



Review article

The memory systems of the human brain and generative artificial intelligence

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ABSTRACT

Generative Artificial Intelligence foundation models (for example Generative Pre-trained Transformer – GPT – models) can generate the next token given a sequence of tokens. How can this ‘generative AI’ be compared with the ‘real’ intelligence of the human brain, when for example a human generates a whole memory in response to an incomplete retrieval cue, and then generates further prospective thoughts? Here these two types of generative intelligence, artificial in machines and real in the human brain are compared, and it is shown how when whole memories are generated by hippocampal recall in response to an incomplete retrieval cue, what the human brain computes, and how it computes it, are very different from generative AI. Key differences are the use of local associative learning rules in the hippocampal memory system, and of non-local backpropagation of error learning in AI. Indeed, it is argued that the whole operation of the human brain is performed computationally very differently to what is implemented in generative AI. Moreover, it is emphasized that the primate including human hippocampal system includes computations about spatial view and where objects and people are in scenes, whereas in rodents the emphasis is on place cells and path integration by movements between places. This comparison with generative memory and processing in the human brain has interesting implications for the further development of generative AI and for neuroscience research.

1. Introduction

A key interdisciplinary research area at present is the relation between the brain and generative AI: how similar are their computations? One aim of this paper is to describe the computations that take place in the human brain when a whole memory of a past recent episode is recalled from a partial retrieval cue, and to compare this with the computations made in generative AI when it generates an answer to a question about what happened recently. Given the major differences in the way in which the computations are performed, a second aim is to consider some implications for generative AI in the future. The evidence about the operation of the hippocampus is based on evidence available in humans and other primates, which shows that locations being viewed in spatial scenes are important in the spatial representations, and how the locations of objects and people in spatial scenes are important in human episodic memory [1–3]. This is in contrast to modelling of what is found in rodents, which considers rodent place cells and path

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integration between places [4–11]. The reasons for this paper are thus to consider similarities and differences between what is computed in the human brain and in generative AI models, taking as an example the generation in humans of a whole memory when a part of it is provided as a recall cue [1–3]. Key differences are the use of local learning rules with the information available in the presynaptic and postsynaptic rates in the hippocampal-neocortex system for the storage and recall of episodic memory, whereas in AI, deep learning is involved which makes the details of the operation of the system more opaque [2]. Given what can be achieved by the human brain, there are implications for AI systems of the future.

2. Generative AI

Generative AI is generative in the sense that given some sequence of input tokens, it can generate the next token [12]. A token might be a word, and this approach can be used for natural language processing, for example in Chat GPT-4 (openai.com). These Foundation Models do this by being trained on enormous datasets, of for example text, and from all these exemplars can estimate a likely next token given the sequence of input tokens that they have just been given [12]. The answers provided by generative AI may thus not be the correct answer to a question asked in the input sequence, but are based on the process just described. What is provided is just the most likely next token given all the text etc on which the network was trained. Given its vast amount of training data, the AI network may form a compressed representation of all its training data such that the compressed representation may include commonalities extracted from different examples in the training data [12]. Details of the many variations of the methods used in generative AI, and of

