by simulations (Rolls, 1995; Rolls et al., 2024c). We now consider the theory of each part of the hippocampal memory system.

We note that, for decades, a competing account of hippocampal function, largely based on recordings of individual neurons in rodents – ‘place’ and other cells – has emphasized the spatial operations that hippocampal networks might perform in order to facilitate navigation towards a goal (see e.g. O’Keefe (1990)). The discovery of grid cells (Hafting et al., 2005; Moser et al., 2017), upstream of the hippocampus, has indicated that at least some complex spatial computations are carried out before the hippocampus is reached. It has also been proposed that place cells arise as a result of the operation of a memory system (Benna and Fusi, 2021). Nevertheless, space is an important component of episodic memory (Rolls and Wirth, 2018; Rolls, 2023c), and we will see below how the intrinsic variability with which spatial representations may be acquired as a result of self-organization in the hippocampus (Cerasti and Treves, 2013) may lead to entirely new constraints on the storage capacity of hippocampal networks (Schönsberg et al., 2023).

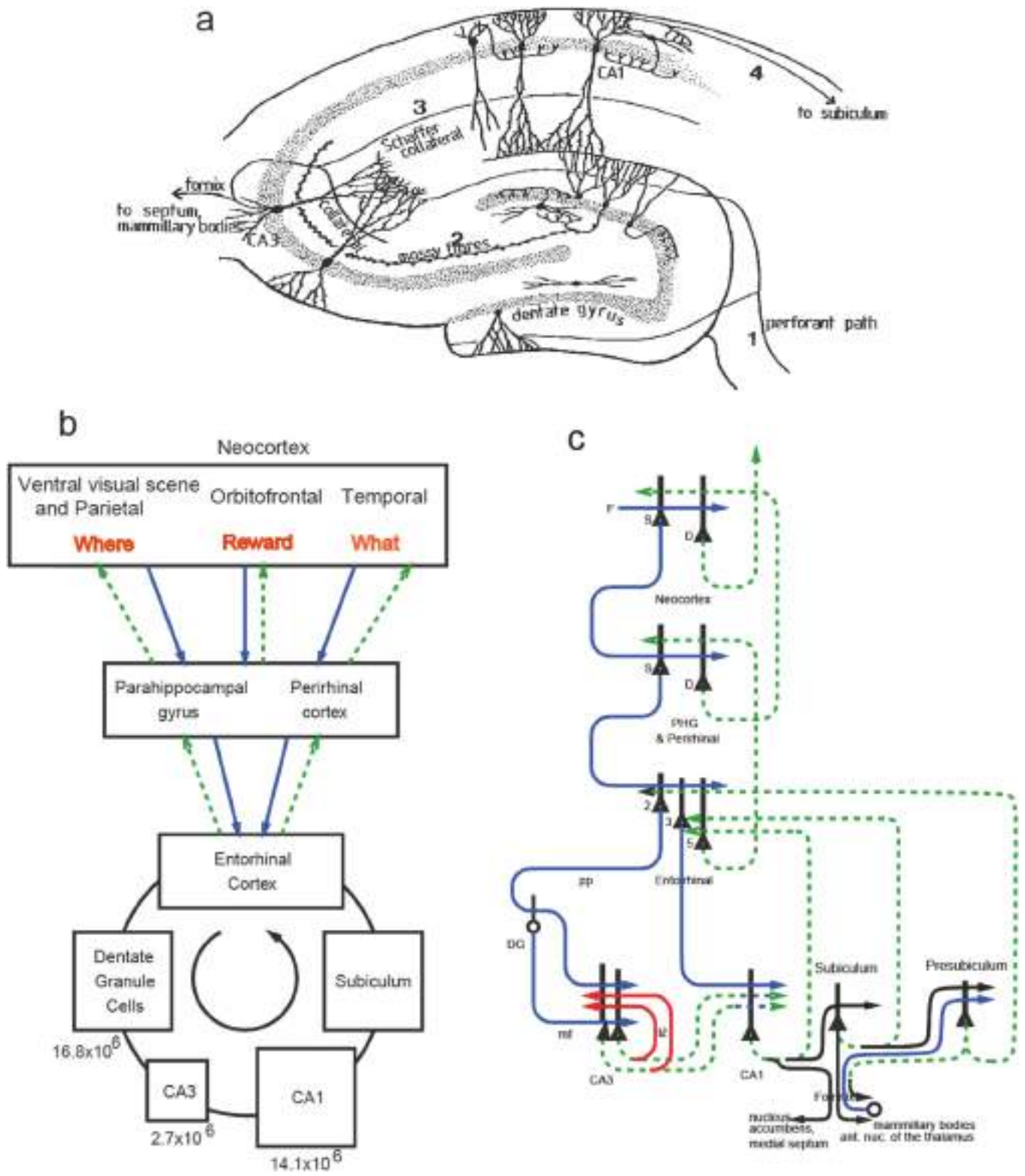
2. Dentate granule cells

There are only perforant path inputs from entorhinal cortex to the dentate granule cells, and no (excitatory) recurrent collaterals, and therefore this was proposed to operate by competitive learning and to operate as a pattern separation network to reduce redundancy in the inputs and to produce a sparse representation that helps to decorrelate the inputs to CA3 produced during the learning of different episodic memories (Rolls, 1989b).

This theory was later applied (Rolls et al., 2006; Treves et al., 2008; Si and Treves, 2009) to show how competitive learning in the dentate could convert the non-sparse medial entorhinal cortex grid cell representations (Moser et al., 2014b; Moser et al., 2015; Moser et al., 2017) (that are correlated for different places) to the place cells in the dentate, CA3 and CA1 in which places are represented much more orthogonally than in the medial entorhinal cortex.

The sparseness of the representation produced by dentate granule cells has been confirmed neurophysiologically and through gene expression in rodents (Jung and McNaughton, 1993; Chawla et al., 2005; Leutgeb et al., 2007; Leutgeb and Leutgeb, 2007), and it might be even sparser after excluding immature adult-born granule cells (Piatti et al., 2013). Further, selective lesion experiments of the rat dentate impaired the ability to remember what was present at nearby locations, with evidence also for similar odors, slopes, and visual contrasts, and consistent with the pattern separation hypothesis (Morris et al., 2012; Hunsaker and Kesner, 2013; Kesner, 2013; Morris et al., 2013; Weeden et al., 2014; Kesner et al., 2015; Kesner, 2018).

The few but large mossy fibre synapses of the dentate granule cells onto any one CA3 cell were described as detonators for CA3 cell firing (McNaughton and Morris, 1987). The theory was developed that the low



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Fig. 1. a. Representation of 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’ 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. **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, 2021b).

contact probability of dentate granule cells via mossy fibres with CA3 cells has the effect of selecting different sets of CA3 cells to be active for any one episodic memory, that is, there is a randomising effect to help each CA3 set of cells selected for any one episodic memory to be very different from the set active with a different dentate granule cell input for a different episodic memory (Treves and Rolls, 1992). (Each mossy fibre has about 12 mossy fibre synapses in rats, and each CA3 cell receives from about 48 dentate granule cells (Fig. 2).) The theory is that selecting a random set of different CA3 cells for each episodic memory makes the different episodic memories very different from each other, i. e. uncorrelated (Rolls, 1989b; Treves and Rolls, 1992, 1994). It is of course very important that each episodic memory is as uncorrelated with others as possible: think of remembering where one parked one’s bicycle today compared to all previous days; or of what happened on a particular day two weeks ago.

These roles of competitive learning in the dentate, sparse representations, and the randomising effect of the low contact probability of dentate granule cells via mossy fibres with CA3 cells has been described in more detail elsewhere (Rolls, 2013, 2016a, 2021b), including the beneficial effect of diluted connectivity in competitive networks such as the dentate granule cells, because this helps different neurons to fire differently to different inputs even before associative synaptic modification onto high firing rate neurons during the competitive learning (Rolls, 2016a, 2023c). Interestingly, even the interhemispheric projections onto the contralateral dentate gyrus, by cells other than the granule cells, are understood to reinforce the competition (Yen et al.,

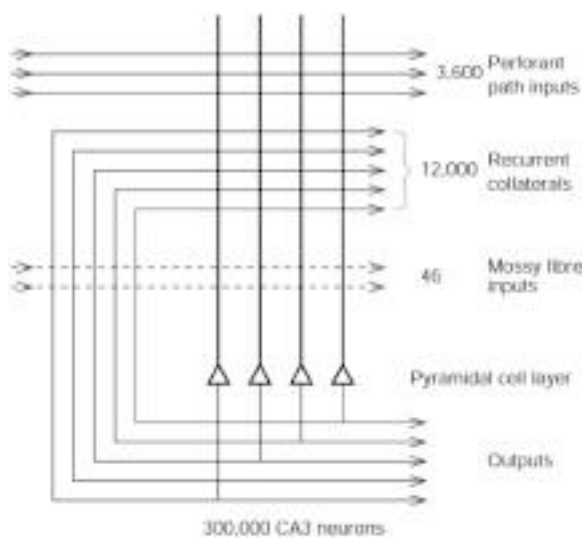


Fig. 2. The numbers of connections from three different sources onto each CA3 cell from three different sources in the rat. (After Amaral et al., 1990; Treves and Rolls, 1992; Rolls and Treves, 1998).

2022). One crucial difference with other forms of pattern separation, nevertheless, is that the one operated by the dentate gyrus is critical in ensuring that CA3 representations are orthogonalized, but appears to be largely irrelevant once they have been learned, that is, in recall (Treves and Rolls, 1992). This was shown by blocking transmission in the DG-to-CA3 synapses (Lassalle et al., 2000) or by lesioning DG altogether (Lee and Kesner, 2004), neither of which impaired the retrieval of information already acquired in CA3.

The contributions of different mechanisms to pattern separation important for high capacity information storage in the CA3 hippocampal network where uncorrelated representations are at a premium are considered in more detail by Rolls (2013, 2016a).

One should be aware, when elaborating quantitative arguments, of the large cross-species differences, even among rodents. For example, bank voles, with about the same body size as laboratory mice, are endowed in the wild with 4 times more DG granule cells, even 5 times when old (Amrein et al., 2004). Allowance should then be made, in theorizing about hippocampal operation based on the few species for which data are available, for the possibility that these species may not be so quantitatively representative of the standard mammalian phenotype (Malikovic et al., 2023). The general qualitative design of the mammalian hippocampus, however, is quite well defined and distinct, for example, from that of birds (Herold et al., 2019), who appear to lack a dentate gyrus (Reiter et al., 2017), despite similar transcriptomics (Tosches et al., 2018). All ideas put forward about the dentate gyrus (see Borzello et al. 2023), therefore, should be regarded as characterizing a mammalian development, which refines and presumably enhances the basic vertebrate structure (Broglio et al., 2015; Fiedler et al., 2021). Among mammals the development of the dentate granule cell system comes in different sizes, which indicates the need for quantitative analyses (Cerasti and Treves, 2010).

3. CA3

3.1. The theory of CA3 (Rolls, 1989b; Treves and Rolls, 1992, 1994)

At the Dahlem conference on the Neural and Molecular Basis of Learning in Berlin in 1985 Rolls proposed that the CA3 operates as an autoassociation network for episodic memory because of its highly developed recurrent collateral system, and the publication came out soon after this (Rolls, 1987). At about the same time, McNaughton and Morris (1987) also considered how the hippocampal CA3 cells might form an associative matrix memory. Before this, David Marr (1971) had performed seminal work on how recurrent collateral connections could be used in associative memories, but had not identified the hippocampal CA3 cells as being involved. Rolls’ proposal (1987) was developed into a theory of hippocampal function in which quantitative estimates of the numbers of synapses on each CA3 neuron, and the dilution of the connectivity, were introduced, together with how other parts of the

hippocampal circuitry were involved in preparing the information for storage in CA3, and in recalling the information back to the neocortex (Rolls, 1989b).

The theory (Rolls, 1989b) was then further developed into a quantitative theory of hippocampal function including of CA3 (Treves and Rolls, 1992, 1994). A key contribution to the quantitative analysis of the CA3 autoassociation or attractor network was the development of the theory of attractor networks beyond that with binary neurons (low or high firing rates), and with full symmetric synaptic connectivity (i.e. without dilution of the connectivity) ensuring an energy landscape, and with a sparseness of the representation of 0.5, in which half of the neurons chosen at random were in a high firing rate state for any one memory pattern to be stored, which is the scenario in which Hopfield (1982) was able to estimate the storage capacity of the attractor network. The storage capacity is the number of different memories that could be stored and retrieved, and was $0.14 N$, where N is the number of neurons in the autoassociation or attractor network (Hopfield, 1982). (In the analyses of the storage capacity of neuronal networks (Hopfield, 1982; Amit et al., 1985; Tsodyks and Feigelman, 1988; Amit, 1989; Rolls and Treves, 1990; Treves, 1990, 1991b, a; Treves and Rolls, 1991, 1994; Cerasti and Treves, 2013; Rolls, 2023c), memory pattern refers to the vector of firing rates of the N neurons in the network. Each such memory pattern is referred to as a different memory.) However, Rolls pointed out that in the brain the connectivity between neurons was diluted so that an energy function could not be assumed, that neuronal firing was graded between high and low rates, and that representations were sparse (see Rolls and Treves 2011). As a result, following progress in understanding sparse coding (Tsodyks and Feigelman, 1988), and facilitated by Daniel Amit (1989), a whole series of papers were produced that showed how attractor networks could operate when all of these restrictions were removed (Treves, 1990, 1991b, a; Treves and Rolls, 1991). This analytic work led to the conclusion that an attractor network, such for example as CA3, could work with diluted connectivity, graded firing rates, and with sparse representations such as those found in the brain. (This work advances the Hopfield model (Hopfield, 1982) by incorporating sparse representations, diluted connectivity, and graded firing rates, and does not rely on the binary synaptic weights considered by Marr 1971, which is often referred to as the Willshaw model (Willshaw et al., 1969; Rolls and Treves, 1998).) In this biologically plausible context, the maximum number of patterns, p_{\max} , that can be stored and correctly retrieved is approximately

$$p_{\max} \cong \frac{C^{\text{RC}}}{a \ln(1/a)} k \quad (1)$$

where C^{RC} is the number of recurrent collateral connections onto each neuron, and k is a scaling factor that depends weakly on the detailed structure of the rate distribution, on the nature of the connectivity, etc., but is roughly in the order of 0.2–0.3 (Treves and Rolls, 1991). For example, for $C^{\text{RC}} = 12,000$ associatively modifiable recurrent collateral synapses onto each neuron, and the sparseness of the representation $a = 0.02$, p_{\max} is calculated to be approximately 36,000. For $C^{\text{RC}} = 12,000$ associatively modifiable recurrent collateral synapses onto each neuron, and $a = 0.1$, p_{\max} would be lower, roughly similar to C^{RC} , i.e. 12,000. This analysis emphasizes the utility of having a sparse representation in the hippocampus, for sparse distributed representations increase the number of different memories that can be stored (Treves and Rolls, 1991), essential for an episodic memory (Rolls, 2010, 2016b). This result shown in Eq. (1) is a key part of the analysis included in the quantitative theory of hippocampal function (Treves and Rolls, 1992, 1994).

The sparseness a in Eq. (1) would be for binary neurons the proportion of the population of neurons with high firing rates, and has been generalized to the case with graded firing rate neurons, which are found in the brain (Rolls and Tovee, 1995; Franco et al., 2007; Rolls and Treves, 2011; Rolls, 2023c), to

$$a = \frac{\sum_{i=1,N} (r_i/N)^2}{\sum_{i=1,N} (r_i^2/N)} \quad (2)$$

where r_i is the firing rate (e.g. spikes/s, typically in the range 0–100 spikes/s) of the i 'th neuron in the set of N neurons. The sparseness ranges from $1/N$, when only one of the neurons responds to a particular stimulus (a local or grandmother cell representation (Rolls and Treves, 2011)), to a value of 1.0, attained when all the neurons are responding at the same rate to a given stimulus (Treves and Rolls, 1991; Franco et al., 2007; Rolls and Treves, 2011).

This analysis shows that the number of connections C onto any one neuron is the key factor in setting the maximum capacity of an attractor network with diluted connectivity, such as the CA3 network, and *not* the number of neurons, N , in the network. Given the importance of the number of connections C onto any one neuron in a network, we show from Treves and Rolls (1992) the estimates for these numbers for the rat in Fig. 2. An implication is that with $a = 0.1$, the number of memories that could be stored in the rat hippocampus is in the order of C^{RC} , 12,000. This number of synapses onto each neuron is thus key in assessing the memory capacity of the hippocampus, and evidence on this number in non-human primates and humans would be very helpful. The numbers of neurons in some parts of the human hippocampal system are shown in Fig. 1 (Rogers Flatterly et al., 2020), but the numbers of synapses from different sources onto each neuron type in the hippocampal system are needed, especially for primates including humans. Note that the number of memories is not the same as the number of spatial environments that could be stored in memory, as will be shown below.

