A hippocampal-parietal network for map to action transformation

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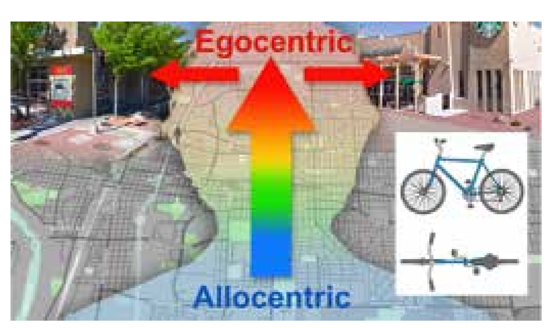
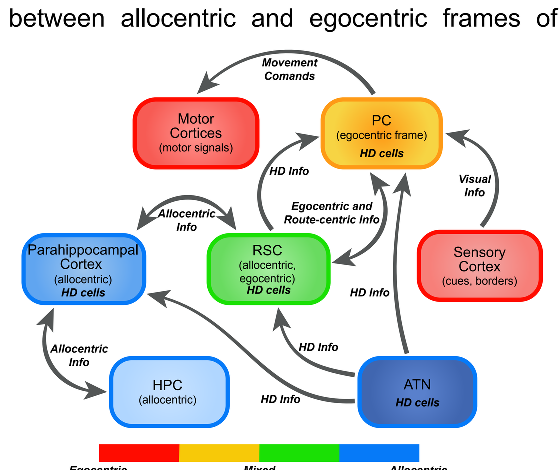
Introduction

In order to survive, animals, including humans, must be able to guide themselves through space and establish enduring memories of these experiences. To navigate in space, animals can reference distant landmarks such as lakes and buildings, which is called an allocentric or viewer-independent frame of reference (i.e., north, south, etc.) [1]; they can also reference their body orientation in relation to cues and make a sequence of actions to the target, which is called an egocentric, viewer-dependent, self-centered, or action-centered frame of reference (e.g., forward, left, etc.) [2]. Allocentric and egocentric frames of reference can interact such that allocentric information can be decoded to determine a subject's egocentric orientation and vice versa. For instance, when using navigating apps while driving, we may need to turn right as it is instructed facing west on the map. In other words, we need to understand that turning right and turning to the west are the same.

The neural representations of this allocentric-egocentric coordination is thought to include the parietal cortex (PC), anterior thalamic nuclei (ATN), hippocampus (HPC), retrosplenial (RSC), and parahippocampal regions [3, 4, 5]. The PC has been linked to the coding of actions and egocentric relationships with landmarks, but also allocentric representatons of space [4, 6, 7], while HPC neurons code for allocentric location [1, 8, 9]. It is hypothesized that the PC-HPC network operates as a system to transform the allocentric representations into egocentric representations and vice versa [3, 4, 10, 11]. Therefore, we set out to target two key nodes in this network, the PC, which contains mixed encoding, and the HPC, which contains predominantly allocentric encoding, while rats performed a task that requires interfacing between allocentric and egocentric frames of reference.

