The Opportunistic PFC: Downstream Modulation of a Hippocampus-inspired Network is Optimal for Contextual Memory Recall

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Abstract

Episodic memory serves as a store of individual experiences and allows for flexible adaptation to environment volatility and goal changes. The selection of episodic memories to recall is often considered to be driven by external sensory cues. Experimental studies suggest that this process is also influenced by internal cues, and that projections from the medial prefrontal cortex to the hippocampus play a role in this contextual modulation. In order to make sense of the biological configuration of prefrontal-to-hippocampus connectivity, we investigate the effectiveness of modulating various layers of a hippocampus-inspired neural network in a contextual memory task. Our results reveal that providing context information to the most downstream regions (i.e. last layers) of the model leads to better performance. In addition, the best average performance is obtained when contextual connections target the regions corresponding to the biological subfields that receive information from the prefrontal cortex, which provides a normative account of the biological connectivity. We relate this work to the need for augmenting reinforcement learning with flexible episodic memory. We make the code available at `https://github.com/HugoChateauLaurent/opportunistic-PFC`.

1   Introduction

Episodic memory is our ability to store and recall memories along with their spatiotemporal context of acquisition. Information about what, when and where events happened in the past can be retrieved and used to make decisions in the present. This cognitive function contrasts with the formation of semantic memories which are decontextualized and cached for efficient use [6]. While heavy inspiration has been drawn from semantic memory to develop deep learning algorithms, artificial agents most often lack episodic memory, and more generally explicit memory, despite their forecasted potential to improve sample efficiency and flexibility [7, 15, 19]. In order to guide behavior efficiently, recalled memories should be relevant to the current situation. More precisely, the memory selection process should be influenced by both contextual and sensory information. In contrast to the information that is directly accessible to the agent through its perception of the environment, contextual information encompasses any internal representation that is not directly perceptible, but is susceptible to help the agent predict future rewards and states. This includes information about the temporal unfolding of events, spatial integration, but also the goals pursued by the agent. Numerous studies have shown the influence of temporal (e.g. [13, 31, 17]), spatial (e.g. [11, 21, 22]), semantic (also investigated in [11]), and goal [1] factors on episodic memory.

The most influential theory of stimulus-driven memory recall states that the hippocampus is able to perform pattern completion on partial and noisy cues by implementing attractor dynamics through recurrent connections in area CA3 [27] (but see [8] for an alternative account in which CA1 performs pattern completion and CA3 learns sequences). With this process, memories to be recalled are those that share similarities with current sensory observations, or in other words, those with the closest attractor. Interestingly, stimulus-driven episodic recall has been implemented in a Neural Episodic Control architecture [24] and shown to improve sample efficiency of classical deep reinforcement learning algorithms. In this study, a Differentiable Neural Dictionary was used to store episodes while the network was playing Atari games, and similarity with the situation faced by the agent was used as a criterion for selecting episodes to recall.

While stimulus-driven retrieval has been studied both empirically and theoretically, much less is known about the contextual modulation of episodic recall. We believe that a better comprehension of the mechanisms involved is necessary to develop a complete theory of episodic memory, but also to develop machine learning algorithms that can comprehend a wider variety of spatiotemporal contexts and direct their behavior towards internal goals. More precisely, synergy between episodic memory and contextual control could yield significant improvements over algorithms that use context alone (e.g. [29, 5, 14, 25, 4]) in terms of sample and parameter efficiency. It is worth noting that Neural Episodic Control [24] was later extended to include a LSTM-based working memory which arguably represents some sort of contextual information and influences episodic recall [12]. Other related works include model-based episodic learning [18], episodic meta learning [20, 26], separate retrieval mechanisms [16], and so on. Yet, this line of machine learning research is largely disconnected from the biology.

Experiments suggest that the prefrontal cortex (PFC) and prefrontal-hippocampal interactions play an important role in this function [2, 10, 17, 21, 22]. In comparison with sensory cortices, PFC is connected to the hippocampus through many pathways (see [10] for a review). Just as sensory information, information represented in PFC reaches the hippocampus through superficial layers of the entorhinal cortex (EC). PFC also directly projects to deeper layers of the EC. In addition, PFC is connected to the dentate gyrus and CA1 through the supramammillary and reuniens nuclei respectively. Strikingly, there seems to be no pathway connecting PFC and CA3 [3].