Another key part of the theory of hippocampal function is the roles of the other two inputs to the CA3 neurons, the dentate gyrus via mossy fibre synapses, and the direct perforant path inputs, both shown with quantitative estimates for the rat in Fig. 2 (Treves and Rolls, 1992). As outlined earlier, the low probability of connections from the dentate granule cells provides a way for a new random set of CA3 neurons to be selected for each new episodic memory, to help by this pattern separation (Rolls, 2013, 2016a) to minimize the correlations between the sets of CA3 neurons used for each episodic memory. Details are provided by Treves and Rolls (1992). This number of connections per neuron (48 in the rat, Fig. 2) is too low to be useful to use the dentate granule cell / mossy fibres connections to CA3 to cue recall in CA3, even if these synapses were associatively modifiable (Treves and Rolls, 1992). Consistent with the theory, the mossy fibre synapses are unique and may not be associatively modifiable (Henze et al., 2000). In contrast, there are many more synapses from the entorhinal cortex via the perforant path onto any one CA3 neuron (Fig. 2), and these are associatively modifiable (McMahon and Barrionuevo, 2002), so it is proposed that these inputs provide the recall cue to CA3 (Treves and Rolls, 1992) which then reverberates through the recurrent collaterals, endowed with similarly associative plasticity (Martinez et al., 2002; Fellini et al., 2009) (cf. (Mehta et al., 1997; Mehta et al., 2000)). The concept is that during learning of a new episodic memory, the entorhinal cortex / perforant path synapses from active entorhinal neurons become associated with the firing of whichever CA3 neurons have been selected by the dentate / mossy fibre synapses in what is formally a pattern association network (Rolls, 1989b; Treves and Rolls, 1992). Our quantitative analysis of the number of patterns that can be stored in a pattern association network (Rolls and Treves, 1990) showed that somewhat similarly the number of patterns that can be correctly learned depends on the number of connections C onto each neuron from the to-be-associated pattern, and on the sparseness a of the output representation, in a way that is somewhat similar to what is shown in Eq. 1 for autoassociation networks (see also Rolls 2023c, which includes a description of pattern association networks).

Advances in the theory of CA3 (Rolls, 1989b; Treves and Rolls, 1992, 1994) and new evidence since then are now considered.

3.2. Articulating the model for CA3

3.2.1. The need to store correlated patterns of activity

The formal analyses described above of the storage capacity of autoassociation networks (Hopfield, 1982; Amit et al., 1985; Amit, 1989; Treves, 1990, 1991b, a; Treves and Rolls, 1991) assume random allocation of neurons to discrete memory patterns, so that the correlations between patterns are not different from what would be expected by chance. Therefore, the successful reactivation of a memory pattern would be highly correlated with the pattern itself, and equally correlated with, or ‘distant from’ all other patterns – the set of patterns has no metricity, no distinction between pairs of patterns that are close and pairs that are far away. However, some types of memory imply representations that do have correlations between the different patterns. One example is spatial representations, in which nearby locations in space (place or spatial view) have similar representations, as the metric of space must be reflected, to some extent, in relations between the neural activity patterns that represent it.

A first question that arises is whether CA3 could store episodic memories in which some of the representations were conventional random sets of neurons firing to represent for example an object (neurons 1001–1500 in Fig. 3a), and other sets of neurons that had continuous spatial representations (neurons 1–1000 in Fig. 3a). This was shown to be possible (Rolls et al., 2002). In fact, an attractor network with only continuous, for example spatial, representations is described as a continuous attractor network, and has a flat energy landscape, so is

stable in any location with a small set of neurons active for that location in what is sometimes referred to as a bubble or packet of activity (Tso-dyky, 1999; Rolls et al., 2002; Rolls, 2023c). While such continuous attractors have been shown to be relevant to the coding of simple variables, for which there is no need for learning and memory, for example in the representation of head direction, computationally correlations pose a difficulty for massive learning and memory capabilities. In fact, using a quantification of the metric content of a representation that is applicable to recordings of neural activity (Treves, 1997), it was reported that CA3 expresses representations of lower metric content than neighbouring regions (Treves et al., 1998), which is consistent with the predictions of a network model (Stella et al., 2013). At a more general level, it has been suggested that the hippocampus as a whole represents information episodically, largely stripped of its metric content (Ciar-amelli et al., 2006).

3.2.2. The storage capacity for charts

The next question that arises, then, is what the storage capacity is of an attractor network such as CA3 if it has to store a set of locations produced during navigation in which the representation of each location necessarily overlaps with those of nearby locations. Each ensemble of trajectories through a series of locations in such a space produced for example during navigation has been termed a *chart* (Samsonovich and McNaughton, 1997; Battaglia and Treves, 1998a). It was shown analytically that the number of charts that can be stored in such a network tends to be considerably smaller than the number of random patterns that can be stored in an attractor network, but nevertheless does increase linearly with the number of connections C on each neuron (Battaglia and Treves, 1998a). In a simplified model, each neuron participates in each chart with a place field of standard size, which covers roughly a fraction a of the stored environment; then each chart is equivalent, in terms of memory load, to about $10/(3a)$ discrete attractors, and the maximum number of charts can be estimated by multiplying p_{\max} by $0.3a$ (Fig. 3b). Each such chart can be produced by associative synaptic modification during navigation. This is a key advance in understanding memory storage in a system such as the hippocampus, but an entirely different capacity constraint has been identified recently, considering a model in which place fields are not of standard size and peak rate, as described below.

3.2.3. Remapping

Each time a different chart is used in such a system, for example in

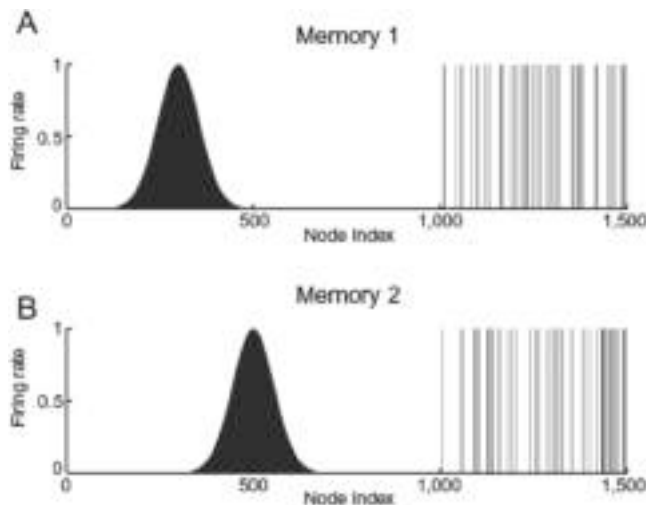


Fig. 3a. The types of firing patterns stored in continuous attractor networks are illustrated for the patterns present on neurons 1–1000 for Memory 1 (when the firing is that produced when the spatial state represented is that for location 300), and for Memory 2 (when the firing is that produced when 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 particular mixed network also contains discrete representations that consist of discrete subsets of active binary firing rate neurons in the range 1001–1500. The firing of these latter neurons can be thought of as representing the discrete events that occur at the location. Continuous attractor networks by definition contain only continuous representations, but this particular network can store mixed continuous and discrete representations, and is illustrated to show the difference of the firing patterns normally stored in separate continuous attractor and discrete attractor networks. For this particular mixed network, 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).

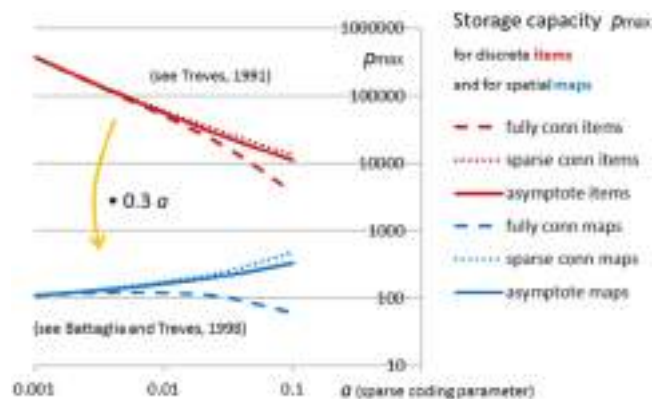


Fig. 3b. The storage capacity p_{\max} for charts, or *maps*, in blue, is contrasted with that for discrete memory attractors (*items*), in red, and plotted as a function of the sparseness a on a log-log scale. The former can be obtained from the latter by multiplying by $0.3a$. Three different connectivity models (fully connected, i.e. $C=N-1$, sparse, $C \ll N$, and a plausible estimate in between, solid curves) differ considerably only for non-sparse memories, $a \geq 0.01$. Note that the plot assumes the somewhat conservative value $C=10,000$, in a model rodent, not $C=12,000$ as in the text.

different spatial environments, the correlations between neurons are different in the different spatial environments. In experiments, when a rat is moved to a different environment, different neurons therefore typically become active, and the correlations between the firing of the neurons change, due to the different topology of the space. (Where is close to where differs between different spaces.) This is described as global remapping (Geva-Sagiv et al., 2016; Schlesiger et al., 2018) and is a quintessentially hippocampal phenomenon (Fyhn et al., 2007; Alme et al., 2014). However, if the spatial structure of the environment remains the same, but for example the visible cues in different parts of the same spatial environment are changed, the hippocampal chart does not need to change, but instead the new cues just have to be associated into the existing chart. This is referred to as local or rate remapping (Leutgeb et al., 2005b). This local or rate remapping appears to be illustrated in macaques when the same spatial environment was retained, but different room cues were substituted (Baraduc et al., 2019) (see also Gulli et al., 2020). That experiment (Baraduc et al., 2019) thus is consistent with the same spatial chart still being used, as described by Battaglia and Treves (1998a), and nicely illustrates rate remapping in primates. The experiment thus appears to show that charts are present in macaques as in rodents, and that local “rate” remapping very well known already in rodents (Wood et al., 1999; Anderson and Jeffery, 2003; Leutgeb et al., 2005a) can also occur quickly in non-human primates. Although the spatial chart was described as a ‘schema’ (Baraduc et al., 2019), we believe that the existing understanding of charts (Samsonovich and McNaughton, 1997; Battaglia and Treves, 1998a) applies, and that the term schema is better reserved for neocortical long-term knowledge-based semantic representations that remain intact after hippocampal damage (Corkin, 2002; Ghosh and Gilboa, 2014; Gilboa and Marlatte, 2017; Farzanfar et al., 2023) (see Section 11.2). Of course, hippocampal episodic memory storage and later retrieval may be useful in building such neocortical representations (McClelland et al., 1995; McClelland et al., 2020; Rolls, 2022), as considered in Section 11.2.

3.2.4. Dynamical 1D continuous attractors

A particular type of continuous attractor represents the unidimensional and unidirectional flow of time, e.g. along a trajectory in space but also in an abstract landscape, of images or thoughts of events. Unlike the *closed* strings, or rings, that encode for example head direction, these attractors can be visualized as *open* strings that link locations in a state space, and we can imagine for example that one open string represents the positions of a rodent along a 1 m linear track. A simple model, with again each neuron participating with one field of standard width randomly placed along each string, and the relative positions of any two connected units stored in the synaptic weight between them with a modified Hebb rule (Zhang, 1996), indicates that there is no cost associated to including time (Spalla et al., 2021). An analytical treatment that extends that of Battaglia and Treves (1998a) shows that a recurrent network can even store a larger number of short trajectories than of point-like attractors, at the price of some rigidity in retrieving them from memory (e.g., at relatively fixed speed). If there is firing frequency adaptation, such continuous attractors spontaneously produce forward or reverse replay, irrespective of the exact circuitry (Treves, 2004).

3.2.5. Spatial 1D continuous attractors

The models above are analytically tractable thanks to the assumption of orderly place fields, one per cell, of standard size, shape and peak rate. Self-organized representations of continuous spatial variables are intrinsically noisier however (Cerasti and Treves, 2013), and the representation of an extended environment has to accommodate multiple fields per cell (Fenton et al., 2008; Park et al., 2011). Recently, recordings from the bat CA1 have shown that the number of fields each cell presents in a 200 m long tunnel is very variable, including their width (length) and peak rate, but all these quantities follow simple statistical distributions (Eliav et al., 2021). Remarkably, it has been

shown that if similar distributions prevail in the spatial representations to be stored in CA3, with a simple Hebbian rule, another independent capacity constraint arises, which amounts to a maximum size of the environment that can be stored in memory (Schönsberg et al., 2023). Effectively, the novel constraint stems not from the interference due to the other environments that the inputs to a cell convey, but rather from the interference between the multiple fields expressed by the cell itself. Which of the two constraints would set the lower bound in a given scenario remains an open question, that awaits first of all the measurement of the relevant variability parameters. The one study that explored the capacity issue in rodents, verifying the orthogonality of the CA3 representations of boxed environments when placed in 11 similar-looking laboratory rooms (Alme et al., 2014) would have to be replicated with more and/or larger environments, presumably by at least an order of magnitude, to get to the expected limit on memory capacity. In summary, self-organisation may produce spatial fields of individual neurons of different numerosity and size, and this appears to set a limit on the number of purely spatial representations that could be stored in an attractor network (Schönsberg et al., 2023). However, further research is needed to examine the situation when continuous spatial representations are combined with discrete representations of objects in an attractor network such as CA3 for episodic memory representations (Del Prete and Treves, 2002; Rolls et al., 2002).

3.2.6. Low capacity for incidental learning

Note that nothing can “force” individuals, human or animal, to push memory performance to their network limits. In an incidental memory task, in which hippocampal activity is crucial for long term consolidation, mice could not remember more than 4–6 different objects (Torromino et al., 2022), even though the objects were more distinct than the 11 rooms discriminated by rats in the spatial situation used by Alme et al. (2014). One may conclude that although mice demonstrate intense curiosity when presented with few objects, they lose interest when exposed to a few more.

3.2.7. Flickering attractors paced by the Theta rhythm

Whatever the capacity constraint, the irregularity due to self-organization makes neural dynamics, that in a regular scenario would simply ‘slide’ towards the attracting manifold, quite bumpy and subject to jolts and stops (Schönsberg et al., 2023). This is consistent with the finding that pattern completion, with competing path integration and visual inputs impinging on CA3 and pointing towards two different attractors A and B, is a rather unpredictable process, with often “flickering” stop-and-go jumps towards A and B, only partially organized by the underlying theta modulation (Jezek et al., 2011). The theta modulation itself, about 30 % in that study if measured on pyramidal cells’ spiking activity, relative to their time average, appears insufficient to robustly switch CA3 between an input-driven and a recurrent-driven mode of operation (Stella and Treves, 2011): rather than an organizing principle, perhaps, theta might contribute to further disorganize an already bumpy pattern completion process, in rodents. This sceptical perspective is corroborated by the recent observation, in CA1, that phase precession and theta sequences may be largely independent, and even mutually avoiding, phenomena in mice (Guardamagna et al., 2023). In any case, we note that the experiment in which the spatial representation switched between A and B in different theta cycles when the test stimulus was ambiguous, provides empirical support for the theory that CA3 operates as an attractor network (Jezek et al., 2011). Further evidence that CA3 does operate as an attractor network is that CA3 but not CA1 utilizes orthogonal representations for any degree of similarity (which is important for attractor networks (Leutgeb et al., 2004)). Further, in a morphing experiment between two spatial environments, it was found that CA3 cells showed an abrupt transition between representing one or the other environment in some training conditions but not in others (Leutgeb et al., 2005a; Wills et al., 2005), as discussed later (Renno-Costa et al., 2014). These types of experiment provide support

for the theory that the CA3 recurrent collateral system operates as an attractor network (Lee et al., 2004; Neunuebel and Knierim, 2014).

3.3. Dynamics of recall: processing speed with integrate-and-fire units in a single attractor network

One way of thinking about the retrieval of the complete memory from a partial, incomplete, retrieval cue in an autoassociation or attractor network is with discrete-time update, in which one iterates several times round the recurrent collateral loop (Hopfield, 1982). Falling into the basin of attraction may take about 10 timesteps. This would be much too slow to be useful in the brain, in which neurons may often have peak firing rates between 10 and 50 spikes per s, and the synaptic and membrane time constants of neurons are in the order of 10 ms. A memory retrieval time of 100 ms for a single attractor network would be very slow, especially in series of cascaded attractor networks such as those present in the cortical hierarchy up each sensory system (Rolls, 2023c).

It was therefore an important advance when realistic dynamics of brain processing were investigated with integrate-and-fire attractor network analyses, and it was shown analytically that an integrate-and-fire attractor network can settle into its basin of attraction in ~ 2.5 time constants of the excitatory synapses: with the time constant of AMPA synapses, taking into account propagation along the dendrite, effectively around ~ 6 ms, the time taken would be of order ~ 15 ms (Treves, 1993; Battaglia and Treves, 1998b). The fast settling can be understood as follows. If some neurons are kept close to their threshold of firing, which means that there is likely to be a low spontaneous firing rate, then very soon after the retrieval cue is applied, some neurons in the population will fire earlier than usual, within for example 1 ms. That influence can then have an effect on other neurons in the population, and already the trajectory towards the basin of attraction has started. This provides a reason for why there is spontaneous firing in the cortex, for if the neurons were left at the membrane potential that is present after a spike, then any neuron would take approximately 20 ms while its membrane potential moved upwards towards the firing threshold before any information processing, including a trajectory towards an attractor basin, could start.

These analyses are supported by integrate-and-fire attractor network simulations, both for single attractor networks (Simmen et al., 1996; Treves et al., 1997), and for series of forward linked attractor networks (Panzeri et al., 2001). In the latter, in a series of 4 forward linked attractor networks with integrate-and-fire neurons modelling networks such as the forward propagation of signals up the visual hierarchy towards the hippocampal system when a signal is presented, the time for each stage even when the attractor dynamics are needed to retrieve information at each stage is ~ 15 ms, producing an overall transmission time of approximately 60 ms (Panzeri et al., 2001), which is sufficiently fast to account for the latency of inferior temporal cortex neurons in macaques of ~ 90 – 100 ms, which includes retinal delays and transmission times to V1 (Rolls, 2023c).