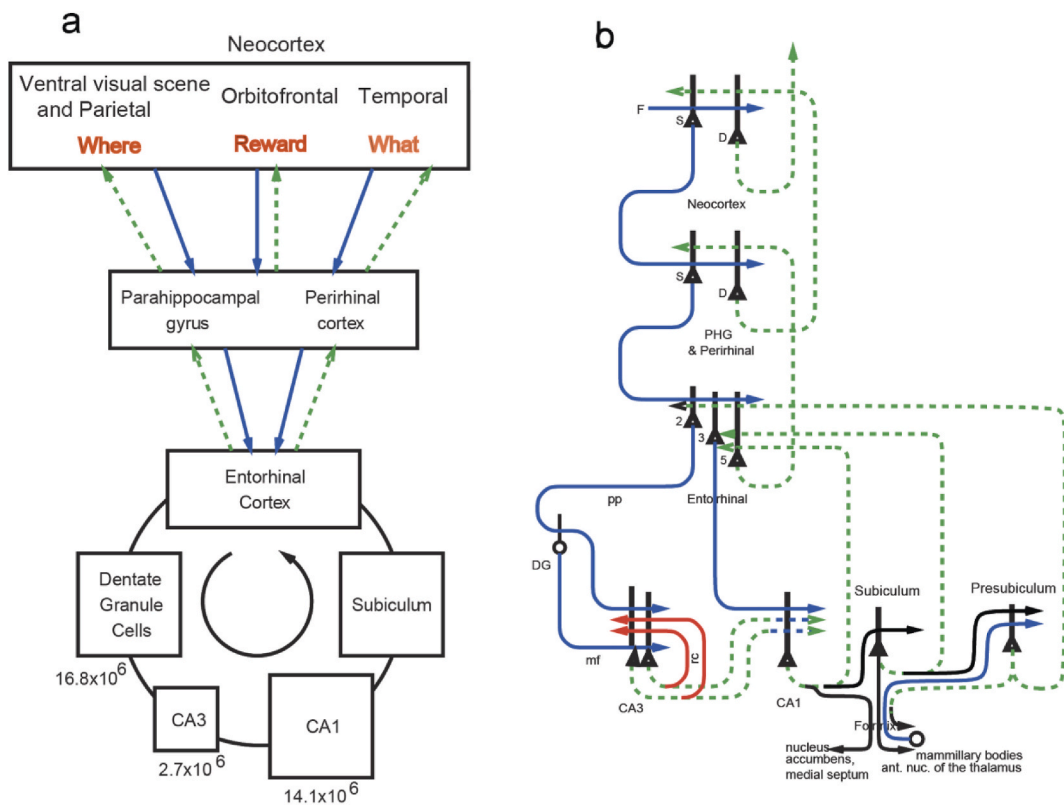


Fig. 1. The human/primate hippocampus receives neocortical input connections (blue) not only from the ‘what’ temporal lobe and ‘where’ parietal and ventral visual scene areas, but also from the ‘reward’ prefrontal cortex areas (orbitofrontal cortex, vmPFC, and anterior cingulate cortex) for episodic memory storage; and has return backprojections (green) to the same neocortical areas for memory recall. There is great convergence via the parahippocampal gyrus, perirhinal cortex, and dentate gyrus in the forward connections down to the single network implemented in the CA3 pyramidal cells, which have a highly developed recurrent collateral system (red) to implement an attractor episodic memory by associating the what, where and reward components of an episodic memory. **a:** Block diagram. **b:** Some of the principal excitatory neurons and their connections in the pathways. Time and temporal order are also important in episodic memory, and may be computed in the entorhinal-hippocampal circuitry [30]. 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 [87] are shown in (a), and indicate very many dentate granule cells, consistent with expansion encoding and the production of sparse uncorrelated representations prior to CA3 [88,89]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the equations used that require deep learning by error backpropagation, are easily available [10,12].

3. Generative AI compared to the generation by the human hippocampal memory system of a complete memory from a partial retrieval cue

It is of great interest to compare this Generative AI with generative processing in the brain, as this is likely to advance our understanding of Generative AI and of brain function. The example of brain function chosen for this comparison is the memory system, in which an incomplete memory retrieval cue is provided, and the brain then generates the rest of the memory. An example is that when provided with a memory retrieval cue, for example a question of who was present at dinner yesterday, the brain can then generate recall of the whole memory of this episode including who was present, where the dinner was, what the discussion was about, and how delicious the food was. The episodic memory system is chosen for the comparison not only because it can generate from a retrieval cue, but also because there is much evidence about the neuronal network computations in the hippocampal episodic memory system, and the ability of the hippocampus to recall whole memories to the neocortex [1–3,13–18]. In this paper, the term ‘prompt’ is used to refer to a linguistic input for generative AI, such as a query question.

The operation of the human hippocampal system for episodic memory can be described with the help of the brain connectivity illustrated in Fig. 1a and b. An episodic memory typically combines in the hippocampus information from the ‘What’ cortical systems (e.g. about objects or individual people), from ‘Where’ cortical systems about the location of the event, and about the Reward or emotional value of the event [2,3,19]. There may also be some information about the sequence of particular events in an episodic memory, such as who arrived after whom for dinner, and the order in which items may have been discussed [20].