In a modeling study similar to ours [23], contextual information was fed to the dentate gyrus to modulate recall, but other prefrontal-to-hippocampus pathways were not considered. Here, we address the question of why PFC targets the hippocampus the way it does, by investigating the effectiveness of potential PFC-hippocampus configurations in a neural network performing a contextual memory task. First, we evaluate the added benefit of providing context at intermediate layers of the network over providing it to the input layer along sensory observations. Second, we test the hypothesis that more downstream modulations (targeting CA1 and the output portion of EC) are more efficient.

2 Methods

2.1 Task

Like the model of [23], our model performed the rodent task described in [21, 22]. Eight object-discrimination problems presented in two different contexts were used to evaluate context-guided memory recall. In a given task $t_i(i = 1, ..., 8)$ and context c, the network learned to choose a rewarded object $R_{i,c}$ over a non-rewarded object $\bar{R}_{i,c}$. In the alternative context c', it learned to choose between the same objects as in context c, except that the non-rewarded object in context c was rewarded in c', and conversely (i.e. $\bar{R}_i^c = R_i^{c'}$ and $R_i^c = \bar{R}_i^{c'}$). As in [23], objects were represented in the network as 6×4 matrices with 6 active entries of value 1 placed at random locations, and other entries with value 0 (fig. 1, table 1).

2.2 Model

The hippocampus model is a 6-layered fully-connected neural network which follows the anatomy of the biological medial temporal lobe. Information flow corresponds to the trisynaptic pathway: Input $\rightarrow EC_{in} \rightarrow DG \rightarrow CA3 \rightarrow CA1 \rightarrow EC_{out} \rightarrow$ Output. The number of neurons in each region is set as the number of neurons in the analog rat region, as retrieved from [9], scaled down by a factor N (see table 2). The network input consists of three pattern slots: two for the objects to choose between

2

Table 1: Input summary. The "Objects" input size corresponds to the product of the number, width and height of input patterns.

Input	Size
Context	2
Objects	$3 \times 6 \times 4$

Table 2: Network summary.

Layer	Output size	Function
EC_{in}	$1.1 \times 10^5 N$	ReLU
DG	$12 \times 10^5 N$	ReLU
CA3	$2.5 \times 10^5 N$	ReLU
CA1	$3.9 \times 10^5 N$	ReLU
EC_{out}	$3.3 \times 10^5 N$	ReLU
Output	$3 \times 6 \times 4$	sigmoid

and one for the rewarded object (table 1). The assignment of R_i^c and $\bar{R}_i^c$ to the first or second slot is random. ReLU was used as the activation function of hidden layers and sigmoid was used in the output layer to map latent activity back to the pattern space (table 2). An additional input was used to modulate different layers of the hippocampal network contextually. It represents the two possible contexts as a 2D one-hot vector. Note that the output layer was never modulated, since it does not model a medial temporal lobe region. CA3 was recurrently connected to store memories. We used the following hebbian rule to update its recurrent weights:

$$\mathbf{M}_t = \lambda \mathbf{M}_{t-1} + \eta \mathbf{CA3}_t \mathbf{CA3}_t^T \tag{1}$$

where $\mathbf{CA3}_t$ is the result of the DG-to-CA3 connection (i.e. before recurrent processing). λ and η respectively denote the rates of forgetting and remembering. During both training and test phases, a single iteration of an attractor network similar to that of [4] and [30] was used for memory retrieval. It yielded a new vector, $\mathbf{CA3}_t^r$, to be passed to the next layer CA1:

$$\mathbf{CA3}_t^r = \text{ReLU}(\kappa \mathbf{CA3}_t + \mathbf{M}_{t-1} \mathbf{CA3}_t) \tag{2}$$

where κ is a decay term.

