A hippocampal-parietal network for map to action transformation

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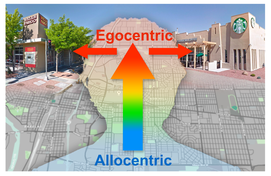
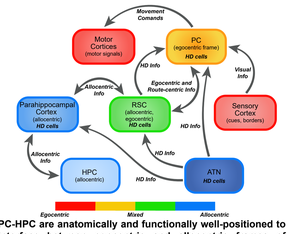
Introduction

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]. There, 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.

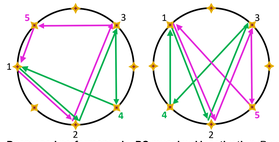


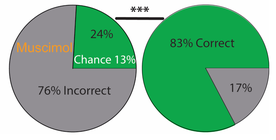
Coordination between allocentric (map-like) and body-centered (egocentric) frames of reference. Our brain maps our position in allocentric coordinates; however, our interactions with the world are body-centered or egocentric by nature (e.g., we turn right at a particular intersection). A fundamental 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 the intersection from the north).



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





PC Inactivation: Allocentric-Memory-Action Trials

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=1) 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=2).

Complex sequence task apparatus:

- Rats were trained on a large circular open field (1.5m in 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.

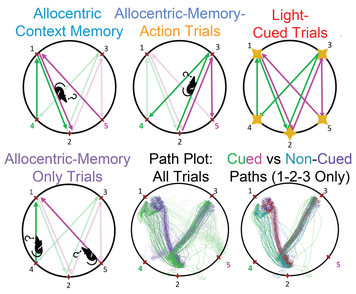
Pretraining:

- Alternation training is achieved using barriers to restrict the movement of the rat to alternating between a pair of light cues on opposite sides of the maze.
- Rats are then trained to follow a light cue to navigate toward all 32 light/reward zones using a random with repeats sequence from the 32 light/reward zones.

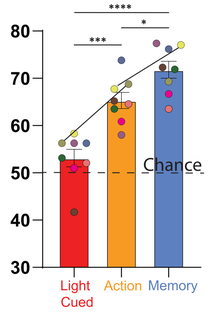
Complex sequence task:

- 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 (control trials) or non-cued (memory trials). On light cued trials, the light is presented at the onset of each segment of the sequence.
- Finally, to test for pure memory or spatial impairments that do not require coordinate transformation, we will assess allocentric memory only trials (4-1 & 5-1).
- 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).

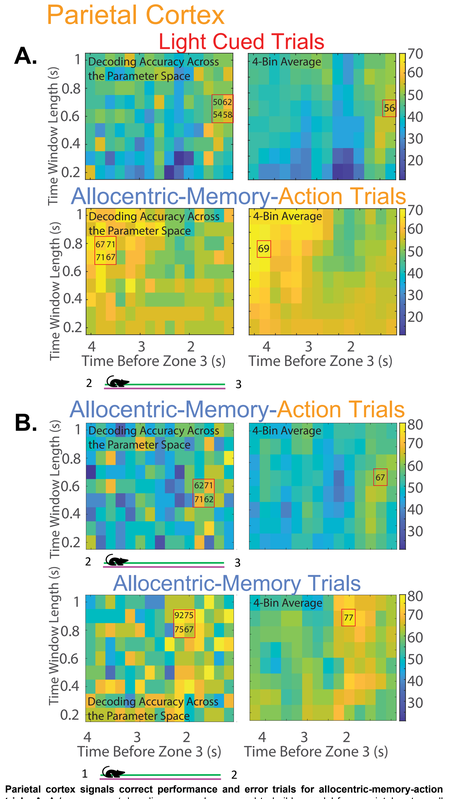
Results



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 4 critical components of this task. *Top Left.* When traversing through zones 1-3 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 Middle*). *Top Right.* Test trials where the rat navigates through the sequence using allocentric orientation are interleaved with light cued trials (both in sets of three) in which the rat is led through the sequence by sequentially active light cues (stimulus response trials). *Bottom Left.* Allocentric memory only trials in which the rat only needs to remember the location of zone 1. *Bottom Middle.* Path plot for a single 50min session showing paths for the 1-2-3-4- and 1-2-3-5- (color-coded) 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 cued vs non-cued trials. Paths on the 2-3 segment again completely overlap for light cued vs. memory trials. Representative example from n=7 rats when performance was close to 70% correct.