For episodic memory, the memory of particular events or episodes, the neocortical representations of ‘what’ (objects, people, represented in the anterior temporal lobe [18]), ‘where’ (viewed spatial location, in scene regions in the ventromedial visual stream [1, 16,18]), and reward value (in the orbitofrontal cortex [2,21,22]) in different parts of the neocortex, reach the hippocampal system (dentate, CA3 and CA1) via the perirhinal, parahippocampal, and entorhinal cortex (Fig. 1a and b). The neocortical information representations typically involve semantic information, such as who knows whom, many of the attributes of each person or object, and schemas of for example what is likely to happen at a dinner party [2,23].

In the hippocampal system circuitry, the (‘standard’ [2,3,15,24]) theory is that the dentate granule cells perform pattern separation on the inputs to make them less correlated with previous inputs (to reduce interference between different episodic memories); the CA3 recurrent associative connectivity operates as an attractor network to associate the ‘what’, ‘where’ and reward inputs currently being received; and the CA1 network prepares a compressed representation for the return pathways back to the neocortex (green in Fig. 1) [2, 15,25,26]. During storage of the episodic memory, these backprojections to the neocortex will be active, and can be associated by pattern association learning with whichever neocortical neurons are firing [2,3,15,26]. During recall of the episodic memory, just part of the episode may be presented, such as ‘what’ information about who was present, the CA3 network operating as an attractor network performs completion and recalls the other components of the episode memory (‘where’ and reward value), and all parts of the memory can be reinstated in different parts (‘what’, ‘where’ and reward) of the neocortex by the associatively modified backprojection synapses onto neocortical neurons [2,3,15,17,25,26]. A property of hippocampal activity is that some neurons are ‘time cells’ that fire at particular times in a fixed sequence [27–30]. Associating items such as objects, places, or reward onto these time cells may provide a way of remembering the order of events within an episodic memory [2,3,20].

A key property of all the computations just described for the neocortical-hippocampal system for the storage and recall of episodic memories is that the key computations are performed by autoassociation (/attractor) networks and by pattern association networks, in which the learning rules are associative and local, i.e. depend on the presynaptic and postsynaptic firing rates [2,3,15,17]. The whole theory is quantitative and analytic using for example approaches developed in theoretical physics [2,3,15,31–34], and has been tested numerically [2,17]. In contrast, the AI approach relies on very different computations, with backpropagation of errors in a hierarchy for which there is no clear architecture or biologically plausible mechanism provided in the brain [2]. An implication is that there may be much to learn from the brain that is relevant to AI, for the human brain solves many complex problems in different ways to those used in current AI.

It is important in understanding the hippocampo-cortical memory system in humans and other primates that what it encodes for memories and navigation is very different from the neuronal representation by ‘place’ cells found in the rodent hippocampus of the place where the individual is located [4,5,35–39]. In contrast, in primates the predominant spatial representation in the hippocampus and parahippocampal cortex is provided by spatial view neurons that code for the location ‘out there’ where the primate or human is looking in space [1,2,40–44]. This discovery, together with much recent evidence from primates [45–49] and humans [50–52] (see the Special Issue of Hippocampus, May 2023), is leading to a revolution in our understanding of hippocampal function in primates including humans, in that this allows memories to be formed of where people and objects are in spatial scenes even though the viewer may never have visited the places being viewed. This is prototypical of human memory, and means that hippocampo-neocortical function as we now understand it is highly relevant to understanding human generative memory brain systems [1,2,40].

Now we can consider whether parts of this hippocampo-neocortical process involved in the retrieval of episodic memories might be described as ‘generative’.

First, the hippocampo-cortical memory recall process is generative in the sense that when prompted with a partial cue for memory retrieval, the whole memory of the episode can then be generated using completion in the CA3 attractor network in the hippocampus, and then recall back to the neocortex. An example is that given the ‘where’ retrieval cue of a dinner that took place in College the previous evening, that retrieval cue leads to recall of ‘what’ information, such as who was present, and what was discussed. That generative outcome has similarities with generative AI.