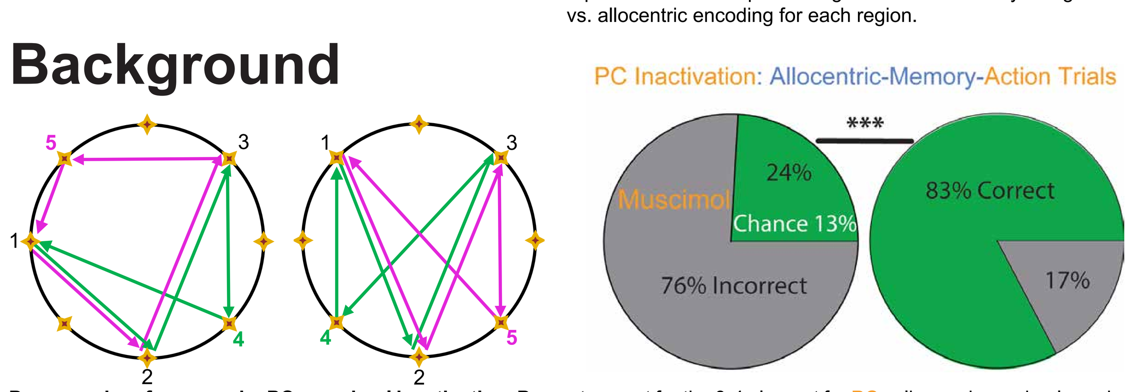


Coordination between allocentric (map-like) and body-centered (egocentric) frames of reference. Our brain maps our position in allocentric coordinates; however, our interactions with the world can be body-centered or egocentric by nature (e.g., turn right at a particular intersection). A fundamental problem is how these frames of reference interact. For example, the action taken at a common city intersection (turn left vs. turn right) is dependent on knowledge of a distant goal location and one's allocentric location in an environment (approaching from the north). Inset. Beyond navigation, object invariance is likely to involve interfacing between egocentric views of the object and allocentric knowledge of the complete object.



PC-HPC are anatomically and functionally well-positioned to interface between egocentric and allocentric frames of reference within a larger network. Illustration of anatomical and functional connectivity of reference frame processing by brain regions that comprise the extended PC-HPC network. HPC and para-hippocampal regions (entorhinal cortex, postsubiculum, and parasubiculum) encode an animal's position in space predominantly in allocentric coordinates. The PC interfaces between egocentric actions, and allocentric spatial and HD information. The HD signal is hypothesized to play a role in transforming between egocentric and allocentric encoding. The PC is centrally positioned within a larger brain network that includes medial temporal lobe regions such as the HPC, as well as motor cortex, sensory cortices, and the RSC. The box colors represent a colormap denoting the relative density of egocentric vs. allocentric encoding for each region.

Background



Decreased performance by PC muscimol inactivation. Percent correct for the 3-4 element for PC saline and muscimol sessions for data from two variations of the complex spatial sequence task. Muscimol infusion significantly impaired 3-4 performance versus saline. *** p<0.001 ***p<0.00001.

Methods

Animals:

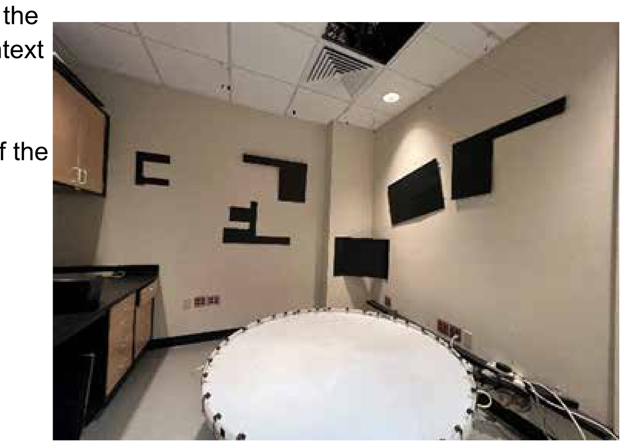
- Long-Evans (n=2) or Fisher-Brown Norway (n=4) rats were housed in a 12:12 hour light/dark cycle.
- Rats were either food deprived to 85% of baseline weight to motivate with Ensure as food rewards (n=1) or stimulation of the medial forebrain bundle as a reward (n=5).

