A Hippocampal-parietal Network for Reference Frame Coordination

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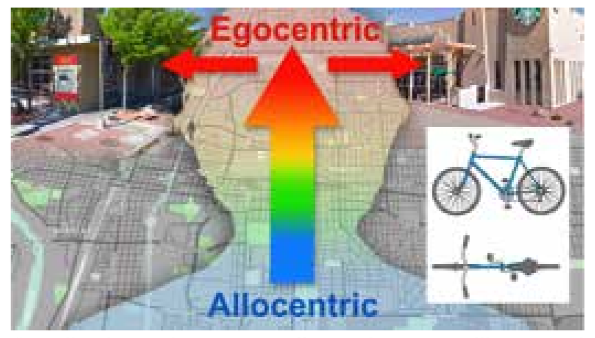
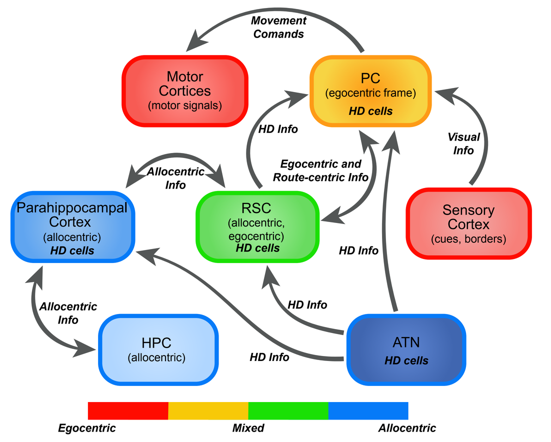
Introduction

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 in order to face west to reach a goal. 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 are best known for coding 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]. Here, we investigated how the hippocampus and PC coordinate between encoding of a previously visited spatial location which informed selection of the appropriate future goal location during a complex spatial sequence task. This task requires rats to remember a prior spatial location and then generate an appropriate future action while traversing a common route. Our results show that both the hippocampus and PC encode and exchange information about the prior and future spatial locations, supporting the notion of a bidirectional network level coordination between allocentric and egocentric perspectives.



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). 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.

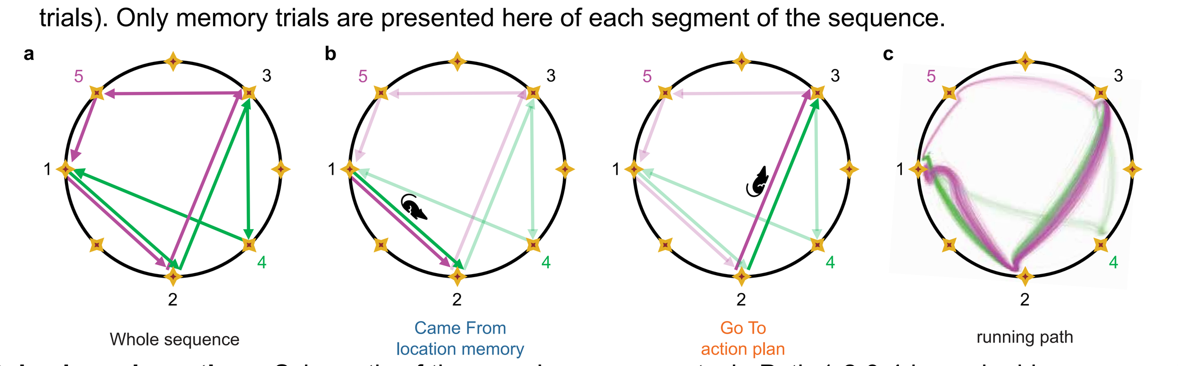
Methods

Animals:

- Fisher-Brown Norway (n=5) 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=4).