Second, insofar as hippocampal circuitry may help with sequence memory using time cells as just described, the hippocampus could enable recall of items back to the neocortex in the temporal order in which they originally occurred, up to the last item in the previously stored sequence, and there is evidence that the hippocampus performs this sequence functionality for places and for objects [20]. Thus if only the first item in the sequence is presented to the human as a recall cue, the human could generate the remaining items in the sequence, and thus in the generative AI sense [12], would be generating the next item or items, given the recall cue that consists of an earlier item in the sequence.

Third, the hippocampo-neocortical system might appear to be different from generative AI, in that if the human system was acting as an episodic memory retrieval system for a particular event, it would recall only exactly what was stored for that particular event, and this might be different from generative AI, which may utilize information learned as a result of many different training examples [12]. But what is stored in the neocortical regions accessed by the hippocampal memory system (anterior temporal lobe for ‘what’ information; medial temporal lobe for ‘where’ information; and orbitofrontal cortex for reward value information [2]), is, as described above, semantic, in that it includes many attributes of people, objects, etc. Given the stochastic dynamics of memory operations in the brain [2,17,53–55], the exact information recalled in the neocortex may not be exactly what was stored. Moreover, what is recalled in the neocortex may be influenced by the semantic structure of the information stored in the neocortex, and that may influence exactly what is present in the recalled neocortical representation. For example, if two of the people in the recalled episodic memory had never been on the same continent previously, that might make the neocortical memory difficult to activate for those two persons together, but easy to activate for one of the people and a second person strongly associated with the first person, resulting in recall of a memory that better might fit the existing semantic structures in the neocortex. Thus in human episodic memory recall, existing semantic knowledge may influence exactly what is generated next in recall, and this is analogous to the situation with generative AI.

In this sense, existing schemas in human semantic neocortical memory may influence what is recalled [2]. Perhaps we could think of some generative AI systems as containing ‘schemas’ due to their vast training that is likely to result in similar sequences of tokens being compressed together. Such a schema might be a doctor’s surgery, in which there would be many elements and events that might be likely to happen in common between different doctor’s surgeries.

Fourth, once an episodic memory has been retrieved to neocortex, it may be rehearsed and thought about more within the neocortical semantic networks [2,17,23], which may in turn modify so that they incorporate information retrieved from an episode, such as modification to neocortical autobiographical semantic memory about interesting discussions held at a particular scientific conference. In this way, the episodic memory may lead to the generation of new semantic representations in the brain [2]. That is something that is much more difficult for generative AI, in that the information trained into GPT-4 was correct in 2021, and when the information needs to be updated with new data, the process is very time-consuming, costly, and compute-intensive [12].

Fifth, after an episodic memory has been retrieved using the hippocampus to neocortex backprojection retrieval pathways (green in Fig. 1), the planning and imagining systems in cortical regions such as the prefrontal cortex that utilize attractor networks [2] can become active [56,57], and can be triggered into thinking about the possible implications for the future of the recalled information. These are neocortical mechanisms that contribute to prospective memory [58] after recall using the hippocampo-neocortical connections (Fig. 1). Prospective memory involves the use of information from the past and the present to generate predictions about the future [58], may be implemented by the network mechanisms referred to here [2], and is inherently constructive [59,60].

Sixth, the human brain appears to use several separate types of memory system, a neocortical long-term memory for semantic representations based on previous experience, and a hippocampal system for episodic memory [2,3,13,14]. This enables real-time collection of new memories about particular events in the hippocampal system, separate from long-term semantic memory which though may gradually benefit from what has been learned from episodic events. In addition, there are several short-term memory systems in the human brain [2]. These are not properties of generative AI systems, which might benefit from these different types of architecture and memory systems.