A further fascinating perspective was opened by the discovery (Tsodyks and Sejnowski, 1995) that the dynamics towards an attractor can stampede outside of the limits imposed by mean-field theory, as had been assumed in previous analyses (Treves, 1993). This seems to happen when the network is already within the basin of attraction, and proceeds towards its bottom with self-reinforcing, effectively explosive rapidity (Battaglia and Treves, 1998b).

Thus the dynamics of attractor networks with integrate-and-fire neurons is sufficiently fast for them to be biologically useful, not only in the hippocampus, but also in the whole series of paths to the hippocampus and throughout the neocortex (Panzeri et al., 2001) (see Fig. 1 for some of the stages).

3.4. Is idiothetic update implemented in CA3?

Given the emphasis of representations of place in the rodent hippocampus, and findings that they can be updated by self-motion when environmental cues are obscured (O'Keefe, 1979; Burgess and O'Keefe, 1996; McNaughton et al., 1996; Hartley et al., 2014; Moser et al., 2017), it has been proposed that path integration to compute self-motion (idiothetic) update of place cell firing could be implemented in the CA3 attractor network (McNaughton et al., 1996). The hypothesis is that integration using head direction cells (Ranck, 1985; Muller et al., 1996; Taube et al., 1996; Robertson et al., 1999) together with motion cells (such as hippocampal whole body motion cells in primates (O'Mara et al., 1994), or the rodent equivalent termed 'speed cells' found in the rat medial entorhinal cortex (Kropff et al., 2015) and parahippocampal cortex (Spalla et al., 2022)) would perform the place update. In this scenario, the CA3 neurons would act as a continuous attractor network (Rolls, 2023c) for place, possibly pre-wired before any associative learning (Colgin et al., 2010), and the head direction and motion signals would modulate the strength of the recurrent synapses in the appropriate direction to move the bubble or packet of neuronal activity that represents the current place (McNaughton et al., 1996; Stringer et al., 2002; Stringer et al., 2004).

One difficulty with such a scheme is conceiving CA3 as having ready, pre-wired, smooth continuous attractors for any need that may arise during the lifetime of the animal, except perhaps as a confused motley of fragments (Farooq and Dragoi, 2019). However, contra this, mechanisms have been proposed for how continuous spatial representations could be learned in an attractor network with stimuli from the environment (Stringer et al., 2002; Stringer et al., 2004; Rolls and Stringer, 2005; Stringer et al., 2005).

Second, recordings from CA1 place cells in bats flying in a long non-descript tunnel show considerable variability (Eliav et al., 2021), which indicates already a 'bumpy' quasi-attractor in CA3 (Schönsberg et al., 2023). If the CA3 network in richer, more ecological, environments strongly associates objects with places for episodic memory (Rolls et al., 2002), then the continuous attractor representing even simple 1D trajectories would become so much bumpier (or riddled with disorderly valleys in the energy landscape) that accurate path integration would probably fail (Schönsberg et al., 2023).

Third, there is evidence that in rodents the medial entorhinal cortex mediates self-motion update of place using continuous attractor mechanisms involving grid cells (Fyhn et al., 2004; McNaughton et al., 2006; Giacomo et al., 2011; Moser et al., 2014a; Moser et al., 2014b; Moser et al., 2017) (see Section 10.5), so this computation may be performed before the hippocampus is reached.

In primates, in which spatial view cells are present, the idiothetic update must involve computations about viewed space, and about eye position in the head. This computation appears to take place not in the hippocampus but in the dorsal visual system, with the transform from retinal to head based coordinates being performed in parietal neocortical regions such as LIP (see Rolls, 2020). A mechanism involved appears to be gain modulation, for example of retinal position by eye position to produce a visual representation of space in head-based coordinates (Salinas and Abbott, 1996; Salinas and Sejnowski, 2001). This gain modulation system operates much better if it is complemented by slow learning with a short-term memory trace (Rolls, 2020). A theory involving gain modulation with slow learning shows how further coordinate transforms to produce world-based representations of visual space in the parietal cortex area 7 (Snyder et al., 1998) and posterior cingulate cortex (Dean and Platt, 2006) could take place in the parietal cortex, which then transfers this idiothetically updated information to the parahippocampal gyrus for navigation and memory in the dark or when the view details have been obscured (Rolls, 2020; Rolls et al., 2022b; Rolls, 2023b; Rolls et al., 2023a).

This evidence shows that idiothetic update appears to be performed in rodents for place using blind path integration of place representations

using head direction, speed, and distance travelled, and that provides a rodent model for navigation (McNaughton et al., 1996; Edvardson et al., 2020). In contrast, human navigation is not blind, but can use spatial view cells and views of the spatial scene to recognise landmarks and navigate using vision, using path integration across spatial views when in the dark or when the view is obscured, providing a different, vision-based, approach to navigation in primates including humans (Rolls, 2020; Rolls et al., 2022b; Rolls, 2023b; Rolls et al., 2023a).

3.5. One hippocampus in rodents, two hippocampi in primates including humans

A feature of the CA3 to CA3 cell recurrent collateral connections is that they spread throughout the anterior-posterior and dorsal-ventral extent of the hippocampus in the rat. This is even more the case in macaques, in which the CA3 to CA3 connectivity is even more extensive (Kondo et al., 2009). The computational significance of this is that associations for episodic memory can be made between *any* representations (including what, where, reward, time), which is a requirement of an episodic memory system in which all the events that are part of an episodic memory must be associated together. This is a key feature in the theory of the hippocampus (Rolls, 1989b; Treves and Rolls, 1992, 1994; Kesner and Rolls, 2015; Rolls, 2018, 2023c), that the CA3 autoassociation or attractor network is a single network allowing associations between any of the inputs that it receives. This is a unique contribution of hippocampal computation, for the neocortex is organised into different regions specialised for different functions, and does not have a single region where any representation could be associated with any other representation (Rolls, 2023c).

This widespread CA3-CA3 connectivity thus provides an anatomical basis for associations between any events to be formed. That is not inconsistent with the evidence that the neurons in the input and output regions of the hippocampus, and even perhaps within CA3, are specialised, with the dorsal (rodent) / posterior (primates including humans) more implicated in finer spatial processing, and the ventral (rodents) / anterior (primates including humans) more involved in gross spatial processing (Kjelstrup et al., 2008) and in reward and emotion-related functions (Strange et al., 2014; Zeidman and Maguire, 2016; Bubb et al., 2017; Brunec et al., 2018; Lee et al., 2023).

It is interesting that the CA3-CA3 connectivity in rodents extends across the midline, so that computationally rodents have a single hippocampus. However, in primates including humans there is much less hippocampal system connectivity across the midline, and so there are two separate hippocampi (Amaral et al., 1984). Consistent with this relative separation of the hippocampal CA3 in the two hemispheres, there is specialization of function of the right vs left hippocampus in humans, with the right hippocampus more involved in spatial memories, and the left more in language-related memories (Burgess et al., 2002; Crane and Milner, 2005; Barkas et al., 2010; Bonelli et al., 2010; Sidhu et al., 2013).

3.6. The roles of diluted connectivity between CA3-CA3 neurons for the attractor theory

The connectivity between CA3-CA3 neurons is diluted: in the rat $C = 12,000$ synapses per CA3 neuron, and there are 300,000 CA3 neurons (Fig. 2), so the dilution is 0.04, or if we take into account the inter-hemispheric connection in rodents 0.02. We have seen above that the attractor properties of networks with this amount of dilution are maintained (Treves, 1991a; Treves and Rolls, 1991).

However, it has been shown that the dilution of connectivity in cortical attractor networks (hippocampal and neocortical) can be advantageous (Rolls, 2012b). If we assume that connections between pairs of neurons are made randomly (and there are insufficient genes to specify the details of which neuron connects to which, given that there are in the order of 25,000 genes and 10^{15} neurons in the cortex (Rolls

and Stringer, 2000)), then if we had as many neurons N in a cortical attractor network as there are connections per neuron C , by chance some pairs of neurons would have more than one connection between them. This has been shown to seriously distort the energy landscape, and thereby reduce the number of memories that can be stored in the network (Rolls, 2012b). So dilution in cortical attractor networks is useful in terms of the memory capacity.

But having N larger than C can have another beneficial effect. The large N has the effect of smoothing out the stochastic noise in the population of neurons caused by the almost random (Poisson) firing times for a given mean rate of cortical neurons, and that can help to realise the maximum capacity of attractor networks (Rolls and Webb, 2012).

3.7. Forgetting

As noted above, attractor networks have a limited storage capacity (Hopfield, 1982; Amit et al., 1985; Amit, 1989), which can be increased if sparse representations are used (Treves, 1991a; Treves and Rolls, 1991). If that capacity limit is reached, then catastrophic forgetting occurs, and most of the memories may become unretrievable. In these circumstances, forgetting in attractor networks has a useful function, to avoid the critical capacity being reached.

One way that forgetting occurs is that with the sparse distributed representations found in the brain (Rolls and Treves, 2011; Rolls, 2023c), any new memory pattern with a random set of neurons will by chance have some neurons in common with the already stored random memory patterns, and overwriting of old memories will gradually occur, in what has been described as a palimpsest (Nadal et al., 1986). The crucial synaptic type of learning for this is heterosynaptic long-term depression, which refers to the weakening of inactive synapses onto active neurons (Rolls, 2023c). This emphasises the importance of further research on heterosynaptic long-term depression, for it is also key to the operation of pattern association (Rolls and Treves, 1990) and competitive networks (Rolls and Treves, 1998; Rolls, 2016b, 2023c). The importance of forgetting in the CA3 attractor network (due to the capacity limits of attractor networks referred to above and analysed quantitatively (Hopfield, 1982; Amit et al., 1985; Amit, 1989; Treves, 1991a; Treves and Rolls, 1991; Rolls, 2023c) and specified in Eq. 1) emphasises the importance of recalling information from the hippocampus and storing it in the neocortex, where the memory capacity is much larger (see Section 11).

Another form of forgetting is just an exponential-like decay of synaptic strength (Nadal et al., 1986), and it is possible that reconsolidation, the process by which a memory may be restored after it is recalled (Debiec et al., 2002; Lee et al., 2017; Haubrich and Nader, 2018), may help where decay of synaptic weights may be a problem (Rolls, 2023c).

3.8. Sequential recall of the components of episodic memory: time cells

Episodic memories may involve several events that occurred in a particular order. One way in which sequential memories could be stored in an attractor network such as CA3 is by using temporally asymmetric synaptic weights, such as might be implemented by spike-timing dependent plasticity (Markram et al., 2012; Fremaux and Gerstner, 2015). The simplest, early model of this mechanism (Sompolinsky and Kanter, 1986) was based on discrete attractors, which would imply a saltatory or stuttering retrieval process at the time scale of tens of ms; a refined model is based on continuous attractors (Zhang, 1996), which have been shown to come 'for free' in terms of storage capacity (Spalla et al., 2021). Both versions foresee a straightforward flow along a given stored sequence, but remain underdefined as to what may happen at choice points, if e.g. two episodic memories share a portion of their path but then diverge to different endings.

A somewhat different mechanism for remembering the order of items involves time cells, which fire for a short time at different times during periods of 10 s or more (MacDonald et al., 2011; Eichenbaum, 2014;

Howard et al., 2014; Howard and Eichenbaum, 2015; Kesner and Rolls, 2015; Salz et al., 2016; Eichenbaum, 2017; Rolls and Mills, 2019). Time cells are found in CA3 as well as in CA1 (Salz et al., 2016). Objects or places or odours could be associated with the time cells that happen to be active at a particular time in a CA3 associative memory, and that is one way in which the temporal order of items in an episodic memory might be stored and later recalled in the correct sequence (Rolls and Mills, 2019). The proposed mechanism is the use of the slowly ramping (decaying over 100 s or more) firing rates of some lateral entorhinal cortex neurons (Tsao et al., 2018), which can be used in competitive networks in the hippocampal system to produce time cells (Rolls and Mills, 2019). This mechanism can produce forward and also reverse replay (Rolls and Mills, 2019) (see Section 6). Hippocampal, especially CA3, lesions do impair object, place, and odour sequential memory (Kesner and Rolls, 2015).

Note that while a *bona fide* time cell would be active at the same time relative to a “starting point” across all situations, in a specific context a cell active at some point of a short continuous attractor is functionally indistinguishable from a (non-ramping, but place-like) time cell; so in practice the two mechanisms are not completely separable.

4. CA2

According to the widely used Lorente de N6 terminology, between CA3 and CA1 there are CA2 neurons, a relatively small set (perhaps 5 % of the number of CA3 neurons (Tirko et al., 2018; Shinohara and Kohara, 2023)), often not included in theories of the hippocampus (Rolls, 1989b; Treves and Rolls, 1994). We now provide a brief update and consider their potential computational roles.

The CA2 neurons appear to have some CA2-CA2 recurrent collaterals, but not highly developed ones that merge with those of the CA3 autoassociation system. The CA2 neurons project to CA1 stratum oriens inhibitory neurons, and mediate feedforward disinhibition on CA1 (presumably via another inhibitory synapse) (Tirko et al., 2018). This facilitates long-term potentiation of CA3 inputs onto CA1 neurons. This functionality of CA2 may be to enable oxytocin or acetylcholine to facilitate CA3 to CA1 connectivity, with the actual computation just being the usual one for CA3 to CA1 (described in Section 5) (Tirko et al., 2018). Indeed, given that CA2 seems to influence CA1 via two serial inhibitory interneurons, it is most unlikely to convey specific high dimensional information. So it may just be a simple facilitator of the standard operation of the massive number of excitatory CA3 synapses onto CA1 neurons. Oxytocin activates the CA2 neurons, and acetylcholine is one of the other key CA2 modulators (Tirko et al., 2018; Liu et al., 2022).

What does this CA2 to CA1 circuitry implement? The CA2 region is implicated in social memory (Dudek et al., 2016; Lin et al., 2018; Tirko et al., 2018; Oliva, 2022), with a direct path from the lateral entorhinal cortex to CA2 tuned to convey information that is important in social memory (Lopez-Rojas et al., 2022). Overall, the CA2 cells are thus directly excited by lateral entorhinal cortex inputs, are also excited by oxytocin, act to facilitate CA3 to CA1 transmission, and play a role in social memory and thereby behavior.

5. CA1

The major input numerically to CA1 is provided by the CA3 neurons, and this is a strong input, stronger than the numerically smaller direct perforant path input from the entorhinal cortex to CA1, which has been described as having a modulatory role (Remondes and Schuman, 2002; Zhao et al., 2020). There are approximately 10,000 CA3 inputs to each CA1 neuron in rodents, and there are more CA1 neurons (approximately 420,000) than CA3 neurons (300,000) (Schultz and Rolls, 1999). This expansion recoding is even greater in humans (2.7×10^6 neurons in CA3, and 14.1×10^6 neurons in CA1 (Fig. 1)) (Rogers Flattery et al., 2020). CA1 neurons do not have recurrent collaterals.

The theory (Rolls, 1989b; Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994) given this architecture is that CA1 acts as a competitive network with associative modification of CA3 to CA1 synapses (Rolls, 2023c), to recode the CA3 representation in which the parts of an episodic memory are necessarily separate and can be associated together in the CA3 autoassociation network, into a more categorised, compact, representation in which the parts need no longer be separate, and which can act as a better cue for the recall process to recall memories back to the neocortex. Consistent with this role, there is expansion recoding provided by the increase in neuron numbers from CA3 to CA1, which is greater in humans with much more neocortex than in rodents. The expansion recoding is a way to decorrelate the different sets of neurons firing for each different memory to be recalled to the neocortex, and this expansion recoding that can be achieved in competitive networks benefits from sparse representations which contribute to the decorrelation of the representations of different memories (Rolls, 2023c).

There is also a numerically smaller direct input to CA1 from the entorhinal cortex (Fig. 1), and its computational function is less clear. One proposal was that the direct entorhinal cortex input to CA1 might act as a teacher or forcing input, with which the CA3 output might be associated (McClelland et al., 1995; McClelland et al., 2020) in what would be a pattern association network (Rolls, 2023c). That would seem unlikely given the observed weakness of the direct entorhinal input to CA1, however what matters is that this input should produce sufficient contrast among CA1 cells during learning. If the CA3 input appears to drive CA1 in a familiar context (Zhao et al., 2020) this may simply indicate that the association with CA3 activity has been successfully established. We have shown how to quantify the amount of information retrieved in CA1 in this scenario (Treves, 1995; Schultz and Treves, 1998); and also suggested that the direct entorhinal cortex input to CA1 may enable some of the original information present in the entorhinal cortex to be combined with the CA3 output to produce a richer recall cue to the neocortex (Rolls, 1989b; Treves and Rolls, 1994).

The new anatomical perspective on CA1 is actually some 300 million years old: it is the realization, from comparative neuroanatomy (Striedter, 2016), that it is more the scarcity of CA1 collaterals, rather than their abundance in CA3, which may represent the mammalian innovation, along with the insertion of the dentate gyrus. The beginnings of a differentiation between CA1 and CA3 has been seen in some non-mammalian species (partly reviewed in Fiedler et al. 2021), but the question of which homologies can be defined between components of the hippocampal formation remains controversial (e.g., do CA3 and CA1 correspond to different parts of the small-celled division of the lizard medial cortex, or would that be just CA3? (Striedter, 2016)), ultimately pointing at the inadequacy of a binary homologous/non-homologous dichotomy.