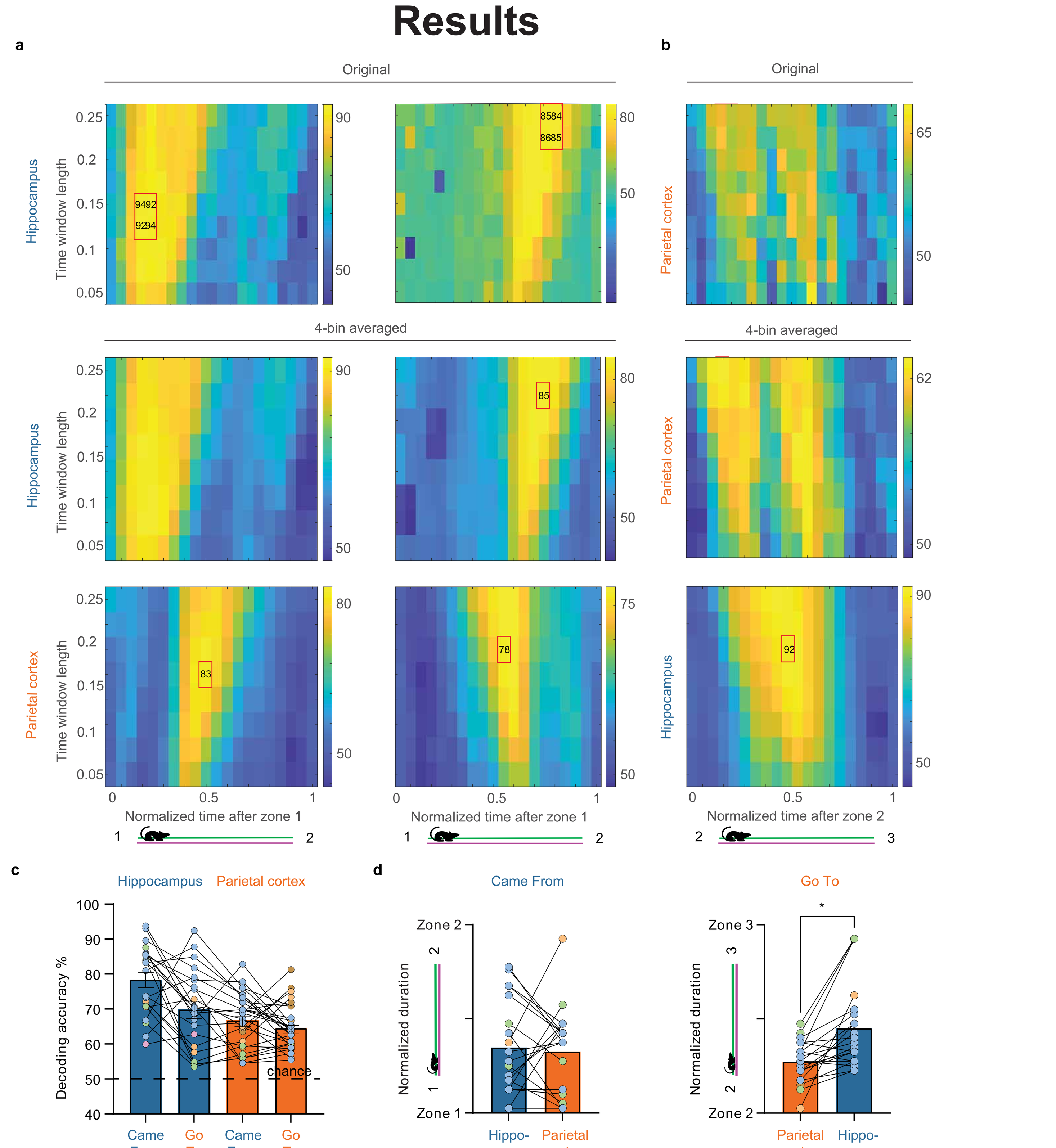
Complex sequence task:

- 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.
- 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.

