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EDITORIAL

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Hippocampal system neurons encoding views in different species: Introduction to the Special Issue of Hippocampus 2023

Vision is paramount to the other senses in humans. A visual evaluation of scenes allows remembering where objects and rewards are in the world, and supports a sense of self-location with respect to the external world. In line with the importance of scenes, neurons that respond to what is being viewed in a scene are found in the primate hippocampus, and these are likely to be useful for memory and/or navigation. These neurons contrast with hippocampal rodent place cells that respond to a rodent's position in space. As the primate and rodent visual systems differ in important ways, these important differences are likely to influence hippocampal representations across species. However, in rodents, place cells can be reset by a view of the environment, so views are important in rodents too. However, the hippocampal visual representations do differ in key ways between primates and rodents. In addition to these view and place representations in primates and rodents, there is increasing evidence for the existence of view-related neurons in rodents. For example, allocentric or egocentric landmark/object neurons and boundary vector neurons have been found in the rodent entorhinal cortex, subiculum, and retrosplenial cortex, and these are likely to be useful for memory and/or navigation.

The aim of this Special Issue of Hippocampus (2023) is to bring together papers that address view representations in the hippocampus and closely related brain systems of any species including humans, in order to understand better how view representations are involved in hippocampal function, and commonalities and differences across species, with the aim to advance our understanding of hippocampal function in memory and navigation.

1 | VIEW REPRESENTATIONS IN RODENTS, NATURE AND FUNCTIONS

The controlling effect of visual cues on allocentric hippocampal place cell was demonstrated shortly after they were discovered (Muller & Kubie, 1987). But while these allocentric codes were described in rodents, research in nonhuman primates described the egocentric nature of stimulus encoding in neocortical regions such as the parietal cortex. It remained unknown whether such egocentric codes, representing the position of a stimulus relative to the self, were also present in the rodent. In this issue, several papers describe newly discovered egocentric codes, highlight the similarities with those found in primates, and propose models based on these codes to account for place codes or goal-directed navigation.

Wang, Lee, Rao, Doreswamy Savelli and Knierim (2023) describe neurons in the rat lateral entorhinal cortex that represent the angular bearing of objects and boundaries in an egocentric frame of reference, with new results on the deep layers of the lateral entorhinal cortex. They report that cells in the deep layers of the entorhinal cortex are relatively similar to those in the superficial layers of the lateral entorhinal cortex rather than allocentric, hence preserving egocentric information, despite receiving input from CA1.

Alexander, Robinson, Stern and Hasselmo (2023) consider neurons in the retrosplenial cortex of rats that show egocentric coding of the position of boundaries in relation to the animal. They propose a new model allowing a transition from a self-based to a world-based allocentric reference frame that uses theta phase coding instead of gain fields. Their model posits that an allocentric position representation in grid and place cells constitutes the apex of the hierarchical representations of complex scenes, and stems from initial processing of view-based egocentric vector codes.

LaChance and Taube (2023) start with neurons in the rat postrhinal cortex that respond to the egocentric (observer-centered) bearing and distance of the boundaries, or geometric center, of an enclosed space. They present a model that with the addition of a head direction signal shows how in rodents these egocentric view signals could be transformed into goal-directed behavior, thanks to a difference in bilateral representation of motion parallax.

Lee, Shin and Lee (2023) note the presence of hippocampal formation spatial view neurons in primates, and the importance of scene processing in humans. Based on the presence of recently discovered scene-based processing in the rodent hippocampus, similar to that found in primates, they propose a unifying framework across species for understanding how scene information underlies memory. They argue that it will be important to further investigate rodent hippocampal system neurons in scene-based tasks.

2 | VIEW REPRESENTATIONS IN PRIMATES

Hippocampal function is believed to build a representation of the world, which allows the encoding of the stimuli's position with respect to each other in an allocentric reference frame. In which reference frames are views encoded? In this issue, several papers provide grounds to discuss the nature of the allocentric representation in primates and its relationship with egocentric representations given that the world is sampled from a first-person perspective.

Yang, Chen, and Naya (2023) consider the allocentric (world-based) encoding of hippocampal view neurons and raise the issue of how the background plays a role in a first-person view-dependent encoding and retrieval of a scene. They show how an allocentric representation is progressively constructed in the hippocampus by combining cortical signals pertaining to object identity and their foveal background.

Rolls (2023a) considers the allocentric spatial view cells in primates that respond to viewed locations in scenes relatively independently of the place where the individual is located, and shows that these representations are ideal for episodic memory of where objects or rewards have been seen in viewed space, and also for navigation guided by viewed landmarks. He also describes recent analyses of effective connectivity in the human brain that show how a ventromedial visual pathway reaching the medial parahippocampal cortex where the parahippocampal scene area is located provides a basis for scene representations to be built by combinations of overlapping viewed features in scenes.