6. The entorhinal cortex

6.1. Rodents

The discovery by the Moser lab of grid cells in the rodent entorhinal cortex (Fyhn et al., 2004; Hafting et al., 2005; Fyhn et al., 2007), unforeseen in earlier studies, has led to a remarkable series of other empirical findings, of computational studies and of theories, which fall outside the scope of this review. Grid cells represent places by hexagonal place grids and are involved in idiothetic update of place, as described by a number of possible computational mechanisms (Kropff and Treves, 2008; Giocomo et al., 2011; Moser et al., 2015; Gerlei et al., 2021). The main effect this has had on understanding the hippocampus, however, is that it has largely resolved the tension between the memory account, originally based on the observation of memory deficits in hippocampally lesioned patients, which had led to the model by David Marr (1971), and the spatial computer account, based on recordings of place cells in rodents moving around in a box, which had led to the idea that the

hippocampus could implement some sort of vector algebra (O'Keefe, 1990). The beautiful, geometrically precise spatial selectivity observed in grid cells indicates that spatial operations on the relevant inputs, whichever operations and inputs they may be, are carried out upstream, before reaching the hippocampus. On the other hand, the temporal coincidence between rigid dislocations of the grid pattern and global remapping in hippocampal place cells (Fyhn et al., 2007) indicates a tight coupling between the two populations. There is interest in how grid cells might be instrumental in the generation of the place fields of place cells (Solstad et al., 2006), and one proposal is that competitive learning can perform the transformation (Rolls et al., 2006; Si and Treves, 2009). There is now interest in how the tight coupling between entorhinal grid cells and hippocampal place cells may arise from the mutual interactions between systems with similarities and equally clear differences (Stella et al., 2012; Kanter et al., 2017; Agmon and Burak, 2020). It remains largely unknown how such interactions may be expressed outside of the simple spatial tasks typically used to study grid cells and their phenomenology.

A major computational implication of the discovery of grid cells, irrespective of the mechanisms that lead to the grid cells, is that some of the spatial operations that had been earlier ascribed to the hippocampus (O'Keefe, 1990) are probably carried out upstream. One should not forget that many other types of cell selectivity have been observed in medial (Spalla et al., 2022) and lateral (Huang et al., 2023) entorhinal cortex, and that extensive collateral connections even across the midline (Caputi et al., 2022) may also allow for some object-place associations to be implemented upstream of the hippocampus, at least in rodents. Such conjunctive representations may be useful in a number of brain regions outside the hippocampus, including the prefrontal cortex (Rigotti et al., 2013).

6.2. Primates including humans

In macaques, a grid-cell like representation in the entorhinal cortex has been found, but the neurons have grid-like firing as the monkey moves the eyes across a spatial scene (Killian et al., 2012; Rueckemann and Buffalo, 2017; Meister and Buffalo, 2018; Garcia and Buffalo, 2020). Similar competitive learning processes to those suggested for rodents (Rolls et al., 2006) may transform these primate entorhinal cortex 'spatial view grid cells' into primate hippocampal spatial view cells (Rolls, 2021c), and may contribute to the idiothetic (eye movement-related) update of spatial view cells (Robertson et al., 1998). The existence of spatial view grid cells in the entorhinal cortex of primates is predicted from the presence of spatial view cells in the primate CA3 and CA1 regions (Rolls, 2013; Kesner and Rolls, 2015; Rueckemann and Buffalo, 2017). Moreover, some of these 'spatial view grid cells' have their responses aligned to the visual image in that they reflect which visual image is being viewed (Meister and Buffalo, 2018), as predicted (Kesner and Rolls, 2015).

In the human entorhinal and cingulate cortex neurons with grid-like response properties have been reported (Jacobs et al., 2013; Nadasdy et al., 2017), and there is neuroimaging evidence that is potentially consistent with this (Julian et al., 2018; Nau et al., 2018). This is further evidence for the concept that representations of locations being viewed in space "out there" is a key property of spatial representations in the hippocampal system of primates including humans. One should note that even in rodents, in which the grid cell phenomenon is striking and well-defined, no quantitative measure of gridness with a clear bimodal distribution has been reported, suggesting that, instead of a sharply defined separate category of grid cells, one should refer to neurons with a spatial selectivity that shows variable degrees of propensity towards a rigid hexagonal firing pattern. It may well be that in primates neurons with such a clear propensity are significantly fewer (Spalla et al., 2022). Interestingly, a recent study indicates that the hexagonal modulation seen in some fMRI studies may be due to a clustering of head direction selectivity, independent of the presence of grid cells *per se* (Bin Khalid

et al., 2022).

7. Recall of memories from the hippocampus back to the neocortex

7.1. The mechanism of recall from the hippocampus back to the neocortex

After episodic memories have been stored in the hippocampus, they must be recalled at some time to be useful. Moreover, as we have shown above, the hippocampal CA3 system has a limited memory capacity, and it is essential that hippocampal memories are recalled to the neocortex for possible consolidation there before they are lost by overwriting / forgetting in the hippocampus (see Section 3.7). David Marr (1971) promised a theory of recall from the hippocampus, but never produced one. Rolls (1989b) produced a theory of recall from the hippocampus as follows, using the backprojection connections from the hippocampus to the neocortex shown in green in Fig. 1. The theory is that during storage in the hippocampus, the backprojection connections to the neocortex shown in green in Fig. 1 from CA1 become active, and that pattern association learning (Rolls, 2023c) occurs between the active backprojection synapses and the active neocortical neurons. Then later, when a partial recall cue originating in a particular neocortical (e.g. place or view) region reached the CA3 neurons via the direct entorhinal cortex inputs to CA3, then CA3 performs pattern completion, the full representation in CA3 then activates the correct set of CA1 neurons through those synapses modified during learning, and then CA1 activates the correct neocortical neurons at each stage in the backprojection synapses (Rolls, 1989b).

The theory was made quantitative (Rolls and Treves, 1994; Treves and Rolls, 1994) by mapping the pattern association along each of the several backprojection stages back towards the neocortex (green in Fig. 1) onto several iterations round the recurrent collateral loop of an autoassociation network (such as CA3 in Fig. 1). That analysis showed that the maximum number of memory patterns p_{\max} that can be recalled back to neocortex is approximately

$$p_{\max} = \frac{C}{a \ln\left(\frac{1}{a}\right)} k \quad (3)$$

where C is the average number of backprojection synapses onto any one pyramidal cell from the preceding stage, and k is a factor that depends weakly on the detailed structure of the rate distribution, on the connectivity pattern, etc., but is roughly in the order of 0.2–0.3 (Treves and Rolls, 1991). The sparseness a in this equation is the population sparseness in the backprojection pathways (Treves and Rolls, 1991; Franco et al., 2007). A more recent development is that with threshold-linear neurons and sparse coding, an associative learning rule is as good a rule as any other for learning the synaptic weights, and this applies to attractor networks, as well as to pattern association networks invoked here as a mechanism of recall from the hippocampus to the neocortex (Schönsberg et al., 2021). That is, the Gardner approach which was applied to binary neurons (Gardner, 1988) has been shown to apply to threshold-linear units.

This is the only quantitative theory of backprojections from the hippocampus, or indeed between neocortical regions, that we know. It is also the only account of why in the neocortex there is such a large number of backprojection synapses onto a neocortical pyramidal cell, approximately the same number as forward connections. It is advantageous that the backprojection synapses are mainly on the apical dendrites of cortical pyramidal cells in layer 1, for the input there is weak though sufficiently strong to implement recall provided that there is no strong forward bottom-up input that would shunt the backprojected recall input; so that during strong bottom-up inputs, the backprojected memory recall would not dominate the firing. This scenario for a neocortical module is shown in Fig. 4 (Rolls, 2021f). It is shown that a

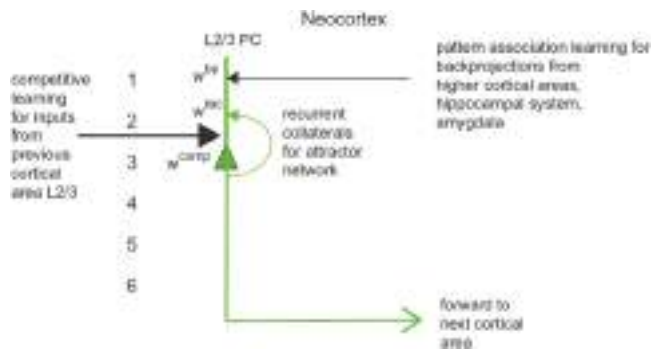


Fig. 4. The neocortical model that combines competitive learning using the forward inputs from the preceding cortical region, with associatively modifiable recurrent collateral synapses to form an autoassociation attractor network to maintain neuronal firing for short periods, and with pattern association learning to implement recall or top-down attention using cortico-cortical backprojections originating from for example the hippocampus. L2/3 PC is a layer 2/3 pyramidal cell. The thick line above the pyramidal cell body is the dendrite, receiving inputs from the previous cortical area that operates by competitive learning using the synapses w^{comp} , from the recurrent collaterals that operate as an attractor network using synapses w^{rec} , and back-projections from higher cortical areas for memory recall and top-down attention that operate by pattern association learning using the synapses w^{bp} . 1–6: the layers of the neocortex. (From Rolls 2021. The connections of neocortical pyramidal cells can implement the learning of new categories, attractor memory, and top-down recall and attention. *Brain Structure and Function* 226: 2523–2536.)

population of pyramidal cells can implement new learning based on forward inputs when they are present using competitive learning, and at the same time can train the recurrent collaterals to implement an attractor network for later short-term memory, and can simultaneously train the backprojections as a pattern associator to implement later top-down recall (from e.g. the hippocampus) and top-down attention. Later, when a forward input is not present, recall can be initiated by the backprojections, and the activity can be maintained in short-term memory by the autoassociation recurrent collaterals (Rolls, 2021f) (Fig. 4).

It is emphasised that this theory of the recall of information from the hippocampus back to the neocortex uses purely local associative synaptic modification rules that are biologically plausible, and has nothing to do with error backpropagation learning in deep networks (LeCun et al., 2015) which is not known to be biologically plausible (Rolls, 2023c).

A further development has been on understanding the diluted connectivity in the back-projection pathways from the hippocampus to the neocortex. The backprojection pathways have diluted connectivity in that each neocortical neuron may receive up to in the order of 10,000 backprojection synapses, yet the total number of neurons at each neocortical stage in the backprojection hierarchy shown in Fig. 1 has very many more neurons than this, at least 10 times as many neurons as there are synapses per neuron. This diluted connectivity in the back-projection pathways is advantageous, for it is likely to reduce the probability of more than one connection onto a receiving neuron in the backprojecting pathways. It has been shown that if there were more than one connection onto each neuron in a pattern associator, this would reduce the capacity of the system, which in this case is the number of memories that can be recalled from the hippocampus to the neocortex (Rolls, 2015).

For the theory of recall (Rolls, 1989b; Treves and Rolls, 1994; Rolls, 2023c), the backprojection pathways for at least one stage from CA1 going back to neocortex must be associatively modifiable. A similar approach to hippocampo-neocortical recall has been adopted by others (McClelland et al., 1995; McClelland et al., 2020), but they proposed that the key stage was from CA3 to CA1 with the direct entorhinal input to CA1 being a teacher, but that is inconsistent with the evidence that

the CA3 to CA1 inputs drive the CA1 cells much more strongly than do the direct entorhinal cortex inputs (Zhao et al., 2020).

This theory of hippocampus to neocortex recall (Rolls, 1989b, 2023c) shows how during the learning of the episodic memory, the backprojections are trained to ‘point to’ the correct cortical neurons that are active by pattern association learning. The implication is that the full representation of faces, objects, places, rewards etc is in different neocortical regions as described more fully elsewhere (Rolls, 2023c), and that the full information is not actually in the hippocampus. The hippocampus is in this conceptual framework like an indexing system, that can learn what neocortical neurons in completely different neocortical regions are simultaneously active during the formation of an episodic memory, and can later recall those neocortical neurons back into activity later using a sparse code (Schönsberg et al., 2021). Teyler and DiScenna (1986) had the general idea of the hippocampus as a pointer, but did not describe how the hippocampus could be a pointer, and had no theory of the operation of the system.

What is the memory capacity of the whole neocortex-hippocampus-neocortex architecture illustrated in Fig. 1? This was analysed using a simulation of the whole neocortex-hippocampus-neocortex system scaled as shown in Fig. 5 (Rolls et al., 2024c). It is known with sparse representations that the capacity of the CA3 autoassociation network should be approximately C^{CA3} where C^{CA3} is the number of recurrent collateral connections onto any one neuron (Eq. 1), that the capacity of the multistage backprojection system from CA1 via the entorhinal cortex to the neocortex should be approximately C^{BP} where C^{BP} is the number of backprojection connections onto any one neuron (Eq. 3), and that the capacity of the entorhinal to CA3 neurons used to trigger recall by pattern association is approximately C^{EtoCA3} where C^{EtoCA3} is the number of associatively modifiable synapses onto each CA3 neuron from the entorhinal cortex, given the capacity of pattern association networks (Rolls and Treves, 1990; Rolls, 2015). Provided that C^{EtoCA3} was set to the same value as C^{CA3} and C^{BP} , the whole neocortex-hippocampus-neocortex system could be trained up to capacity C , corresponding for example to $p=12,000$ memories if C^{CA3} etc is 12,000. (Of course, as shown in Eqs. 1 and 3, the sparseness of the CA3 and backprojection connectivities are important, and remain to be fully established empirically in the brain (Rolls and Treves, 2011), but for these simulations, the values shown in Fig. 5 were used.) This is useful new evidence that the whole neocortex-hippocampus-neocortex system can be trained up to capacity (Rolls et al., 2024c). However, given that C^{EtoCA3} is lower than the other C values, in practice C^{EtoCA3} may limit the capacity of the whole neocortex-hippocampus-neocortex system somewhat (Rolls et al., 2024c). These analyses underline the importance of measuring the number of synapses C onto any one neuron in memory systems such as the neocortex-hippocampus-neocortex system, and further evidence about C^{EtoCA3} in primates including humans would be of great interest. A key point is that the capacity of most associative neural systems in the cortex in which diluted connectivity is present is determined by the number of connections C on any one neuron, not by the number N of neurons in the network (Rolls and Treves, 1990; Treves, 1991a; Treves and Rolls, 1991; Rolls, 2012b, 2015, 2016a, 2023c).

In the context of the recall of information from the hippocampus to the neocortex, it has been suggested that hippocampal replay may be important. Some hippocampal neurons display replay in which the neurons represent a sequence of places etc, and this can be in a forward or reverse direction, happens very rapidly, and has been proposed might be involved in hippocampo-neocortical recall (Wilson and McNaughton, 1994; Foster and Wilson, 2006; Chen and Wilson, 2017; Foster, 2017; Berners-Lee et al., 2022). No account was provided of how the appropriate neocortical regions would be activated by this replay, nor of what reverse replay might be useful for. It has been shown in the model of hippocampal time cells that performs competitive learning on inputs from lateral entorhinal cortex temporal ramping cells, that replay and reverse replay can arise as a side effect of what is being computed, namely cells that fire at a particular time in a sequence (Rolls and Mills,

What and Where neocortical modules shown in Fig. 5, and then measuring the time after a retrieval cue was applied to the neocortex. What module for recall to be produced in the neocortex Where module. It is important that the whole process should be relatively fast, taking for example not much longer than 100 ms, because the theory of recall from the hippocampus to the neocortex requires that during learning, the backprojection inputs to the neocortex from the hippocampus are present while the neocortical neurons are still being activated by their incoming forward inputs, to allow pattern association learning between the activity in the backprojection paths and the currently firing neocortical neurons (Rolls, 1989b; Treves and Rolls, 1994). By training the synaptic weights in the architecture shown in Fig. 5 in a rate-coded simulation, and then importing those synaptic weights into an integrate-and-fire simulation, it was found that the time for recall from the neocortex via the hippocampus and back to the neocortex was indeed in the order of 100 ms (Rolls et al., 2024c). This research (Rolls et al., 2024c) highlighted some key factors involved in the dynamics and operation of neocortex-hippocampus-neocortex circuitry.

First, it was found that some associative recall of Where from What could occur even if the CA3-CA3 autoassociation synapses were disabled. The associative process that implemented this was that from CA3 to CA1, which is known to enable different inputs to CA1 to be associated together by competitive learning, which is associative (Schultz and Treves, 1998; Schultz and Rolls, 1999). Thus provided that the What and Where inputs from the neocortex via the entorhinal cortex and dentate granule cells activate different CA3 neurons, as the theory holds, then some associations can be learned in the CA3 to CA1 pathway even without the CA3-CA3 connectivity operating as an autoassociation network (Rolls et al., 2024c). However, if the CA3-CA3 connectivity was allowed to operate as an autoassociation network, then the performance and memory capacity of the circuitry shown in Fig. 5 was much better, and up to the theoretical capacity (Rolls et al., 2024c).

Second, it was clear that the neocortex-hippocampus-neocortex circuitry has other places than CA3 that can operate as attractor networks (Rolls et al., 2024c). One such attractor network is formed by the entorhinal cortex to CA3 to CA1 to entorhinal long loop, which with its associatively modifiable excitatory synapses forms an attractor network that can maintain neuronal activity. Second, attractor networks are formed by the loop back from entorhinal cortex to neocortex formed by the associatively modified backprojections. Those loops can also maintain firing in an attractor state. In addition, the whole long loop from neocortex to entorhinal cortex to CA3 to CA1 to entorhinal cortex and back to neocortex can because of the associatively modified excitatory synapses in it provide for continuing neuronal activity to be maintained in an attractor state. These findings emphasise that the computational importance of the CA3-to-CA3 autoassociation network is not in maintaining neuronal firing, but instead in enabling associations to be formed between activity from different parts of the neocortex such as What, Where and Reward (Fig. 1), which can be implemented in the hippocampus because these separate neocortical types of representation (What in inferior temporal visual cortex, Where in the parahippocampal scene area, and reward in the orbitofrontal cortex) can be brought together for associations between them to be learned in the single network that is CA3. That is what this computational theory holds is a key aspect of the operation of the neocortex-hippocampus-neocortex system.