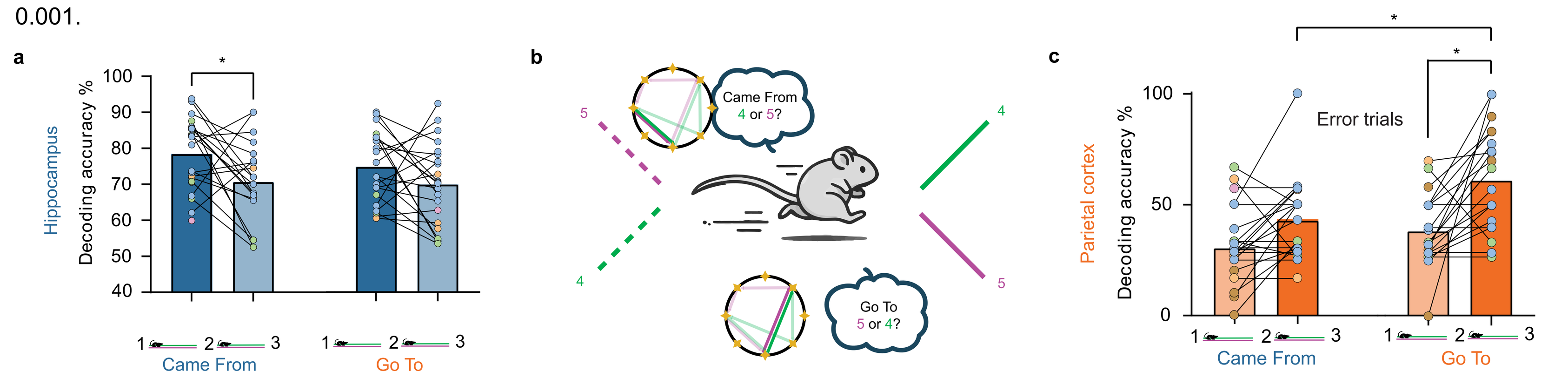


Behavior schematic. a, Schematic of the complex sequence task. Path 1-2-3-4 is marked in green, and 1-2-3-5 is marked in magenta. **b,** To navigate the spatial sequence, the rat must remember where it "Came From" during segment 1-2 (left) and subsequently use this information to generate a plan for where it will 'Go To' during segment 2-3 (right). **c,** Example of the running path during one behavior session.