Corrigan, Gulli, Doucet, Mahmoudian, Abbass, Roussy, Luna, Sachs and Martinez-Trujillo (2023) show that during navigation in a virtual environment, specific views, containing task-relevant objects, elicit selectivity in a high proportion of macaque hippocampal neurons, and an even higher proportion of lateral prefrontal cortex neurons. Place selectivity was scarce and generally dependent on view.

Zhu, Lakshminarasimhan, and Angelaki (2023) describe hippocampal neurons, in freely moving macaques, that respond to the view of the environment toward which the animal is facing, and for which the place where the head is located is not a key variable so that these are not place cells. They then emphasize how posture such as head tilt is another dominant tuning variable for primate hippocampal neurons and could provide an egocentric reference frame to view-dependent perception. They also argue that eye movements during navigation primarily embody subjects' beliefs generated by their hippocampal internal model, or primarily reflect active sampling for improving their internal model.

3 | FLEXIBLE REPRESENTATIONS AND MEMORY STORAGE CAPACITY IN HUMANS

An important issue is what is represented in the human hippocampus, and the implications that this may have for memory storage. If the memories to be stored have overlaps, then this may reduce the storage capacity of the memory system. Moreover, if neurons are used flexibly in different tasks, this also may reflect overlaps between memories. Three papers address such issues at the individual neuron or population of neurons levels.

Donoghue, Cao, Han, Holman, Branmeir, Wang and Jacobs (2023) show how neurons encoding visual stimuli in the human medial temporal lobe display context-dependent flexibility in tasks such as a spatial navigation task and working memory task. This raises the interesting issue about how the task being performed can influence the activity of hippocampal neurons, and alter their functional coding properties dynamically to represent different information.

Quian Quiroga (2023) considers the “concept cells” found in the human medial temporal lobe including the hippocampus and suggests that a model of partially overlapping assemblies is well suited to cope with memory capacity limitations. He further suggests that the flexible nature of hippocampal codes is due to a temporary use of the hippocampus for unconsolidated information, while only relevant information is represented in long-term concept cells, which according to Quian Quiroga are central to human's cognitive abilities.

Ryom, Stendardi, Ciaramelli and Treves (2023) consider a model based on long-range neocortical connections and ask whether there are purely computational constraints that require cooperation between the hippocampus and neocortex in the associative storage and retrieval of snapshot compositional memories. Their analysis shows how the storage capacity for compositional representations such as views is constrained by the statistics of the compositionality and in particular by the correlations between them. They describe conditions in which, in their model, cortical–hippocampal interactions may help disambiguation between overlapping memories and participate in semantic or schema based versus episodic memories in humans.

4 | COMMENTARIES ON ISSUES RAISED IN THIS SPECIAL ISSUE

Han, Donoghue, Cao, Kunz, Wang and Jacobs (2023) consider issues raised in the Special Issue of Hippocampus on View Representations and argue that a promising research strategy is the use of multitask experiments, or more precisely switching between multiple task contexts while recording from the same neurons in a given session could be a fruitful approach to better understand the nature of hippocampal representations across different cognitive domains.

Wirth (2023) discusses how rodents' and primates' differences in visual perception may impact the way the brain constructs egocentric and allocentric reference frames to represent stimuli in space. While both rodents and primates have egocentric spatial reference frames that are suitable for navigation, the primate hippocampus may rely more heavily on an egocentric reference frame that relates to the first-person perspective characteristic of a primate's field of view. She argues that an allocentric reference frame in primates may be more of a semantic construct and that views based on the first-person perspective are a powerful tool for probing episodic memory across species.

Rolls (2023b) considers how allocentric spatial view representations are important not only for understanding episodic memory, which requires an allocentric representation that is nevertheless subject to view-dependent effects that are found on different sides of a scene, but also in a sense provide the world-based anchoring of place cells in rodents to the world, and how they relate to concept cells and the semantic systems found in humans. Rolls emphasizes that egocentric representations may be fine in primates for implementing actions in peripersonal space and in rodents for avoiding obstacles, but allocentric view representations are essential for remembering where objects and people have been seen in the world, and for navigation.

Edmund T. Rolls[1,2]
Sylvia Wirth[3]

[1]*Oxford Centre for Computational Neuroscience, Oxford, UK*
[2]*Department of Computer Science, University of Warwick, Coventry, UK*
[3]*Institute of Cognitive Science Marc Jeannerod, Centre National de la Recherche Scientifique UMR5229, and University of Lyon 1, Bron, France*

Correspondence
Edmund T. Rolls, Oxford Centre for Computational Neuroscience, Oxford, UK.
Email: Edmund.Rolls@oxcns.org

Sylvia Wirth, Institut des Sciences Cognitives Marc Jeannerod, Bron, France.
Email: Sylvia.Wirth@isc.cnrs.fr

ORCID

Edmund T. Rolls https://orcid.org/0000-0003-3025-1292
Sylvia Wirth https://orcid.org/0000-0001-7002-329X

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