Complex sequence task apparatus:

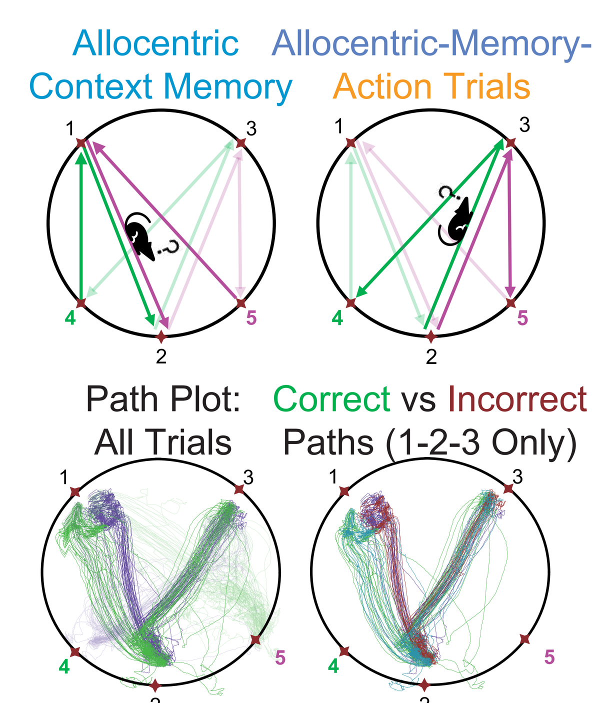
- Rats were trained on a large circular open field (1.5m diameter) with 32 light cues evenly distributed around the perimeter.
- Rats were trained to navigate to a series of spatial locations in a sequence, 1-2-3-4-1-2-3-5- to get rewards at each spatial location.
- Landmarks were distributed around the room for spatial orientation.

Complex sequence task:

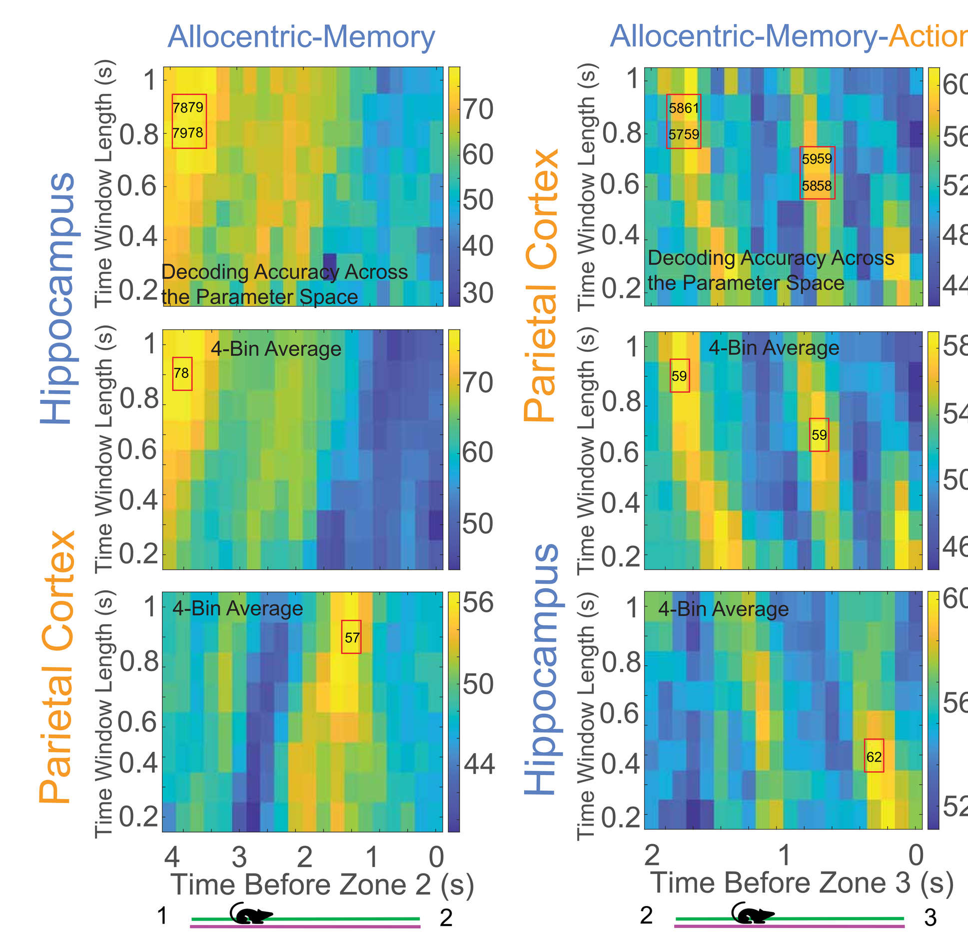
- The route is composed of a path sequence with a repeating element followed by a divergent path (1-2-3-4-1-2-3-5-).
- The repeating path segment (1-2-3) is followed by one of two distinct actions and therefore belongs to two spatial contexts. Thus, the rat must maintain a spatial allocentric context memory and translate the appropriate action for the context. Specifically, in context 5-1-2-3-4, the rat must go to 4 for reward, while in context 4-1-2-3-5 the rat must go to 5.
- The task is composed of alternating sets of trials in which the sequence is cued or non-cued (memory trials). Only memory trials are presented here. of each segment of the sequence.
- Recording and inactivation experiments begin when the rat achieves 70% correct on zone 4 and 5 (i.e., before the task has become highly repetitive).