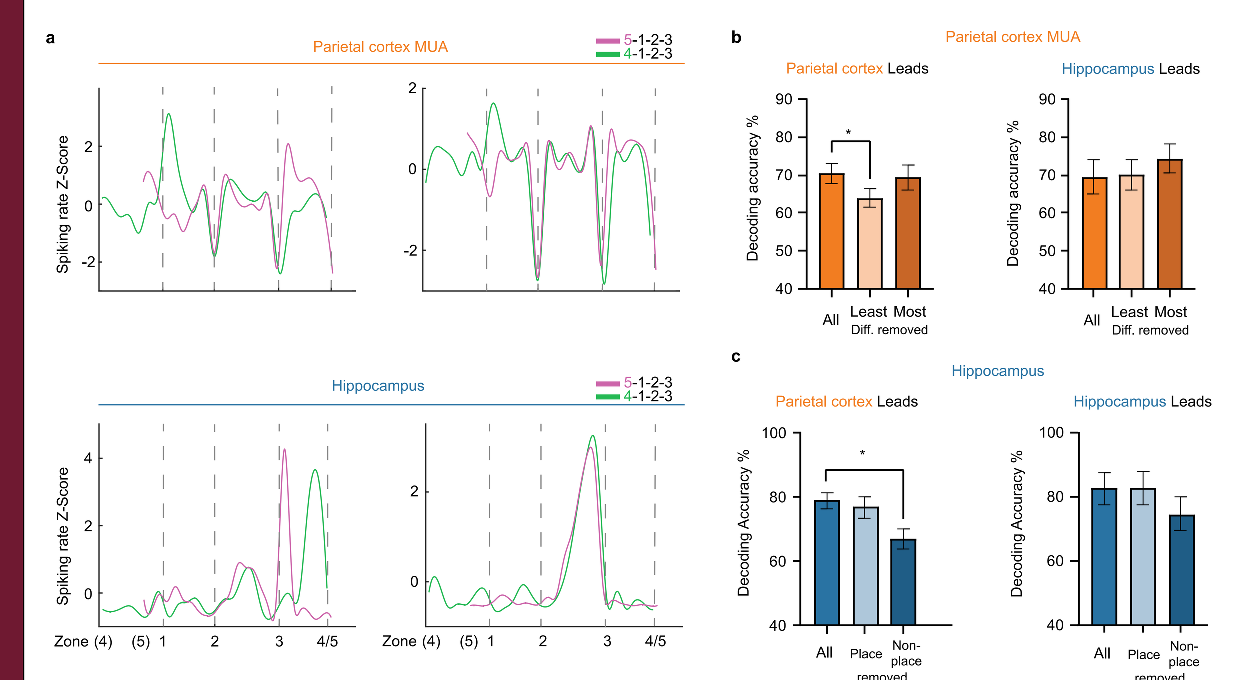
Results



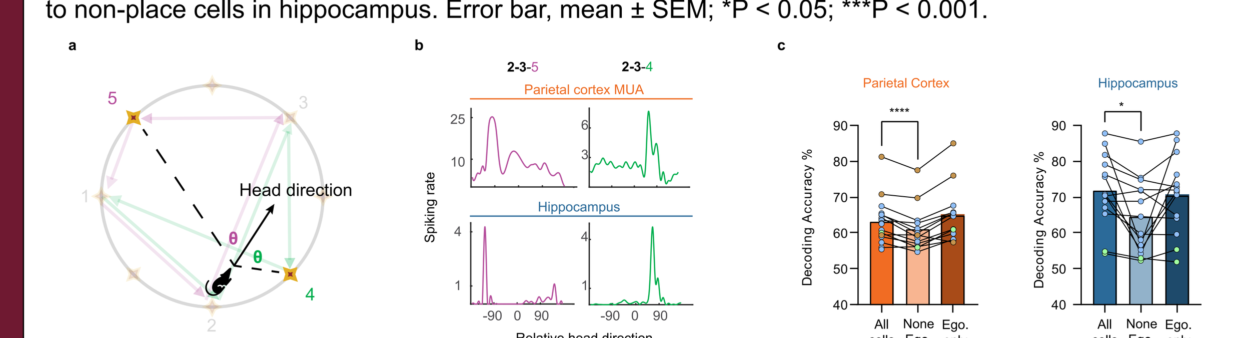
Temporal Decoding Reveals Sequential Patterns Across Hippocampus and PC of 'Came From' and 'Go To' Information. a, Examples of temporal decoding matrices for 'Came From' decoding during segment 1-2. *Top*: Original hippocampal decoding matrix. Horizontal axis is normalized time, and vertical axis is window size (proportion of normalized segment time). *Middle*: Each set of 4 adjacent bins is averaged to produce an average decoding matrix so that the peak in the parameter space can be extracted. *Bottom*: Averaged decoding matrix for PC. Color bar: Decoding accuracy (percent). **b,** Examples of temporal decoding matrices for 'Go To' decoding during segment 2-3. *Top*: Original PC decoding matrix. *Middle*: PC 4-bin averaged decoding matrix. *Bottom*: Hippocampus 4-bin averaged decoding matrix. **c,** Decoding accuracy varied across 'Came From' and 'Go To' decoding in hippocampus and PC. **d,** Temporal order of decoding peaks for 'Came From' decoding in segment 1-2 (*left*) and 'Go To' decoding in segment 2-3 (*right*). 'Came From' decoding leads in hippocampus or PC mixedly, while 'Go To' decoding happens in PC significantly. *P < 0.05; ***P < 0.001.



Over the Full 1-2-3 Segment, 'Came From' Decoding Becomes Less Accurate While 'Go To' Decoding Becomes More Accurate. a, Hippocampal (top) 'Came From' and 'Go To' decoding varies across segments 1-2 and 2-3, with 'Came From' being less accurate during segment 2-3. **b,** Schematic illustrating the two ways in which error trials can be decoded. 'Came From' decoding can suggest that the rat may have remembered the wrong zone, predicting that it will make an error. In contrast, 'Go To' decoding can predict an error by indicating that the rat will 'Go To' the wrong zone. Note that the latter case could arise either because the rat remembered the wrong zone or selected the wrong action (i.e., 'Go To' decoding is better suited for predicting errors). **c,** Error trial prediction from decoding data for segments 1-2 and 2-3 varied significantly for PC MUA. Specifically, error decoding for 'Go To' was more accurate for segment 2-3, and error trial decoding was also more accurate for 'Go To' than for 'Came From' decoding in the 2-3 segment. *P < 0.05.



Route-centered Coding in PC When PC Leads and Place Cells in Hippocampus when Hippocampus Leads May Underlie 'Came From' Decoding. a, Examples of activity rate z-score normalized to mean firing rate and split by path 5-1-2-3 (magenta) and 4-1-2-3 (green) from PC MUA (top) and hippocampal single cells (bottom). **b,** Removing route encoding PC MUA impairs decoding, but only when PC is leading hippocampus for 'Came From' decoding during segment 1-2. **c,** Removing non-place cells impairs decoding but only when PC is leading, suggesting that PC conveys 'Came From' information to non-place cells in hippocampus. Error bar, mean ± SEM; *P < 0.05; ***P < 0.001.



Egocentric Tuning to Future Goal Locations During the 2-3 Segment Underlies 'Go To' Decoding in PC and Subsequently in Hippocampus. a, Schematic of relative goal location fixed with respect to the current head direction (i.e., egocentric goal direction). **b,** Examples of egocentric tuning in PC MUA (top) and hippocampal single cells (bottom) split by path 1-2-3-4 (left, green) and 1-2-3-5 (right, magenta). **c,** 'Go To' decoding accuracies of PC (top) and hippocampus (bottom) varies when egocentrically tuned (or not tuned) cells or MUA are removed. Specifically, there is a significant reduction in decoding accuracy when egocentrically tuned cells or clusters are removed, but not when non-egocentrically tuned cells or clusters are removed. *P < 0.05; ****P < 0.001.

Conclusions

- 'Came From' and 'Go To' signals are both apparent in hippocampus and PC but at different times.
- 'Came From' decoding may emerge from PC route-centered encoding when the PC signal appears before the signal in hippocampus.
- 'Came From' decoding in PC may be relayed to hippocampal non-place cells when PC is leading, whereas when hippocampus is leading, both place and non-place cells in hippocampus contain sufficient information to accurately decode the 'Came From' location.
- Egocentric tuning to future goal locations may underlie the 'Go To' decoding signal observed first in PC and then in hippocampus.

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