We thus see many differences in kind between what is implemented in generative AI with its implementation of an ability to predict the next token, and the mechanisms in the brain that are triggered by memory recall to lead to prospective thinking and also creativity. Creativity in the brain is supported by probabilistic computations triggered by the almost random timing of neuronal action potentials that generate ‘noise’ in the brain and facilitate jumping to new locations in the energy landscape making the operation of the human brain probabilistic [53,61–65]. Moreover, thoughts about thoughts, and in particular higher order syntactic thoughts, may be useful in correcting mistakes in human thinking, to improve creativity by selecting useful new ideas generated by the stochastic dynamics of the brain [2,66,67]. Generative AI has been described as ‘stochastic parroting’ [68], in that it predicts the next item based on an agglomeration of vast training of sequences, though perhaps it does more than stochastic parroting [69]. In contrast, in humans there is continuous updating of the semantic system that in part utilizes the hippocampal episodic memory system; what is recalled from the hippocampal episodic memory system can be influenced by what is already in the neocortical semantic memory system; and once the information is recalled to the neocortex then neocortical processing can perform logical, spatial, and reasoning operations at which generative AI systems can notoriously fail, because they are parroting [70].

4. AI-based approaches to understanding hippocampal memory function

There have been some generative AI approaches to understanding hippocampal function [6–10]. However, these have involved models of place cells found in rodents, and self-motion update of place representations to generate maps. One problem is that place cells, which encode where the individual is located, are the predominant spatial representation in the rodent hippocampus [4,5,35–39]. In contrast, in primates the predominant spatial representation in the hippocampus and parahippocampal cortex is provided by spatial view neurons that code for the location ‘out there’ where the primate or human is looking in space [1,2,40–44]. This

discovery is supported by much recent evidence from primates [45–49] and humans [50–52]. Thus these AI-based studies do not address what is found in the hippocampus of humans and other primates, or the generation of a whole memory from any part in the human hippocampal memory system. A second problem is that these AI-based approaches to understanding hippocampal function rely on deep learning, so are likely to not be biologically plausible (see below and [2]).

Another approach has been a hybrid approach [71], using a relatively standard biologically plausible neuronal network approach to modelling the hippocampus that includes an autoassociation network [3,15,17], implemented with a modern Hopfield network [72], but combining this with generative models (variational autoencoders) for the connectivity between the neocortex and the hippocampus. A problem again with this approach is that the generative autoencoder requires deep learning, and is impenetrable in exactly what is computed at different levels of the network [2,73].

5. Implications

The differences in what is being computed in the neocortex and how it is computed [2] vs in generative AI [10,12] have clear implications for the design of future AI machines, and for understanding the great differences between generative computations in the brain and generative AI.

First, generative AI algorithms, and approaches to understanding hippocampal function using them [6–10], use backpropagation of error, which seems physiologically implausible for there is no generally accepted way understood by which the appropriate errors for every neuron at every level of a cortical hierarchy could be fed back to update all the synaptic weights. The connections and operation of the cerebral cortex do not seem to support backpropagation error learning, but instead learning does occur using local learning rules [2].

Second, deep learning does not provide reasoned explanations for how it reached its answers and is somewhat impenetrable in that it cannot explain the particular evidence by which it produced a particular result [73], whereas humans are able to provide reasoned arguments for their choices. Indeed humans can think about their own thoughts, and this may be helpful in correcting errors in first order thoughts [66], and that is a process that needs development in AI.

Third, generating creative thoughts in the brain may involve stochastic jumping to nearby parts of a semantic space driven by the stochastic nature of neuronal spike timing in the brain which is close to Poisson [2,53,62], and generative AI is not naturally creative, for it aims to generate the next most likely token in a sequence given its previous training.

Fourth, it has been argued that predictive coding and active inference are key properties of the human brain [74–79], and this is different from generative AI.

Fifth, the power of learning by error backpropagation and the multiple parameters by which the learning can be optimized make it possible to mimic properties of what is found in the brain, for example neuronal activity in the inferior temporal visual cortex [80–83], but this does not mean that we understand better what computations are being performed and how they are performed in the brain. This is partly because exactly what is learned in deep learning is somewhat impenetrable [73], and partly because the brain probably does not implement backpropagation error learning in deep networks but computes by different principles [2,84–86].

Data availability statement

No new data were collected as this is a review paper.

Ethics statement

No new data were collected as this is a review paper.

CRediT authorship contribution statement

Edmund T. Rolls: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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