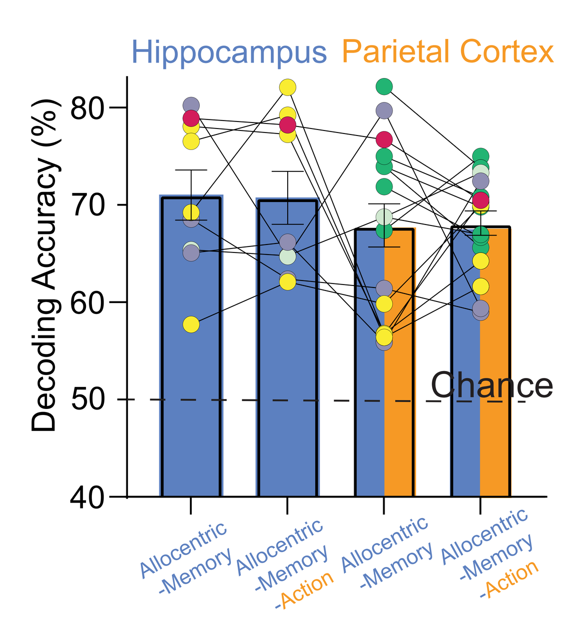
Results



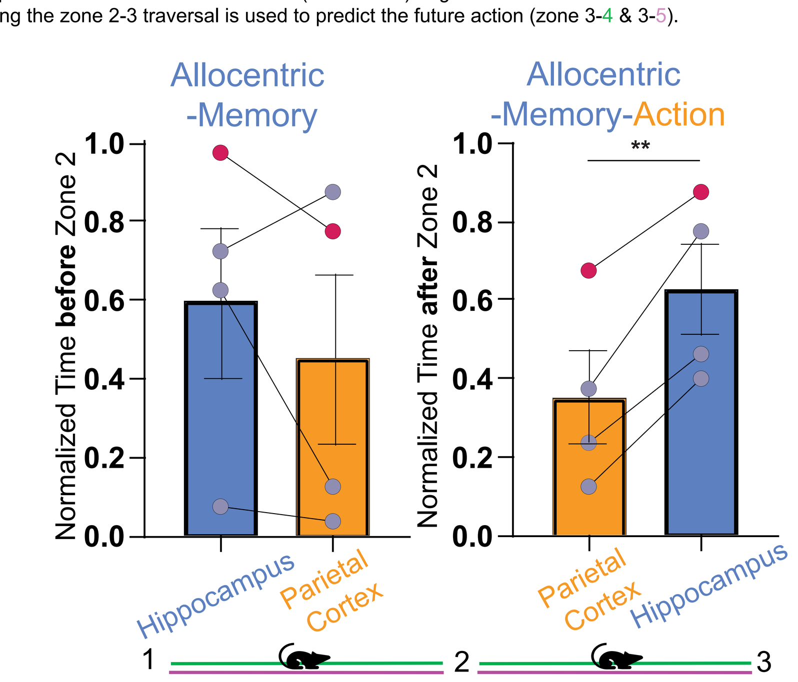
Complex Spatial Sequence Task. Schematic for the repeated elements sequence in the complex spatial sequence task. Zones are numbered clockwise starting at the top left. The rat always starts at zone 5 and continues to zones 1-2-3-4-1-2-3-5-. There are at least 2 critical components of this task. *Top Left.* When traversing through zones 1-2-3 the rat must keep track of its allocentric spatial context to coordinate the memory for the allocentric context with the correct egocentric action to reach zone 4 or 5 (*Top Right*). *Bottom Left.* Path plot for a single 50min session showing paths for the 1-2-3-4- and 1-2-3-5- segments of the task. Paths overlap for the 2-3 segment. Divergence at 1 caused by coming from 4 vs 5. *Bottom Right.* Same path plot but only for the 1-2-3 segment and color coded for correct vs incorrect trials. Paths on the 2-3 segment again completely overlap for correct vs. incorrect trials.