2.3 Training and hyperparameterization

All task-context combinations were presented once during each epoch, in random order. Similarly to the recently proposed autoencoder model of the hippocampus [28], the network learned to output its input, namely the two input object patterns and the rewarded one. Thus, the loss function to be minimized was the mean squared error between the input and the output. Learning was online, as training examples were presented one by one. The rewarded pattern was provided as input to the network during training, but was masked during test (i.e. values of the third input slot were set to 0). In the test phases, a trial was considered correct when the pattern stored in the third slot of the output was closer to the rewarded pattern than the non-rewarded one, as assessed by the mean squared error. Unless otherwise mentioned, networks were trained during 100 epochs, and hyperparameters were selected randomly to ensure robustness of the results. These include N, the learning rate, κ, λ and η. The same hyperparameterization was shared along configurations of modulated layers to allow for the use of paired difference statistical tests.

3 Results

Performance was evaluated according to which layers were modulated by contextual information (fig. 2, left panel). The depth of the layer receiving contextual input (ranging from $EC_{in} : 1$ to $EC_{out} : 5$) positively correlated with performance (Spearman's $r(1250) = .34, p < .001$). Wilcoxon Signed-ranks tests indicated that performance was significantly lower when context was provided to EC_{in} (Median $= 66.88\%$) than when provided to DG (Median $= 78.16\%, z = -4.28, p < .001$), CA3 (Median $= 82.88\%, z = -5.98, p < .001$), CA1 (Median $= 84.97\%, z = -8.67, p < .001$) or EC_{out} (Median $= 85.66\%, z = -9.54, p < .001$). Modulating either CA1 (Median $= 84.97\%$) or EC_{out} (Median $= 85.66\%$) gave the best results, and did not differ significantly ($p = .29$). We then tested whether the effects of modulating individual layers would add up when multiple layers received contextual information. We found that modulating both CA1 and EC_{out} was more efficient (Median $= 89.97\%$) than modulating CA1 (Median $= 84.97\%, z = -3.44, p < .001$) or EC_{out} (Median $= 85.66\%, z = -2.39, p < .01$) individually (fig. 2, right). We investigated the relationship between
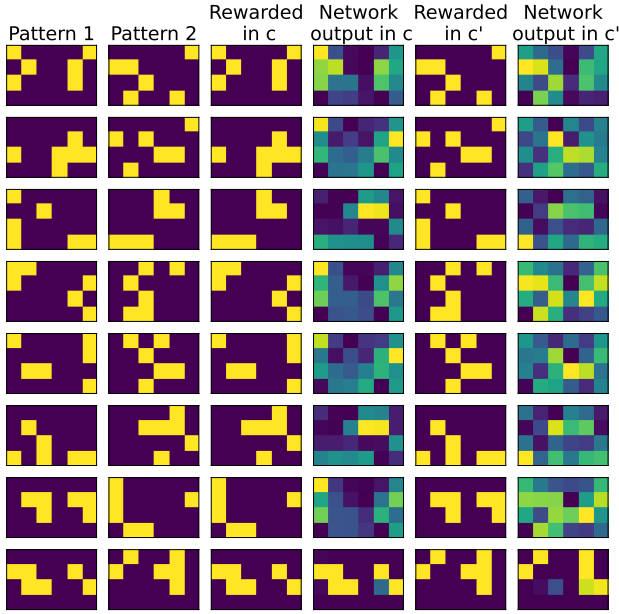
Figure 1: Example series of eight tasks. Here, the network was trained during 1000 epochs and parameterized with $N = .001$, a learning rate of $10^{-4.5}$, and $\kappa = \eta = \lambda = .5$. The output shown was taken from the test phase.
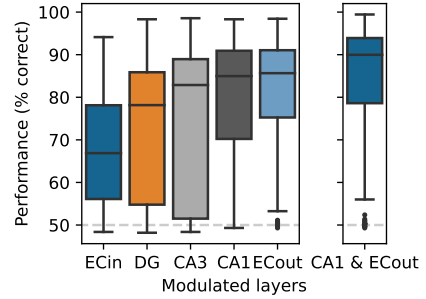