Third, the multiple sets of associatively modifiable excitatory connections in the neocortex-hippocampus-neocortex circuitry (Figs. 1 and 5) just described make the whole system susceptible to runaway excitation and uncontrolled high firing rates throughout the system. To control the potential runaway excitation, careful inhibition within each network is needed by the local inhibitory neurons, and it was found that in addition to this, neuronal temporal adaptation and presynaptic temporal adaptation / depression were important (Rolls et al., 2024c). This emphasises the potential computational importance of adaptation evident in the firing rates of cortical neurons, and this deserves much

further exploration to help understand better the low firing rates that are typical of hippocampal neurons (Rolls et al., 1997; Robertson et al., 1998; Rolls et al., 1998; Georges-François et al., 1999).

7.3. Memory consolidation, and recall from the hippocampus back to the neocortex

This theory of hippocampal function shows that the memory capacity of the hippocampal system is limited to a number of memories determined by the number of recurrent connections C on any one CA3 neuron. With sparse representations, the estimate of the number of memories that could be stored in the rodent can numerically exceed the estimate of $C=12,000$ for the number of recurrent collaterals onto any one CA3 neuron, also in rodents. C may be a little higher in humans, but evidence on that is still needed. In any case, at first glance it may seem like a loose, rather high upper limit, especially considering that a parallel memory capacity estimate for the neocortex cannot be really produced or even defined, given the complex correlational structure of memories in the neocortex. A simple quantitative comparison between memory storage in the hippocampus and neocortex can however be worked out, roughly, by focusing on *information* capacity. This refers to the total amount of information I_{\max} deposited on a system of synapses, given in the simple case of p discrete orthogonalized representations as $p \times i_p$, where i_p is the information contained in a single activity pattern or memory representation (with sparser representation, p_{\max} increases and i_p decreases). With associative mechanisms for memory storage and retrieval, the maximum amount of information has been hypothesised to never exceed 0.2–0.3 bits per participating synapse (Kropff and Treves, 2005), hence a comparison of how much can be stored in the recurrent CA3 system vs. in recurrent synapses between pyramidal cells in the neocortex can be reduced to a comparison between their number. Assuming further that the number of recurrent synapses per pyramidal cell is not too different between the two structures, the comparison is further reduced to that between the respective numbers of cells. In rats, there are estimated to be $\sim 3 \times 10^5$ pyramidal cells per side in CA3 (Amaral et al., 1990), and no more than $20\text{--}25 \times 10^6$ in the neocortex overall (Mortera and Herculano-Houzel, 2012), i.e., a ratio of 1:40 at most. In humans, a similar comparison would yield a ratio in the order of 1:2,000 (West and Gundersen, 1990; Azevedo et al., 2009). Therefore, the total memory capacity of the neocortex is to be regarded as potentially very high, even if semantic memories are primarily in the human anterior temporal lobe and its connected cortical regions (Rolls et al., 2022a). Given the overwriting of hippocampal memories and forgetting considered in Section 3.7, this constitutes a key computational argument for recalling information from the hippocampus to the neocortex, where it can be stored in partly different forms as semantic and long-term autobiographical memories.

In addition to this key computational argument for recalling episodic information about particular events back to the neocortex for consolidation in the neocortex, other arguments have been put forward, including the slow learning that might be useful to reorganise information storage in semantic neocortical memory systems (McClelland et al., 1995; McClelland et al., 2020), and evidence from for example the possible temporal gradient of retrograde amnesia following hippocampal damage (Scoville and Milner, 1957; Squire, 1992; Squire et al., 2015; Fernandez and Morris, 2018; Moscovitch and Gilboa, 2022). There is also some evidence that new semantic learning is impaired in people with hippocampal damage that occurs after early development (Carlesimo, 2022). However, the issue of systems-level consolidation is still under discussion (Moscovitch and Gilboa, 2022). In these circumstances, the quantitative arguments about the limited storage capacity and forgetting in the hippocampal system compared to the neocortex as described here are of particular importance.

8. Representations in the hippocampus: what is stored and recalled

What is represented in the hippocampus is important to understand its computational operation. At the time that the hippocampal theory was developed (Rolls, 1989b; Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994), the evidence was mainly from rodents, and was that place cells that represent the place where the rodent is located is what is represented in the hippocampus (O'Keefe, 1979; McNaughton et al., 1983; O'Keefe, 1984; Muller et al., 1991; Markus et al., 1995; Hartley et al., 2014). Later, entorhinal cortex cells representing a grid of places where the rodent is located were discovered (Fyhn et al., 2004; Moser et al., 2014b; Moser et al., 2015; Edvardsen et al., 2020), and the Nobel prize was awarded for the discovery of place cells and grid cells in the rodent hippocampus in what was described as a GPS-like system. Many approaches to hippocampal computations are thus related to spatial processing of the place where the individual is located (McNaughton and Morris, 1987; McNaughton and Nadel, 1990; O'Keefe, 1990; Burgess et al., 1994; Burgess and O'Keefe, 1996; McNaughton et al., 1996; Bicanski and Burgess, 2018; Edvardsen et al., 2020).

However, even by the time of the hippocampal theory (Rolls, 1989b; Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994), it was being discovered that while the primate hippocampus may have some place cells (Rolls and O'Mara, 1995), many primate hippocampal neurons respond to the location "out there" in space being viewed, and not to the place where the individual is located (Cahusac et al., 1989; Miyashita et al., 1989; Rolls et al., 1989; Feigenbaum and Rolls, 1991; Rolls and O'Mara, 1995). Further studies, including in locomoting macaques, showed that these spatial view cells have an allocentric representation of space that is relatively independent of head direction, eye position, and the place where the individual is located (Rolls et al., 1997; Robertson et al., 1998; Rolls et al., 1998; Georges-François et al., 1999). These CA3 and CA1 and parahippocampal cortex spatial view cells were linked to hippocampal episodic memory by the further discoveries that in an object-spatial view location memory task some hippocampal neurons respond to a combination of spatial view and object ('what' and 'where') (Rolls et al., 2005b) (with combination-responding neurons also now implicated in episodic memory in humans (Kolobius et al., 2023)); that in a reward-spatial view task some hippocampal neurons respond to a combination of high (or for others low) reward value and spatial view ('reward' and 'where') (Rolls and Xiang, 2005); and that some hippocampal neurons respond in a one-trial object-spatial view task to the object or view being recalled when it is not being shown on the screen (Rolls and Xiang, 2006). The discoveries that many primate hippocampal neurons can respond to locations being viewed or gazed at "out there" in space has been confirmed in macaques (Wirth et al., 2017; Baraduc et al., 2019; Mao et al., 2021; Tan et al., 2021; Yang et al., 2023; Zhu et al., 2023), marmosets (Martinez-Trujillo et al., 2023; Piza et al., 2024), and humans (Ekstrom et al., 2003; Staresina et al., 2019; Tsitsiklis et al., 2020; Donoghue et al., 2023).

This revolution in our understanding of what is represented in the primate and human hippocampus (Rolls, 2023d, b, c) is consistent with the hippocampal theory (Rolls, 1989b; Treves and Rolls, 1992; Rolls and Treves, 1994; Treves and Rolls, 1994), which can deal with these types of spatial representation. For example, continuous spatial representations and discrete object representations can be associated together in the same single attractor network (Rolls et al., 2002). In another example, spatial view cell representations can be set up in continuous attractor networks (Stringer et al., 2005; Rolls et al., 2008). These types of spatial scene representation are present in the parahippocampal cortex in what is termed the parahippocampal scene (or place) area (see Section 11.1). The theory is that these provide the 'where' inputs to the hippocampal episodic memory system in primates including humans (see Section 11.1). At the same time, the hippocampal theory does deal with a rodent hippocampal system in which associations are made

between place representations, and objects (including odours) and/ or rewards/ goal for episodic memory and navigation in rodents.

It is of interest that neurons in the bat hippocampus can represent where another bat is, consistent with representations "out there", and also the place where the bat is (Omer et al., 2018); that the auditory and visual spatial locations are not in register as a spatial map (Geva-Sagiv et al., 2016); and that theta is not present in bats (Eliav et al., 2018), providing further doubt about much computational importance of theta for hippocampal function.

The representation provided by spatial view cells in the primate hippocampus and parahippocampal gyrus is in an allocentric coordinate framework in the sense that it depends on the location being viewed in the world and is relatively independent of eye position, of head direction, and of the place where the individual is located (Rolls et al., 1997; Rolls et al., 1998; Georges-François et al., 1999; Rolls, 2023d, b). This is to be contrasted with an egocentric coordinate framework, in which the representation of the spatial location is relative to the individual, for example to the left of the head. These spatial coordinate frameworks are conceptually different from viewpoint-dependent frameworks, which refer to the fact that the left-right relations in any viewed scene depend on the location of the viewer (Rolls, 2023d). For example, if we look at a view of Paris from the South, we will see on our left (West) the Eiffel Tower, then the Louvre, and then on our right (East) the Centre Pompidou. But if we move our viewpoint to be from the North, then we will see on our right (West) the Eiffel Tower, then the Louvre, and then on our left (East) the Centre Pompidou. The same happens if we view a map of Paris. If we view the map in the usual way with North at the top of the map, but then rotate the map so that South is at the top, then everything will be left-right reversed from our viewpoint. The same properties apply to objects (Rolls, 2023d). If we view the front cover of a book, the spine is on our left. But if we view the back cover of the book, the spine is on our right. Yet the spatial relations of the parts of the book as an object remain the same. [Optic flow also reverses in a similar way. If we view a person rotating clockwise about their body axis, the optic flow will be from our right to our left. But if the person is inverted and continues rotating clockwise about their body axis, then the optic flow will be reversed, and this object-based motion is encoded by neurons in the cortex in the superior temporal sulcus (Hasselmo et al., 1989b), and can be learned by slow learning (Rolls and Stringer, 2006).] Viewpoint-dependent frameworks always apply when we view a scene or object, and are part of the physics of the world, and should be clearly distinguished from allocentric vs egocentric spatial coordinate frameworks where these terms are defined as above. Indeed, it is suggested that the term egocentric should only be applied to egocentric vs allocentric spatial coordinate frameworks as defined above, and one or the other (or perhaps a mixture) will apply. Egocentric as defined above refers to coordinates relative to the head or body, and only sometimes applies. In contrast, viewpoint dependency *always* applies. It is suggested that it is important therefore to distinguish between an egocentric coordinate framework, and viewpoint dependency, and not to conflate them. This has some interesting implications for representations in the brain: they could use an allocentric spatial coordinate framework, yet must also be viewpoint-dependent (Rolls, 2023d). Further, viewpoint dependency is important for navigation when actions need to be taken (Rolls, 2023d). In the Paris example above, if one is to the South, one turns left to reach the Eiffel Tower, but if one is to the North, one turns to the right to reach the Eiffel Tower.

9. Concept cells in the hippocampus and neocortex

Quian Quiroga (2023) has argued that concept cells, which can be activated by any one of a range of attributes such as the sight of a person, the sight of a spatial view or location associated with that person, the sound of the person's voice, and the name of the person (Quian Quiroga et al., 2005; Quian Quiroga, 2012; Fried et al., 2014; Ison et al., 2015; Rey et al., 2015; De Falco et al., 2016; Rutishauser, 2019; Gastaldi et al.,

2021), may be unique to humans. This deserves further consideration in terms of our understanding of representations in the hippocampus and neocortex, in macaques as well as in humans (Rolls, 2023d).

When we discovered neurons in the macaque cortex in the anterior part of the superior temporal sulcus that respond to moving objects such as the sight of a head making or breaking social contact (Rolls et al., 1987; Hasselmo et al., 1989a; Hasselmo et al., 1989b), we also discovered nearby neurons that responded to auditory stimuli including vocalization (Rolls et al., 1987). The concept was that these two representations might be brought together in these cortical regions to form representations that could be activated by the sight of for example the lips moving to vocalize, and by the sound of the vocalization being made (Rolls et al., 1987). That has in fact now been shown to be the case, in that 76 % of neurons in face patch AF in the macaque cortex in the superior temporal sulcus were significantly influenced by the auditory component of a movie with faces that elicited neuronal responses, most often through enhancement of visual responses but sometimes in response to the auditory stimulus alone (Khandhadia et al., 2021). This type of neuron in macaques is thus multimodal, and can be activated by corresponding stimuli in the visual and auditory sensory modalities. That would appear to satisfy at least part of what a concept cell is. The concepts represented by these neurons in the third visual cortical stream are often about the social significance of stimuli (Pitcher et al., 2019; Pitcher and Ungerleider, 2021; Rolls, 2023c; Rolls et al., 2023a; Rolls, 2024). Given these multimodal cells in the macaque neocortex which projects to the hippocampus, multimodal cells may also be expected in the hippocampus. Indeed, visual-auditory multimodal neurons have also been observed in the macaque hippocampus (Tyree et al., 2023).

In another example from macaques, hippocampal spatial view cells in macaques are involved in memory, in that they can become associated with an object in an object-location-in-scene memory task (Rolls et al., 2005b; Rolls and Xiang, 2006), and with a reward in a reward-in-scene memory task (Rolls and Xiang, 2005). Thus a macaque single hippocampal neuron might respond to the sight of an object, or the sight of the place where it is located. In this sense, the responses of macaque hippocampal cells can be somewhat like those of concept cells (Rolls, 2023b). However, the macaque cells may be essentially specialized for particular associations that occur in an episodic memory, whereas neurons in the human temporal lobe cortical regions outlined in black in Figs. 7a and 7b of Rolls et al. (2022a) are more likely to be long-term semantic representation cells.

One property that is different of course for human concept cells is that they can be activated by the word that represents the concept, for example by the person's name, where the name is an arbitrary symbol to stand for the object or concept. Moreover, these semantic representations can then be used in syntactic operations, in ways that are at least starting to be investigated in neuroscience using computational modelling of how syntactic operations might be performed by biologically plausible attractor networks, and using investigations of effective connectivity (Rolls and Deco, 2015; Rolls et al., 2022a; Rolls, 2023c). However, in humans, the situation may be further subdivided, in that the left hippocampal system may be specialized for these language and word-related types of episodic memory (Bonelli et al., 2010; Sidhu et al., 2013), whereas the right hippocampal system may be more specialized for spatial representations and perhaps more like that in macaques (Burgess et al., 2002; Crane and Milner, 2005; Barkas et al., 2010).

In summary, it appears that some neurons with properties typical of concept cells are found in macaques, in terms of being multimodal, which is part of what is implied by "concept cell". However, the concept cells in humans may be specialized for language-related processing, and in that respect are more developed than the concept cells present in macaques (Rolls, 2023d). This is to be expected, if the selectivity of cells is the statistical outcome of a process of self-organization of what is relevant for the individual, rather than being pre-wired according to some universal mammalian instructions.

10. The human orbitofrontal and ventromedial prefrontal cortex can control memory consolidation in the hippocampus and neocortex

When episodic memories involving for example spatial view cells and objects (Rolls et al., 2005b; Rolls and Xiang, 2006) or rewards (Rolls and Xiang, 2005) are formed in the hippocampus, recent connectivity studies in humans provide evidence for connectivity from the orbitofrontal cortex in part via the pregenual anterior cingulate cortex to the septal nuclei and basal forebrain nucleus of Meynert (Rolls et al., 2022b, 2023b) which contain cholinergic neurons that project to the hippocampus and neocortex respectively (Mesulam, 1990; Zaborszky et al., 2008; Zaborszky et al., 2018) (yellow in Fig. 10). In that the orbitofrontal cortex represents reward value, aversive stimuli, and non-reward (Rolls, 2019a, b; Rolls et al., 2020a; Rolls, 2023a, c; Zhang et al., 2024), this provides a way in which the storage of episodic memories can occur especially well when environmental reinforcement contingencies are present or change. In a corresponding way, the orbitofrontal cortex via the ventromedial prefrontal cortex (vmPFC) has connectivity to the basal forebrain cholinergic neurons, which provide for the consolidation of semantic memories to be influenced particularly when there is a reward, punishment, or non-reward component (Rolls, 2022). These cholinergic systems are implicated in the synaptic mechanisms involved in episodic memory storage in the hippocampus, and memory consolidation involving the formation of semantic memories in the neocortex (Hasselmo and Bower, 1993; Hasselmo, 1999; Hasselmo and McGaughy, 2004; Hasselmo and Giocomo, 2006; Giocomo and Hasselmo, 2007; Hasselmo and Sarter, 2011; Newman et al., 2012).

A second key reward-related component of memory consolidation is that reward value can be stored in the primate (Rolls and Xiang, 2005) including human (Rolls, 2022; Rolls et al., 2023b) hippocampus as part of an episodic memory (via the pathways shown in Fig. 10), and can later be recalled to the neocortex, allowing any value that the episodic memory may have to be assessed, and thus by influencing whether further neocortical processing occurs, to influence whether the episodic memory is consolidated into long-term neocortical memory (Rolls, 2022, 2023c).

Reward-related mechanisms such as this are thus proposed to be key in understanding memory consolidation in the hippocampus and neocortex (Rolls, 2022, 2023c).