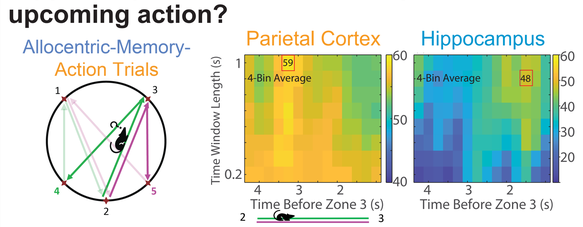


PC ensembles encodes the upcoming action and also the allocentric spatial context but only for memory trials and not light cued trials. PC activity was accurate in predicting performance for action and memory trials and significantly higher than for making the same prediction for the interleaved sets of trials where a cue light led the rat from zone 2-3 (logistical regression; p<0.01; support vector machine – not shown; p<0.05), suggesting HPC and PC are less critical for cued navigation. Mean +/- SEM and decoding accuracy for each data set (color coded for data set pairs – cued vs memory) are shown for n=8 data sets from 2 rats.



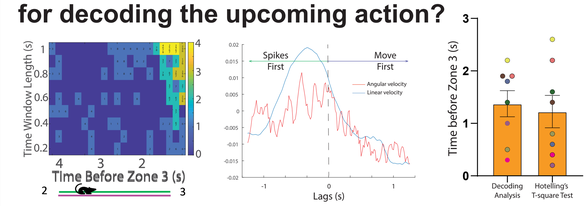
Parietal cortex signals correct performance and error trials for allocentric-memory-action trials. A. A *leave one out* decoding approach was used to build a model from parietal cortex cell activity during the zone 2-3 traversal to predict the future choice for the zones in the sequence which require translating the spatial context memory into the appropriate action (zone 3-4 & 3-5). Example heatmaps of the decoding parameter space for action (*Top Left*) and light cued trials (*Bottom Left*). Each set of 4 adjacent bins is averaged and the peak is selected from this averaged heatmap to ensure that decoding accuracy represents a peak in this parameter space (*Right*). The corresponding data points are connected with a line between the light cued group and the action group (adjacent bar plot to the left). **B.** Example heatmaps of the decoding parameter space for action (*Top Left*) and memory trials (*Bottom Right*). The corresponding data points are connected with a line between the action group and the memory group in the adjacent bar plot to the left.

Hippocampal ensembles do not predict the upcoming action?



Hippocampus does not signal correct performance and error trials for allocentric-memory-action trials. HPC decoding performance for predicting traversal from zone 3-4 & 3-5 was lower than parietal cortex (n=1 rat).

Do anticipatory motion tuned modules account for decoding the upcoming action?



Motion tuned modules that anticipate upcoming action do so at a similar time relative to the choice point compared to decoding from the population of modules. *Left.* Heatmap showing the number of single modules that significantly predicted the upcoming action across the parameter space (Hotelling's T-square test). Example module (#7) shows consistent self-motion turning across data sets for forward/right motion (not shown). Cross-covariance for the same data set of absolute angular velocity and linear velocity (*Middle*). The peak in number of modules anticipates forward and angular motion. The time of the peak in the number of modules that show significant decoding and the peak in the decoding parameter space is similar for all data sets (*Right*).

Conclusions

- Parietal cortex is robustly engaged only when the task demands required use of allocentric context memory to select the appropriate action.
- Parietal cortex ensembles signal not only the upcoming action but also the allocentric context.
- Hippocampus population activity is at chance levels for predicting the rats behavior for allocentric-memory-action trials.
- Some PC modules anticipate action at the choice point and this anticipatory encoding may also be reflected in the decoded upcoming action in the population because the anticipatory timing is similar for decoded ensembles and single modules
- Together our data suggests that parietal cortex is critical for translating allocentric context memory into egocentric action.

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