Figure 2: Recall performance when different layers are contextually modulated.
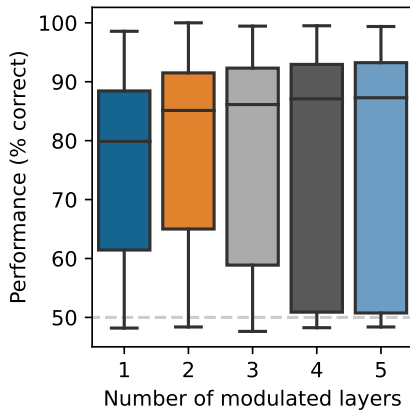

Figure 3: Recall performance when a different number of layers is contextually modulated.
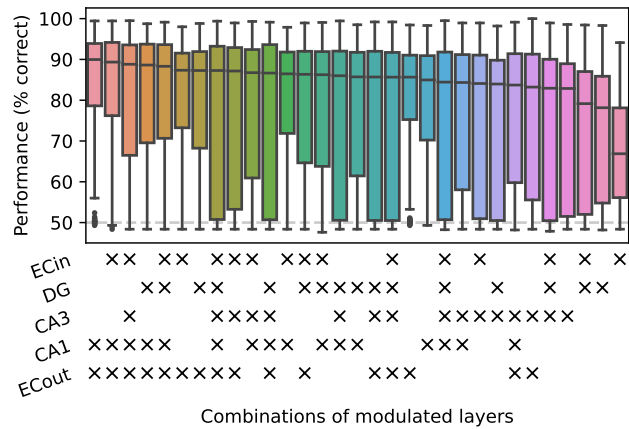

Figure 4: Recall performance of all possible modulatory configurations, ordered by their median.

4

the number of modulated layers and performance by generating all possible combinations of targeted layers. As shown in figure 3, the relationship was weakly positive (Spearman's $r(7750) = .08$, $p < .001$), and seemed to stagnate when more than 2 layers received contextual information. In fact, Mann-Whitney U tests revealed that while modulating two layers was significantly more efficient (Median $= 85.13\%$) than modulating one (Median $= 79.88\%$, $U = 1,365,367$, $p < .001$), modulating five (Median $= 87.28\%$) did not yield significantly better results than modulating two (Median $= 85.13\%$, $U = 292,927$, $p = .05$).

Over all configurations, the best performance was obtained when CA1 and EC_{out} were simultaneously modulated (fig. 4), and the worst configuration was to modulate EC_{in} alone. Surprisingly, the second best configuration was to modulate EC_{in} in addition to CA1 and EC_{out}. We also noted that EC_{in} was more present than CA3 and DG in top configurations, and that CA3 was the least present.

4 Discussion

Our results provide support for a role of prefrontal projections to CA1 and deep layers of the EC in top-down control of memory retrieval. A general trend was that modulating the last layers was more efficient than modulating upstream layers, suggesting that PFC is opportunist and biases processing at the end of the information flow. The fact that PFC generally targets high-level sensory regions of the brain suggests that these results might extend to non-mnemonic cognitive control. Projections to superficial layers of the EC were found to be the most inefficient yet not significantly detrimental when accompanied by downstream modulation. On the contrary, projections to CA3 which seem to be absent in biology, or even to DG, were not found to be very efficient whether being alone or with other prefrontal projections. Results also indicate that feeding multiple layers with the same contextual information is not redundant for the network and can instead improve performance. Yet, the relationship between the number of modulated layers and performance does not seem to be straightforward, as adding more modulations did not necessarily improve performance and rather increased variance (fig. 3).

These preliminary results along with the study of [23] open up a new line of research dedicated to the understanding of controlled episodic memory using computational tools, with a focus on the hippocampus and PFC. For example, the model could be extended with a biologically motivated monosynaptic pathway (i.e. a shortcut connection from EC_{in} to CA1). Other tasks could also be considered to further disentangle the selective role of each prefrontal-hippocampal pathway. For example, the need for cognitive control could be increased by generating patterns with more spatial overlap. Sequence memory tasks could also be investigated. Interestingly, it has been reported that inactivating either the entorhinal or thalamic afferences from PFC led to qualitatively different sequence memory impairments [17]. We believe that this research avenue will yield significant improvements of episodic reinforcement learning algorithms, as simple stimulus-driven recall will be augmented with contextual cues, goal-directedness, and possibly sequence modeling.

Acknowledgements

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