In this context of reward-related representations in the orbitofrontal cortex and ventromedial prefrontal cortex (Rolls, 2022, 2023c), it is notable that damage to the ventromedial prefrontal cortex (vmPFC) can impair episodic memory (Bonnici and Maguire, 2018; Clark et al., 2018; McCormick et al., 2018; Ciaramelli et al., 2019; Clark et al., 2019; De Luca et al., 2019; McCormick et al., 2020; McCormick and Maguire, 2021). The observation that vmPFC patients mind-wander less, and when they do they tend to focus on the present (Bertossi and Ciaramelli, 2016) has led to the proposal that the vmPFC (working with other prefrontal cortex regions) may contribute to the scaffold for extended streams of thought (and may not insert snapshots of scenes retrieved from the hippocampus, which are equally vivid in patients with vmPFC lesions). These scaffolding processes useful for prospective thinking operate with other prefrontal cortex regions and could include retrieval of entire episodes as well as the construction of hypothetical scenarios, the formulation of plans, etc (Ciaramelli and Treves, 2019).

However, the damage that produces these impairments can extend into the pregenual anterior cingulate cortex, and damage in the human orbitofrontal cortex / vmPFC / pregenual anterior cingulate cortex is likely to damage the connectivity of these cortical regions to the cholinergic neurons that influence the hippocampus via the septal region and the neocortex via the basal forebrain nucleus of Meynert, as described above (Fig. 10). Accordingly it is proposed (Rolls, 2022) that interference with acetylcholine as a key modulator of hippocampal function (Hasselmo and Giocomo, 2006; Giocomo and Hasselmo, 2007; Hasselmo and Sarter, 2011; Newman et al., 2012; Zaborszky et al., 2018)

that is involved in memory storage is likely to contribute to the memory deficits that follow damage to these orbitofrontal / vmPFC regions. Thus it is proposed that these vmPFC cortical regions do not perform computations like those of the hippocampus, but instead modulate hippocampal function to enhance memory storage when rewards, punishers, or novel stimuli decoded by the orbitofrontal cortex are present in the environment (Rolls, 2022, 2023c).

11. Pathways to and from the human hippocampus, and their computational implications for hippocampal function in humans

To help understand the computations performed by the human hippocampal memory and navigation system, it is important to know what information reaches the human hippocampus, and what computations are being performed en route to the hippocampus. This aim has been advanced recently by investigations of the pathways to the human hippocampus, performed by analysing the connectivity of the human hippocampal system with 360 cortical regions identified in the Human Connectome Project Multimodal Parcellation atlas (HCP-MMP1) (Glasser et al., 2016a) extended to include 66 subcortical areas (Huang et al., 2022). The HCP-MMP is a well founded parcellation of the human cortical regions that utilises evidence from anatomy (cortical thickness and cortical myelin), functional connectivity, and task-related fMRI (Glasser et al., 2016a). The Supplementary Material provides a list of the abbreviations of cortical regions in the HCP-MMP parcellation, and Figures to show the locations of the cortical regions in the human brain. The connectivity (Huang et al., 2021; Ma et al., 2022; Rolls, 2022; Rolls et al., 2022b, 2023c, b; Rolls et al., 2023e) was measured using MRI

acquired in more than 170 participants at 7 T in the HCP (Glasser et al., 2016b) with three different types of measure. Effective connectivity measures the connectivity in each direction between each pair of brain regions by utilizing the functional connectivity and a version of the functional connectivity with a delay of 2 s for fMRI (Rolls et al., 2022b) and 20 ms for magnetoencephalography (Rolls et al., 2023d; Rolls et al., 2024b), and was complemented by measurement of functional connectivity, which given that it is based on Pearson correlations, can provide evidence about interactions between brain regions, but not about the direction or causality of effects (Ma et al., 2022; Rolls et al., 2023b). These methods were complemented by diffusion tractography which can measure direct connections between brain regions though not about the direction of connections (Huang et al., 2021; Rolls et al., 2023b). Figs. 6–10 summarize some of the results of these investigations (Rolls et al., 2022b; Rolls et al., 2023a; Rolls et al., 2023b, c; Rolls et al., 2023d; Rolls, 2024), and lead to the following points about the connectivity of the human hippocampal memory and navigation system.

11.1. Spatial scene inputs in humans to hippocampal spatial view neurons

Connectivity is directed to the human hippocampus from a medial posterior part of the parahippocampal gyrus PHA1-3 (which corresponds to TH in macaques) and the adjoining ventromedial visual areas (VMV1-3) (Rolls et al., 2022b; Rolls et al., 2023a) (Figs. 6 and 7). This parahippocampal / VMV region (Sulpizio et al., 2020; Rolls et al., 2024a) is a parahippocampal place area (or Parahippocampal Scene Area, PSA, as it responds to viewed scenes not the place where the individual is located) (Epstein and Kanwisher, 1998; Epstein, 2005;

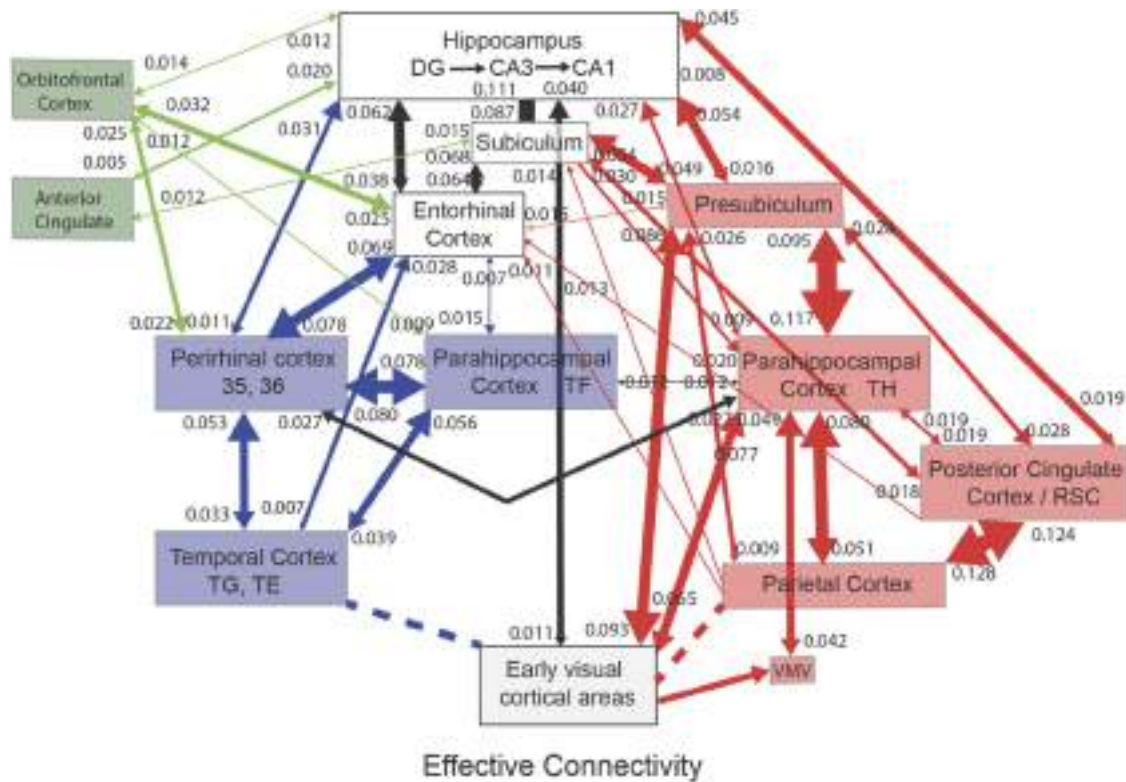


Fig. 6. Summary of the effective connectivity of the human hippocampal system measured across 172 Human Connectome Project participants at 7 T. The maximum value of the effective connectivity is 0.2, and the strength in each direction is shown close to the termination of an arrow. The width of the arrows and the size of the arrowheads reflect the strength of the effective connectivity. For areas such as the temporal lobes, the parietal cortex, and the posterior cingulate cortex, there are several subregions in the HCP atlas, and the value of the strongest effectivity connectivity to or from any subarea is shown in this case. Brain regions that are part of the ventral ‘what’ stream are shown in blue, that are part of the dorsal ‘where’ or ‘action’ stream are shown in red, and that involve the orbitofrontal and anterior cingulate cortex reward value stream are in green. The Ventromedial Visual Areas (VMV) and TH include the parahippocampal place / scene area. The early visual areas referred to here include POS1 and ProS, where the retrosplenial place area is located (Sulpizio et al., 2020; Rolls et al., 2024c). Dashed lines indicate that there are several stages to the connectivity.

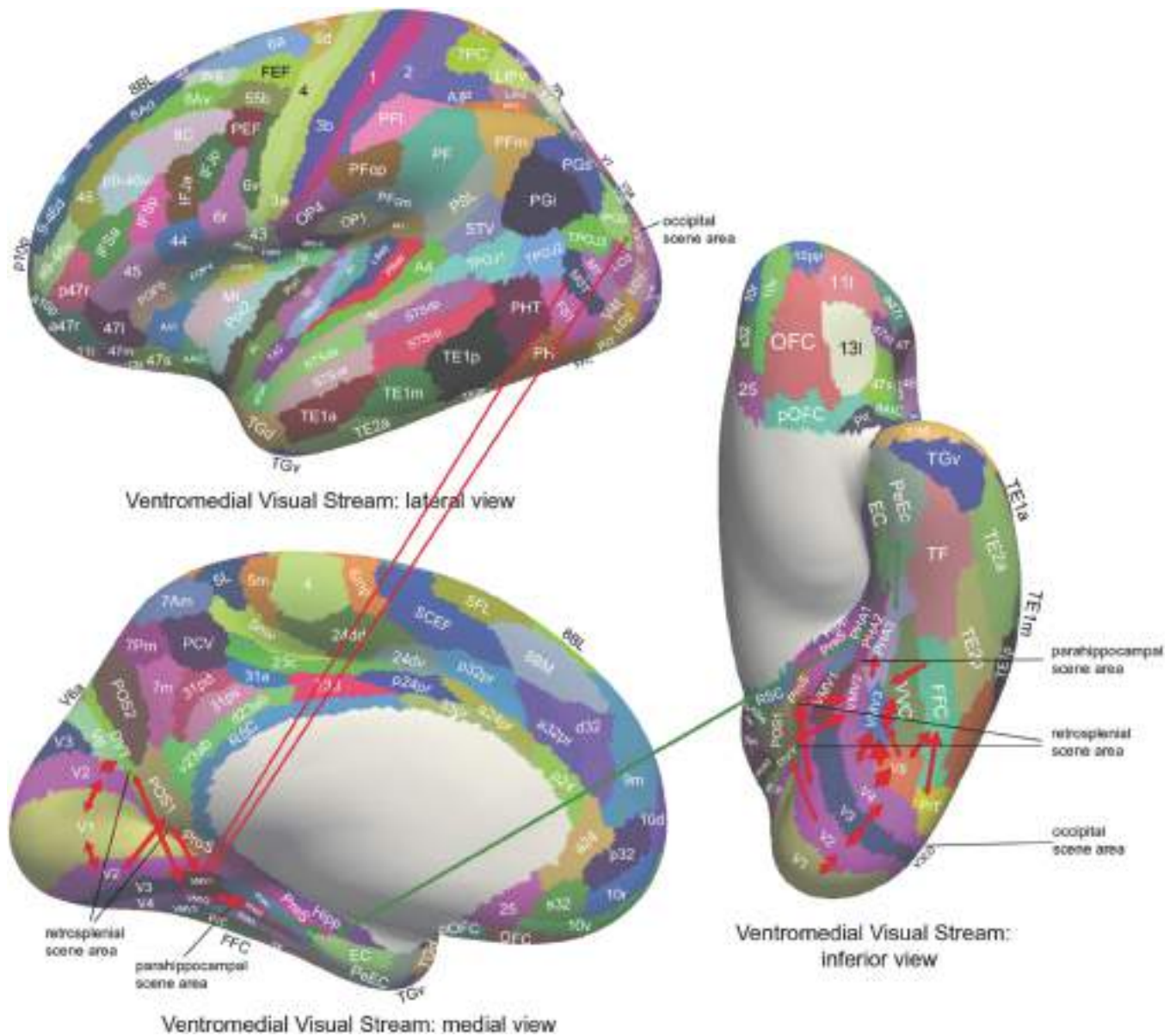


Fig. 7. Effective connectivity of the human Ventromedial Visual Cortical Stream which reaches the parahippocampal gyrus PHA1 – PHA3 regions via ventromedial (VMV) and Ventral Visual Complex (VVC) and ProStriate regions: schematic overview. Visual scenes are represented in the anterior parts of VMV and the posterior parts of PHA1 – PHA3 (Sulpizio et al., 2020) in what is termed the Parahippocampal Place Area, PPA (Epstein and Baker, 2019)). (The PPA might better be termed the Parahippocampal Scene Area PSA as it is the scene being viewed, not the place where the individual is located, that is represented (Rolls, 2023b).) The retrosplenial scene area is in a band of cortex in the Prostriate cortex ProS and Dorsal Visual Transitional cortex DVT that is posterior to region RSC (Sulpizio et al., 2020). The occipital scene area is in V3CD and borders V4 (Sulpizio et al., 2020). The green arrows show how the Ventromedial Visual Stream provides ‘where’ input about locations in scenes to the hippocampal memory system from the medial parahippocampal gyrus PHA1- PHA3 region (which corresponds to TH in macaques). The connectivity from PGp to PHA regions is suggested in the text to be involved in idiothetic update of locations in scenes. The widths of the lines and the size of the arrowheads indicate the magnitude and direction of the effective connectivity. (After Rolls et al. (2023a, 2023d); Rolls et al. (2024b))

Epstein, 2008; Epstein and Julian, 2013; Kamps et al., 2016; Epstein and Baker, 2019; Sulpizio et al., 2020; Natu et al., 2021; Rolls et al., 2024a). Thus the proposal is that the PSA is a route via which hippocampal spatial view cells receive their information about and selectivity for locations in scenes. This direct route (Rolls et al., 2022b; Rolls et al., 2023a) is complemented by connectivity via the posterior cingulate cortex (Rolls et al., 2023e). Indeed, the posterior cingulate cortex has considerable connectivity with the hippocampal memory system and is thereby implicated in episodic memory functions (Rolls et al., 2023e). First, the antero-dorsal parts of the posterior cingulate division in the HCP-MMP (especially 31a and 23d, the precuneus visual region PCV, and also RSC) have connectivity with early visual cortical areas

including those that represent spatial scenes, with the superior parietal cortex, with the pregenual anterior cingulate cortex, and with the hippocampal system. This connectivity implicates it in the “where” component for hippocampal episodic memory and for spatial navigation (Rolls et al., 2023e). Second, the postero-ventral parts of the posterior cingulate division in the HCP-MMP (31pd, 31pv, 7 m, d23ab, and v23ab) have effective connectivity with the temporal pole, inferior temporal visual cortex, cortex in the superior temporal sulcus implicated in auditory and semantic processing, with the reward-related vmPFC and pregenual anterior cingulate cortex, with the inferior parietal cortex, and with the hippocampal system. This connectivity implicates it in hippocampal episodic memory, providing routes for “what,” reward and

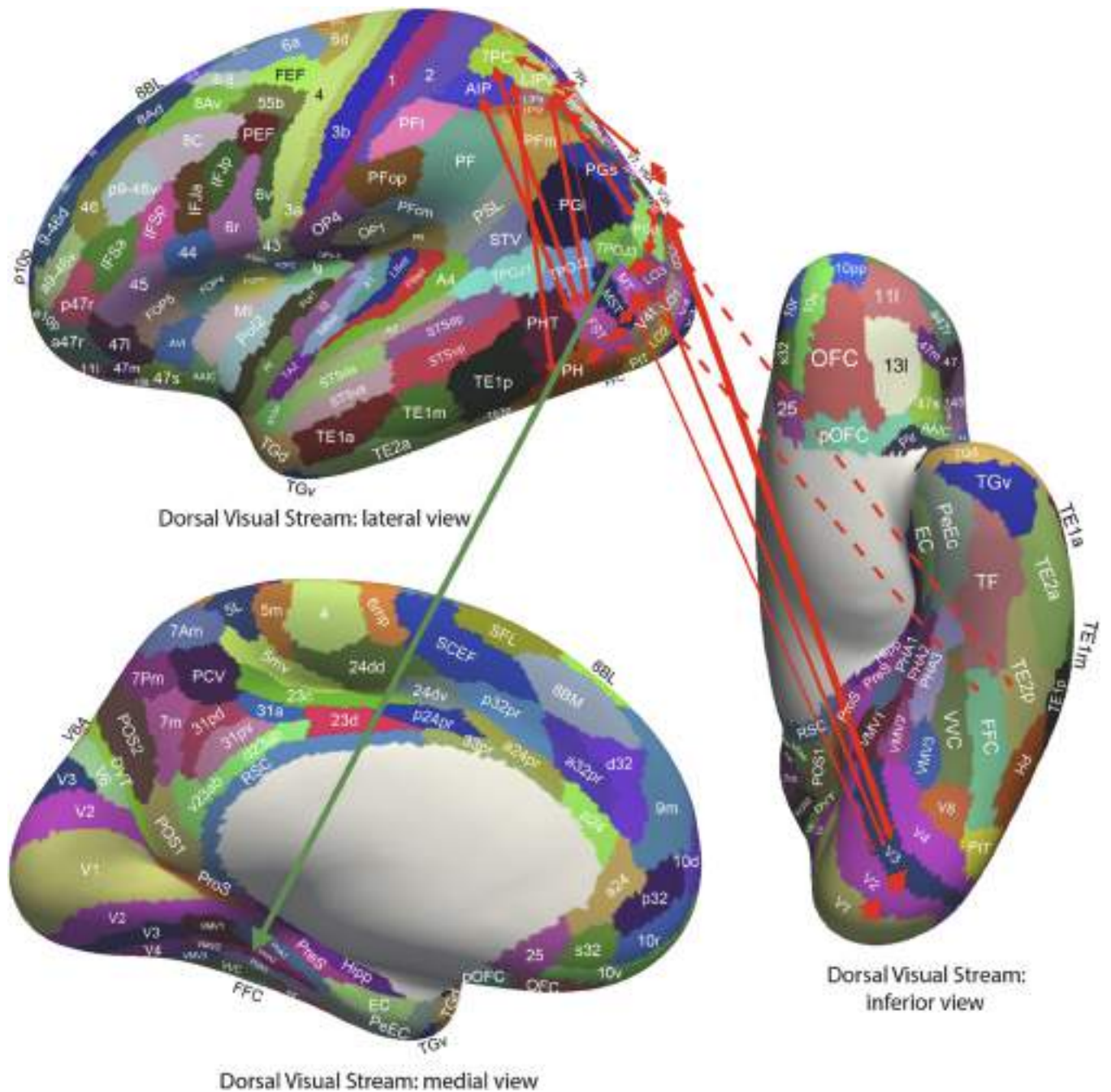


Fig. 8. Effective connectivity of the human Dorsal Visual Cortical Stream which reaches (partly via V3, V3A and LO3) the MT+ complex regions (FST, LO1, LO2, LO3, MST, MT, PH, V3CD and V4t), and then the intraparietal regions (AIP, LIPd, LIPv, MIP, VIP IP0, IP1 and IP2) and then the area 7 regions: schematic overview. Connectivity from the intraparietal and area 7 regions to the inferior parietal cortex region PGp, which in turn has effective connectivity to the parahippocampal scene area in PHA1–3 is shown. Inputs to this dorsal stream from ventral stream regions such as FFC and TE2p are shown with dashed lines. (After [Rolls et al. 2023a](#).)

semantic schema-related information to access the hippocampus ([Rolls et al., 2023e](#)).