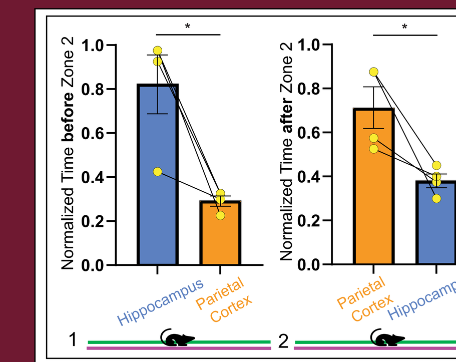
Example heatmaps of the decoding parameter space. We identified optimal decoding parameters for each data set, brain region, and decoding question. The time for which decoding is optimal varies between data sets, thus we used the peak in the parameter space to test the hypothesis that HPC-PC coordination is critical for transforming a remembered allocentric context into egocentric action. Each set of 4 adjacent bins is averaged to ensure that decoding accuracy represents a peak in this parameter space. *Left Column*. A model is built from HPC (*Top* & *Middle*) or PC (*Bottom*) cell activity during the zone 1-2 traversal to predict the place from which the rat had come (zone 4 or 5). *Right Column*. Same as the Left Column but cell activity during the zone 2-3 traversal is used to predict the future action (zone 3-4 & 3-5).



Decoding accuracy is high for PC and HPC for all decoding questions for all but one rat (yellow) which had lower decoding accuracy for PC **but not HPC.** Decoding accuracy for each data set for HPC (Left Bars) and PC (Right Bars). Decoding was accurate in predicting performance for both allocentric-memory and allocentric-memory-action trials. Average accuracies are shown as well as before-after differences across different datasets. Color coding of circles denotes rat identity and lines connect data sets (n = 16 data sets from 4 rats).