The ‘Ventromedial Cortical Visual Stream’ pathway is shown in more detail in [Fig. 7](#), which summarizes how in humans visual information reaches the parahippocampal gyrus PHA1 – PHA3 regions via ventromedial (VMV1-3) and Ventral Visual Complex (VVC) regions ([Rolls et al., 2023a](#); [Rolls et al., 2023d](#); [Rolls et al., 2024b](#)). In this stream there is effective connectivity from V1 > V2 > V3 > V4. Then V2, V3 and V4 have effective connectivity to the VMV regions, which in turn have effective connectivity to PHA1–3, which in turn have effective connectivity directed to the hippocampal system ([Fig. 7](#), green arrows) ([Rolls et al., 2023a](#); [Rolls et al., 2023d](#); [Rolls et al., 2024b](#)). In addition, V2 has

effective connectivity to the transitional visual areas DVT (Dorsal Transitional Visual area) and ProS (the ProStriate region), which in humans are where in the HCP-MMP atlas ([Glasser et al., 2016a](#); [Huang et al., 2022](#)) the retrosplenial place area is located ([Sulpizio et al., 2020](#); [Rolls et al., 2024a](#)); and these regions in turn have effective connectivity to the PHA parahippocampal regions ([Fig. 7](#)) ([Rolls et al., 2023a](#); [Rolls et al., 2023d](#); [Rolls et al., 2024b](#)). In humans, the occipital place area OPA is located in V3CD, V3B, and IP0 ([Sulpizio et al., 2020](#)).

It is proposed that scene representations are built computationally using combinations of ventral visual stream features that when overlapping in space are locked together by associative learning and can form a continuous attractor network to encode a visual scene ([Rolls and](#)

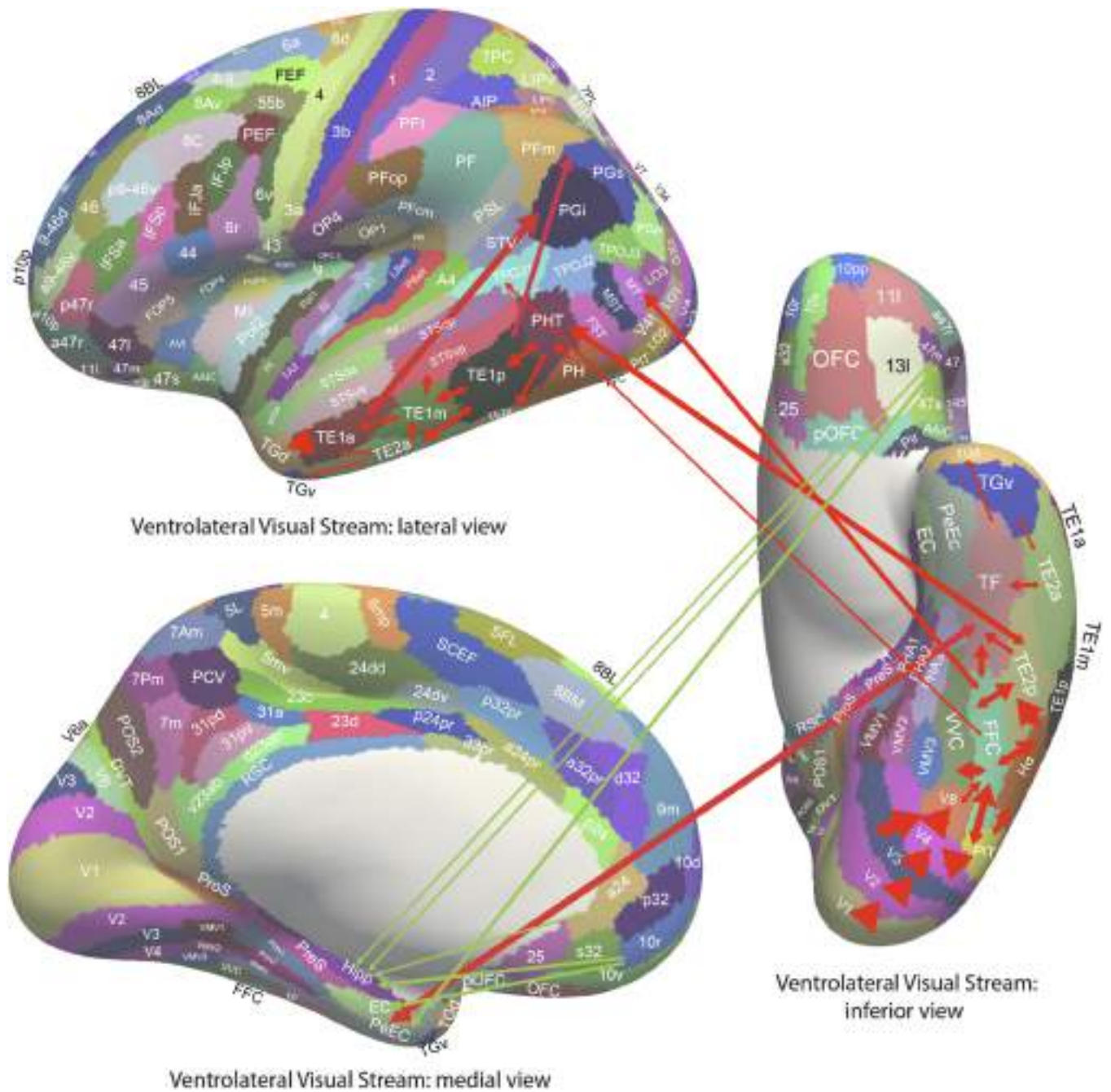


Fig. 9. Effective connectivity of the Ventrolateral Visual Stream which reaches inferior temporal cortex TE regions in which objects and faces are represented (red arrows): schematic overview. One of the red arrows shows how the Ventrolateral Visual Stream provides ‘what’ input to the hippocampal memory system via parahippocampal gyrus TF to perirhinal PeEc connectivity from FFC, PH, TE1p, TE2a and TE2p. The green arrows show how reward regions of the orbitofrontal cortex, vmPFC (pOFC, 10r, 10 v) and pregenual anterior cingulate (a24 and p32), and punishment/non-reward regions of the lateral orbitofrontal cortex (47 m) have effective connectivity with the hippocampus (Hipp), entorhinal cortex (EC), and perirhinal cortex (PeEc). The Ventrolateral Visual Stream also provides input to the semantic language system via TGd. The Ventrolateral Visual Stream also has connectivity to the inferior parietal visual area PFM, PGs and PGI as indicated by 2 green arrows. The widths of the lines and the size of the arrowheads indicate the magnitude and direction of the effective connectivity. After [Rolls et al. \(2023a\)](#).

[Stringer, 2005; Stringer et al., 2005; Rolls et al., 2008; Rolls et al., 2023c; Rolls et al., 2024c](#)) using spatial view cells ([Rolls et al., 1997; Robertson et al., 1998; Rolls et al., 1998; Georges-François et al., 1999; Wirth et al., 2017; Rolls and Wirth, 2018; Tsitsiklis et al., 2020; Rolls, 2022](#)) in the parahippocampal scene (or place) area referred to above, which in turn connects to the hippocampus to provide the ‘Where’ component of episodic memory ([Rolls et al., 2022b, 2023c; Rolls et al., 2024b](#)).

This Ventromedial Visual Cortical Stream for ‘Where’, scene, representations, is a revolutionary proposal in terms of hippocampal theory.

The proposal is that ‘Where’ information, about locations in scenes that are encoded by hippocampal spatial view cells, reaches the hippocampus from the Parahippocampal Scene Area in PHA1-3 and VMV1-3, which has much connectivity with early ventral visual stream cortical areas. Indeed faces are represented near to the Parahippocampal Scene Area in the fusiform gyrus FFC ([Weiner et al., 2017; Pitcher et al., 2019; Natu et al., 2021; Rolls et al., 2024a](#)); ideograms (or logograms) of words are represented just lateral to faces in the visual word form area in the fusiform gyrus ([Dehaene et al., 2005; Dehaene and Cohen, 2011;](#)

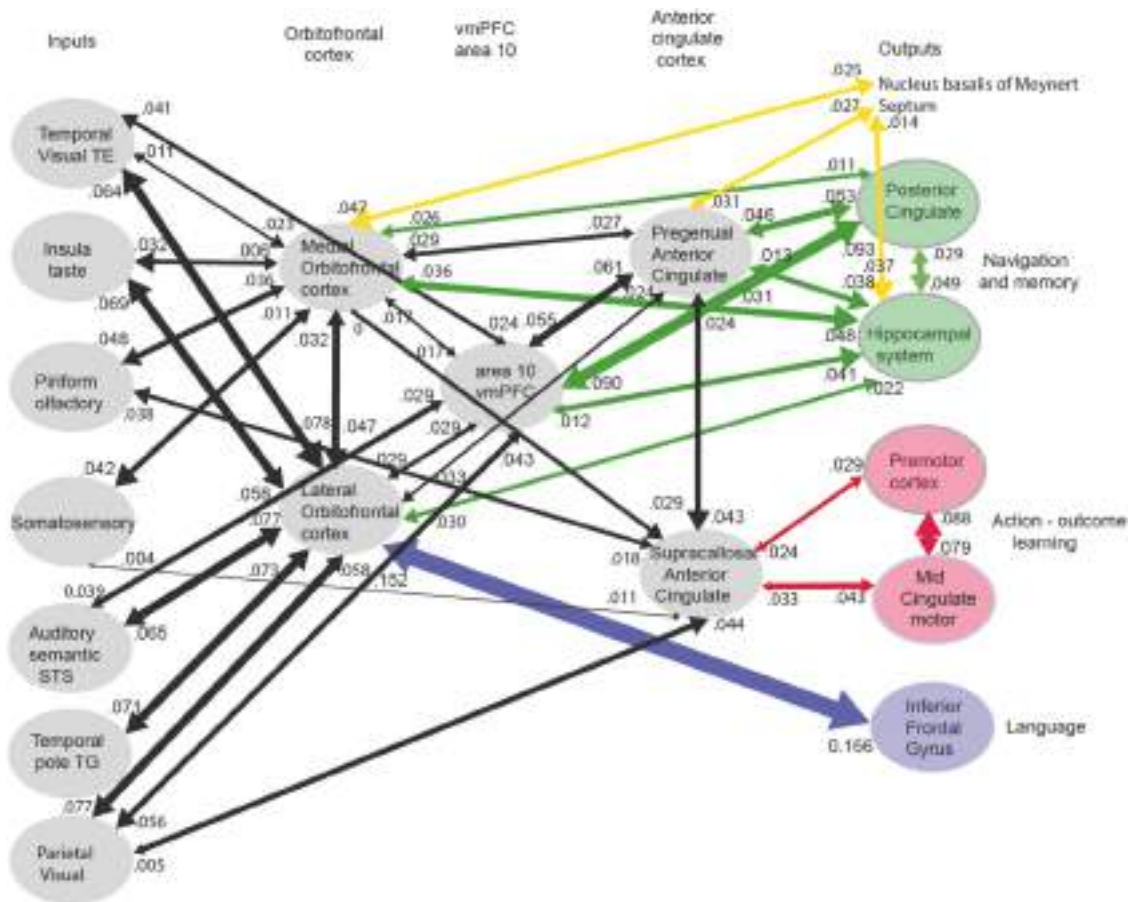


Fig. 10. Synthesis of the effective connectivity of the orbitofrontal cortex, vmPFC, and anterior cingulate cortex shown in the middle, with inputs on the left and outputs on the right. The regions included for each of the 5 central ellipses are as defined in the text (Rolls et al., 2023b). The width 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 PPop, which also connect to the pregenual anterior cingulate but are not shown for clarity; 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. 2023b.)

Caffarra et al., 2021; Yeatman and White, 2021); and cortical regions that represent objects are nearby and project forward into the inferior temporal visual cortical areas involved in invariant visual object recognition (Grill-Spector et al., 2006; Rolls, 2021c, a; Rolls et al., 2023a). However, scenes are likely to be represented by spatially contiguous scene features that become associated together in the correct topological arrangement because of the statistics of the inputs (Stringer et al., 2005; Rolls et al., 2008), and thus visual scene representations are likely to be formed from visual features of the type that are represented in ventral stream visual cortical regions (Rolls et al., 2024c).

Highly relevant to these points is that spatial view cells are found in the macaque parahippocampal gyrus as well as the hippocampus (Rolls et al., 1997; Robertson et al., 1998; Rolls et al., 1998; Georges-François et al., 1999; Rolls and Xiang, 2005; Rolls et al., 2005b) (Section 8). Indeed, it is proposed and likely that many of the neurons in the Parahippocampal Scene (Place) Area are spatial view cells, and that this is how scenes are represented in the primate including human brain.

11.2. The roles of the parietal cortex in the idiothetic update of hippocampal and parahippocampal spatial view cells and scene representations

What has just been proposed in 11.1 raises the question of the role of the parietal cortex, traditionally regarded as the brain region involved in 'Where' representations (Ungerleider and Mishkin, 1982; Pitcher and Ungerleider, 2021), in the responses of hippocampal (and parahippocampal gyrus) spatial view cells. As shown in Figs. 6 and 8, the hippocampal system does receive input from parietal cortex visual regions (Huang et al., 2021; Ma et al., 2022; Rolls et al., 2022b; Rolls et al., 2023a; Rolls et al., 2023c). Inputs are also received via the visuo-motor parts of the posterior cingulate cortex (Rolls et al., 2023e).

In more detail, the effective connectivity of the human Dorsal Visual Cortical Stream is shown in Fig. 8 (Rolls et al., 2023a). There is effective connectivity from parietal cortex regions to the parahippocampal scene area, as illustrated in Fig. 8. Strong effective connectivity is directed from inferior parietal region PGp to the Parahippocampal Scene Areas (PSA) in PHA1-3, which are medial parahippocampal cortical regions that probably correspond to TH in macaques (Fig. 8) (Rolls et al., 2023c). PGp receives its inputs from parietal area 7 regions and intraparietal regions (Fig. 8) (Rolls et al., 2023a) involved in visual motion

analysis and in coordinate transforms from retinal to head-based and then to world-based (allocentric) coordinates (Snyder et al., 1998; Salinas and Sejnowski, 2001; Rolls, 2020). These coordinate transforms are fundamental for self-motion update of scene representations, so that the spatial view neurons in the parahippocampal scene area can represent where in a scene the individual is looking independently of eye position, head direction, and even the place of the head in the environment, when the view details are obscured or in the dark (Robertson et al., 1998; Rolls, 2020). Given these two lines of evidence, it is proposed that the parietal cortex has the role of idiothetic update of the scene representations in the PSA and thereby in the hippocampus (Rolls et al., 2023a; Rolls et al., 2023c). Thus the hypothesis is that the ‘Where’ scene representations in the human ventromedial visual stream are built by combinations of ventral stream spatial features, and the viewed position in the scene is idiothetically updated by coordinate transforms to the allocentric level of scenes (Rolls, 2020) by the parietal cortex inputs to the PSA (Rolls et al., 2023a; Rolls et al., 2023c). This is very different to anything proposed for rodents with their much less well developed and non-foveate visual system, in which path integration over eye position has not been considered.

It is emphasized in this approach that the ‘path integration’ that is required for idiothetic update in humans and other primates involves eye position as well as head direction and the place where the individual is located, and much takes place in the dorsal visual system regions in the cortex in the intraparietal sulcus and area 7 (Rolls, 2020; Rolls et al., 2023c). It is proposed that the computational mechanisms for these coordinate transforms involve gain modulation and a short-term memory trace learning rule implemented in the parietal cortex (Rolls, 2020). This circumvents a real problem with hypothesizing that path integration of any type occurs within the hippocampus in that the energy landscape of any continuous attractor network representation of place or spatial view in the hippocampus that utilised idiothetic update (Stringer et al., 2002; Rolls and Stringer, 2005; Stringer et al., 2005) would be so distorted by association with the ‘What’ and reward information used for episodic memory that it would be very poor at path integration, as the energy landscape would be too bumpy because of the associations (cf. Spalla et al., 2021).

The connectivity from the hippocampus and parahippocampal gyrus to the parietal cortex may further provide a route for allocentric locations in space with associations with rewards, goals, or objects and remembered using hippocampal mechanisms to produce navigation and visuo-motor actions in space that require transforms to egocentric coordinates (Rolls et al., 2023c).

11.3. Ventrolateral visual stream ‘What’ inputs to the human hippocampal system

To add to the recently developing understanding of human hippocampal system inputs, Fig. 9 shows the ventrolateral cortical visual stream in humans progressing via V1 > V2 > V4 > FFC (which contains representations of faces, objects and even words in the visual word form area laterally) > the anterior temporal lobe TE regions (Rolls et al., 2023a) where invariant representations of objects and faces are built (Rolls, 2000, 2021c, a). This pathway provides ‘What’ inputs to the hippocampal memory system via parahippocampal area TF, which is lateral parahippocampal cortex and anterior to the scene area in PHA1-3 (Fig. 9) (Rolls et al., 2023a; Rolls et al., 2024a). TF has effective connectivity to the perirhinal cortex, which in turn has connectivity to the entorhinal cortex, completing a route for ‘What’ visual information about objects and faces to reach the human hippocampus (Rolls et al., 2022b; Rolls et al., 2023a; Rolls et al., 2024a).

11.4. Reward value / emotion-related inputs to the human hippocampus

Reward value and emotion-related inputs reach the human hippocampal system from the orbitofrontal cortex and anterior cingulate

cortex partly via the perirhinal and entorhinal cortex (Figs. 6, 9 and 10) (Ma et al., 2022; Rolls et al., 2022b; Rolls et al., 2023a; Rolls et al., 2023b), and perhaps even more directly (Huang et al., 2021). This important route for reward to gain access to the hippocampus in addition to ‘What’ and ‘Where’ inputs is shown in the updated hippocampal schematic connection diagram in Fig. 1, which shows how reward value information could be associated with ‘Where’ spatial view cell activity in hippocampal CA3.

The connectivity for these reward value and emotion-related inputs to reach the human hippocampus is shown in more detail in Figs. 9 and 10 (Rolls et al., 2023a; Rolls et al., 2023b). The sensory/perceptual cortical regions on the left of Fig. 10 provide visual, taste, olfactory and auditory input not coded in terms of their reward value to the orbitofrontal cortex (Rolls, 2019b, a, 2021c). The representation of these signals in the orbitofrontal cortex is in terms of their reward value, as shown by stimulus-reward learning and reversal; and by satiation which selectively reduces the reward value (Thorpe et al., 1983; Rolls et al., 1994; Hornak et al., 1996; Hornak et al., 2003; Berlin et al., 2004; Hornak et al., 2004; Grabenhorst and Rolls, 2011; Rolls, 2019a; Rolls et al., 2020a; Rolls et al., 2020b; Rolls, 2021d). Reward is represented especially in the human medial orbitofrontal cortex, and punishment and non-reward in the lateral orbitofrontal cortex (Grabenhorst and Rolls, 2011; Rolls et al., 2020a; Rolls, 2023a). The medial and lateral orbitofrontal cortex have effective connectivity to the pregenual anterior cingulate cortex, in part via the ventromedial prefrontal cortex (vmPFC) (Fig. 10) (Rolls et al., 2023b). The medial and lateral orbitofrontal cortex, and the vmPFC, then have effective connectivity with the hippocampal system (perirhinal and entorhinal cortex, and perhaps directly with the hippocampus) (Figs. 9 and 10) (Rolls et al., 2023b). The memory related part of the posterior cingulate cortex provides additional connectivity between these reward-related regions and the hippocampal system (Fig. 6) (Rolls et al., 2022b; Rolls et al., 2023e).

These neural connectivity investigations provide clear evidence on how reward value and emotion-related information can reach the human hippocampal system. It is proposed that in the hippocampus, including in CA3, reward value information can be associated with spatial view information to enable the reward and emotional aspects of episodic memory to become part of the episodic memory (Rolls, 2022; Rolls et al., 2023b). The return pathways from the hippocampus to the orbitofrontal cortex, pregenual anterior cingulate cortex, and vmPFC shown in Figs. 1, 6, 9, 10 provide a route for the reward and emotional value of an episodic memory to be recalled back from the hippocampus to the orbitofrontal and anterior cingulate cortex and vmPFC (Rolls and Treves, 1994; Treves and Rolls, 1994; Rolls, 1995, 2021c), from which it can influence other brain regions involved in actions (Rolls et al., 2020a; Rolls, 2021c; Rolls et al., 2023b).

This connectivity described in humans also shows how a key component of navigation, the goal or reward towards which the navigation is directed, reaches the human hippocampal system, where navigation may be guided by a remembered sequence of spatial view locations encoded by spatial view cells (Rolls, 2021e, c; Rolls et al., 2023b). In fact, it is remarkable how the hippocampal memory and navigation system is a key system towards which reward-related systems such as the orbitofrontal cortex and pregenual anterior cingulate cortex project (Fig. 10) (Rolls et al., 2023b).

In addition, the orbitofrontal cortex and pregenual anterior cingulate cortex have connectivity (yellow in Fig. 10) directed to the human cholinergic basal nucleus of Meynert which projects to the neocortex, and septal region which projects to the hippocampus, and these pathways are proposed to influence memory consolidation including consolidation into long-term semantic memory (Rolls, 2022; Rolls et al., 2023b) (Section 10).

11.5. Perirhinal cortex, recognition memory, and long-term familiarity memory

The perirhinal cortex provides a route in humans for ‘what’ information from ventrolateral visual cortical regions via region TF to reach the hippocampus (Rolls et al., 2023a). Whereas the hippocampus is involved in spatial, object-place, and object-temporal sequence memory, the perirhinal cortex is involved in recognition memory, as shown by the effects of lesions (Baxter and Murray, 2001; Malkova et al., 2001; Buckley and Gaffan, 2006). Moreover, and consistently, the primate perirhinal cortex contains neurons related to the degree of long-term familiarity of objects, with neuronal responses increasing over hundreds of presentations (Hölscher et al., 2003; Rolls et al., 2005a; Rolls, 2008). It has also been suggested that the perirhinal cortex puts together combinations of features to represent complex objects by building conjunctive / configural representations (Bussey et al., 2005). However, when we recorded in the primate perirhinal cortex, we did not find much evidence for very specifically tuned object neurons, but did find that neuronal activity is related to short-term perceptual memory (Hölscher and Rolls, 2002). In the light of this, and the fact that inferior temporal visual cortex neurons do provide very good invariant representations of objects (Rolls and Treves, 2011; Rolls, 2012a), the possibility is suggested that one function of the perirhinal cortex may be to provide a visual short-term memory, which is usually required for the tasks such as oddity with multiple distractors that led to the conjunctive / configural hypothesis (Bussey et al., 2005). Indeed, the visual short-term memory capability of the perirhinal cortex is probably important also for its role in delayed paired-associate learning (Fujimichi et al., 2010).

12. Computational constraints on the storage of information in the cerebral cortex

12.1. Potts attractors

The neocortex has many local attractor networks, as indicated by the local recurrent collateral connections between the pyramidal cells which have a high density only over a few mm, and by the ability of the neocortex to implement short-term memory and pattern completion (Akrami et al., 2009; Rolls, 2016b, 2023c). One way in which the operation of a system with many local attractors that are coupled could be approached is using Potts units, in which each Potts unit might be thought of as representing a local patch of neocortex. This is in contrast to the hippocampus, in which in CA3 we propose that there is a single attractor network.

Treves and colleagues have developed a Potts unit approach to understanding neocortical function inspired by Braitenberg’s observation that in the cortex local intrinsic connections between pyramidal cells, which do not leave the gray matter, and longer-range ones, which connect separate cortical areas with fibers that travel through the white matter, are of similar numerosity; and both, in his perspective, are endowed with Hebbian plasticity and serve to make the cortex an associative memory machine (Braitenberg and Schüz, 1991). He had earlier proposed to consider a ‘skeleton’ cortex reduced, in any given mammalian species, to its N pyramidal cells (N ranging roughly from 10^6 to 10^{10}), organized into \sqrt{N} fictitious ‘compartments’ of \sqrt{N} cells each. If each cell were to receive a synapse from every cell in the same compartment and from a single cell in any other compartment, local and long-range systems would be perfectly balanced (Braitenberg, 1978). The Potts model is based on the suggestion that such compartments (in the human cortex, they would represent 1 mm^2 patches of cortex, roughly the size of a voxel with high-resolution fMRI) operate as local autoassociative networks and are therefore endowed with S local attractor states. The maximum number of such local memory patterns has been estimated analytically to be dependent on the number of local recurrent collaterals per cell in a way similar to that expressed in Eq. (1), but with a proportionality factor reduced by $1/3$ (Roudi and Treves,

2004, 2006). In the Potts model these local networks (i.e. the compartments) are replaced by Potts spins, which are variables that can take S categorical values, representing the local attractors, plus one quiescent state. Rather than discrete spins one can use graded response Potts variables, which then parametrize the degree of similarity of the current state of the cortical patch with each of its S attractors. One advantage is that one can calculate analytically the overall storage capacity of such a model in its basic version (Kanter, 1988) and in its cortically more plausible variants (Kropff and Treves, 2005; Naim et al., 2018). The result is complex, but an approximate formula for the maximum number of randomly correlated memory patterns that could be stored and individually retrieved in a Potts autoassociative network is

$$p_{\max} \approx \frac{CS^2}{4a \ln \left(\frac{S}{a} \right)} \quad (4)$$

where C is now the number of compartments an average compartment is receiving (significant) inputs from, and a is again the sparsity of the cortical representation, here the fraction of compartments not in the quiescent state.

This analytical estimate has been validated by numerical simulations (of the Potts model) and one may think that it implies a very large storage capacity for the human cortex, if one were to consider, for example, that in Braitenberg’s human ‘skeleton’ cortex each compartment is connected to every other compartment, so C could be taken to be $\approx 10^5$, and perhaps S and $1/a$ quite large as well. This would be misleading, however, for several reasons. One is the inherent difficulty of mapping the real cortex onto the crude model and assigning values to its parameters. Each of the C connections to a Potts unit, for example, is actually a tensor with S^2 weights, so it cannot represent 1 or even \sqrt{N} synapses but rather, at the very least, S^2 of them; therefore C should rather be seen as the number of patches or small cortical modules observed to have a significant functional interaction with any given receiving module – from analyses of effective connectivity, one may infer $C \approx 30\text{--}100$ (Rolls, 2023c; Rolls et al., 2023a). Equally difficult is to conceive of a value for S , given that the local cortical networks do not have, to store their S local attractors, the option of using the Dentate Gyrus, in the orthogonalizing role reviewed above for CA3. Moreover, if one were to make reasonable assumptions about C , and S , and perhaps a , they would have to vary in the model depending on which cortical patch each of its units represents. A more fundamental reason that makes it problematic to rely on the storage capacity estimate above is that it is based on the assumption of uncorrelated memory patterns. Specifically, they would have to be, whether orthogonalized or not at the local level, uncorrelated at the global level, which is implausible given the compositional nature of episodic and semantic memories, and on the components presumably having, in the neocortex, stable representations. Thus the episodic memory of a chance encounter, after many years, with a friend in the foyer of the opera theatre might rely on the activation of previously established cortical representations of that friend, of the interiors of that theatre, of the opera being performed, and so on; and it has been shown that if memories are composed of a few large fragments, this leads to a dramatic reduction in autoassociative capacity, so that the effective way to reactivate the composition is to first retrieve its compressed, orthogonalized representation in the hippocampus.

We note that a Potts system could be a model for when an arbitrary set of components have to be associated at one time to store the memory of an episode. In this case the Potts study (Ryom et al., 2023) shows a large reduction in capacity. This reduction of capacity would not apply to semantic memory representations in the neocortex which we assume involve flexible modifications to existing semantic representations. Applied to semantic memory instead, the Potts approach indicates complex dependence of retrieval capability on memory load with a possibility of two phase transitions that remain to be understood

(Boboeva et al., 2018). The implication is that the Potts approach may be useful for understanding the operation and capacity of neocortical semantic memory systems.

12.2. Latching dynamics

The very same compositional nature that makes complex neocortical memory extended traces unsuitable for autoassociative retrieval of what, where and reward combinations that are represented in separate parts of the neocortex, unless aided by hippocampal input, enables instead cognitive processes based on associative thought. This is because the multiple associations encoded in the synaptic weights of representations which serve as components in several memories freely promote transitions that recombine fragments into novel trajectories. Such a process has been called latching dynamics and has been studied analytically and computationally using the Potts model (Treves, 2005; Russo and Treves, 2012). The networks show latching or jumping from one state to another because of temporal adaptation in each of the units. The effectively stochastic character of latching dynamics has been observed to be congruent with the random-walk type of dynamics posited to underlie free recall from short-term memory (Naim et al., 2020; Ryom et al., 2021). More, it facilitates mind-wandering, goal-free and creative lateral thought processes (Viol et al., 2021) possibly with a tendency for frontal cortex to lead the dynamics (Ryom et al., 2024). A discussion of latching dynamics is out of the scope of this review; what is noted here is that it stems from interference effects among memory representations, those that are minimized in the hippocampus by the orthogonalizing effect of the dentate gyrus. Moreover, it may be a key part of prospective thought.

Consistent with this, it has been proposed that creative thought is facilitated by stochastic jumping to new but related parts of a semantic space in attractor networks that is produced by the noise inherent in the almost Poisson spike times of neurons for a given mean rate (Rolls and Deco, 2010). Following up on this hypothesis, it has been found that verbal creativity is associated with higher temporal variability of neocortical functional connectivity (Sun et al., 2019).

13. Conclusions

In this paper, we have appreciated the important advances in understanding hippocampal computations made by many investigators (Marr, 1971; O'Keefe and Nadel, 1978; McNaughton and Morris, 1987; O'Keefe, 1990; McClelland et al., 1995; McNaughton et al., 1996; Samsonovich and McNaughton, 1997; Hasselmo and Giocomo, 2006; McNaughton et al., 2006; Colgin et al., 2010; Hasselmo and Sarter, 2011; Yassa and Stark, 2011; Newman et al., 2012; Yartsev and Ulanovsky, 2013; Neunuebel and Knierim, 2014; Moser et al., 2017; Bicanski and Burgess, 2018; Garcia and Buffalo, 2020; McClelland et al., 2020; Farzanfar et al., 2023; Jeffery, 2023). Against that background, starting with computational hypotheses (Rolls, 1987, 1989b, a, c), we developed a quantitative theory of the storage of information in the hippocampus and its later recall to the neocortex (Rolls and Treves, 1994; Treves and Rolls, 1994). Now, approximately 30 years on, in this paper we have presented updates to this theory, which remains the only quantitative theory of the storage of information in the hippocampus and its later recall to the neocortex.

Key areas for future research identified as a result of what is presented here include:

1. What is the number of synapses on each human CA3 neuron devoted to recurrent collateral connections, which is important to know as this with the sparseness of the representation is the key parameter that sets the memory capacity of the hippocampal memory system (Eq. 1)?
2. What is the capacity of an attractor network such as CA3 when it combines continuous spatial and discrete object or reward

representations (Fig. 3a)? This is important to know, for analytic approaches have so far focussed on either discrete or continuous spatial representations (but see del Prete and Treves (2002)), and it may be that the combination of discrete and spatial representations helps to lift the system out of the reduction in capacity produced by purely spatial representations. From a computational perspective, it would be important to estimate the number of representations that could be stored in an attractor network when some of the information is discrete (e.g. objects), and some is continuous (e.g. spatial). As a reference, with typical values of sparseness, the number of discrete memories that can be stored in the CA3 hippocampal network is approximately equal to the number of recurrent collateral connections per neuron (Eq. 1), which in the rat is approximately equal to 12000 (Fig. 2).

3. Tests of the new theory that the 'Where' spatial view representations in primates including humans are built not by the parietal cortex, but instead by a ventromedial visual cortical stream that utilises feature combinations to build scene feature neurons in a way analogous to object representation building in the ventrolateral visual stream (Rolls, 2021a, 2023c). In this stream, what exactly are the spatial coordinates used in the retrosplenial scene cortex, and what is their relation to dorsal stream networks leading to parietal regions in which coordinate frameworks are changed towards allocentric representations (Rolls, 2020)?
4. Given the discoveries in primates including humans of spatial view cells, what is the role of landmarks in primate including human navigation, in contrast to the self-motion blind update of place representations found in rodents on which some theories of navigation are based?
5. The representations provided by parahippocampal spatial view neurons are allocentric in that they depend on where the individual looks in the scene independently of eye position and head direction and place where the individual is located, but what happens when the individual goes behind the scene, and the egocentric left/right framework becomes reversed (Rolls, 2023d, c)?
6. A new development is the theory that reward value, input to the hippocampus from the human orbitofrontal cortex, is important in memory consolidation, in part via the cholinergic pathways. Further evidence on the importance of these value-based mechanisms in human memory consolidation, and potentially in changes in memory in aging and amnesia related to these mechanisms, will be important.

CRedit authorship contribution statement

Edmund T Rolls: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alessandro Treves:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

None

Data Availability

No data was used for the research described in the article.

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Appendix A. Supporting information

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