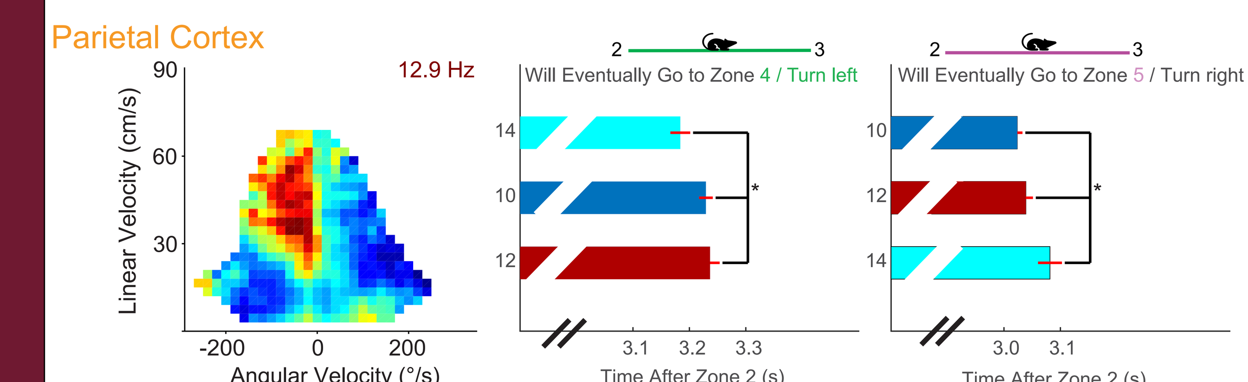


PC decoding peak follows HPC for allocentric memory but precedes HPC for decoding the upcoming action. *Left*. During allocentric-memory trials. HPC decoding peaks lead PC across 4 datasets in 3 rats. *Right*. During allocentric-memory-action trials. PC decoding peaks lead HPC across 4 datasets in 3 rats. Bottom.

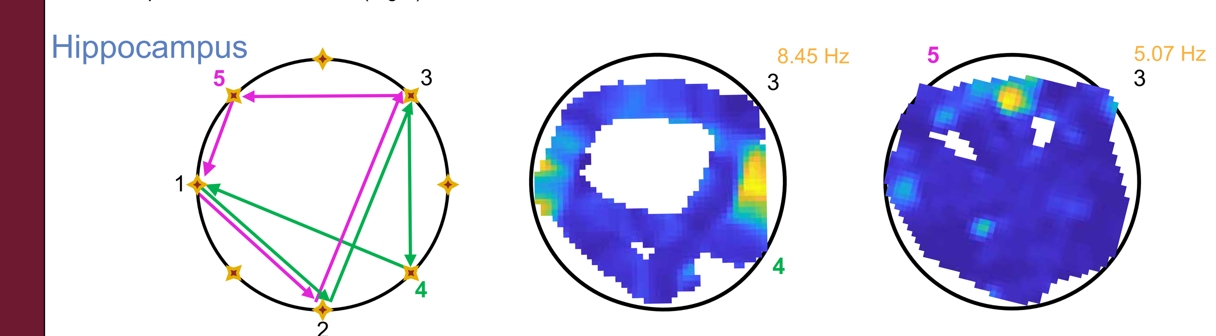


'Yellow' Rat May be Using a fully allocentric strategy as the temporal relationship for 'Going To' decoding is reversed while 'Came From' decoding is identical. *Left*. During the allocentric-memory trials. HPC decoding peaks lead PC across for the yellow rats. *Right*. When decoding the upcoming action PC decoding peaks now follow HPC across 4 datasets in the 'yellow' rat.

What are the Neural Correlates of the Decoding Model?



PC module sequences possibly representing unique action sequences disambiguate future zone 4 vs 5 traversals. *Left*. Example of a PC self-motion tuned module. *Middle*. We used a center-of-mass approach to identify modular sequences during zone 2-3 traversal that coincided with decoding peaks (not shown). Different modular sequences were apparent when decoding predicted a turn to zone 4 versus a predicted turn to zone 5 (*Right*).



Hippocampal Place Cells Could Be the Neural Substrate for Allocentric-Context Memory. Two plots showing the activity of two hippocampal place cells as a heat plot of time-adjusted firing rate, using an evenly spaced color map with max rate indicated in yellow.

Conclusions

Both parietal cortex and hippocampus are engaged (except for one rat...) when the task demands required use of allocentric context memory and to select the appropriate action.

The signal for allocentric context memory appears first in Hippocampus and subsequently in parietal cortex.

The signal for the future action appears after the allocentric context memory and is apparent in parietal cortex and subsequently hippocampus (except for one rat...)

Parietal cortex multi-units activity modular sequences are apparent in close temporal proximity to decoding peaks and disambiguate upcoming action to zone 4 versus zone 5.

Together our data suggests that parietal cortex and hippocampus are critical for transforming allocentric context memory into egocentric action.

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Acknowledgements

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