

## REVIEW

# Computational cross-species views of the hippocampal formation

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## Abstract

The discovery of place cells and head direction cells in the hippocampal formation of freely foraging rodents has led to an emphasis of its role in encoding allocentric spatial relationships. In contrast, studies in head-fixed primates have additionally found representations of spatial views. We review recent experiments in freely moving monkeys that expand upon these findings and show that postural variables such as eye/head movements strongly influence neural activity in the hippocampal formation, suggesting that the function of the hippocampus depends on where the animal looks. We interpret these results in the light of recent studies in humans performing challenging navigation tasks which suggest that depending on the context, eye/head movements serve one of two roles—gathering information about the structure of the environment (active sensing) or externalizing the contents of internal beliefs/deliberation (embodied cognition). These findings prompt future experimental investigations into the information carried by signals flowing between the hippocampal formation and the brain regions controlling postural variables, and constitute a basis for updating computational theories of the hippocampal system to accommodate the influence of eye/head movements.

## KEYWORDS

active sensing, embodied cognition, eye movements, hippocampus, primate

## 1 | INTRODUCTION

The term navigation can be broadly described as the transition of an entity from one state to another (Hinman et al., 2018). It might involve taking a trajectory through physical space (Eichenbaum, 2017) or achieving an understanding in abstract space (Garvert et al., 2017). Perhaps, all movement and thought is navigation. But one thing is clear: navigation is a fundamental cross-species behavior (Poulter et al., 2018; Sosa & Giocomo, 2021). From mice exploring labyrinths (Rosenberg et al., 2021) to bats echolocating in flight (Ulanovsky & Moss, 2007) to monkeys catching fireflies in virtual reality (Lakshminarasimhan et al., 2020) to taxi drivers taking routes from memory (Maguire et al., 2000), species exhibit assorted modes of navigation. Research across species has uncovered many shared motifs, but each species also contributes unique insights toward

understanding the neural mechanisms and cognitive processes underlying navigation.

In this review, we first briefly summarize the similarities and differences between neural responses in the rodent and primate hippocampal formation. We highlight recent works which suggest that instead of (or in addition to) representing one's location, which appears to be the primary function of the rodent hippocampus (HPC), the primate HPC is highly sensitive to the animals' interaction with visual space. Then, we interpret this latter finding in the context of recent behavioral work on humans performing computationally demanding, naturalistic navigation tasks. Specifically, we hypothesize that eye movements shape the activity of the primate hippocampal formation during active sensing because they embody the planning computations facilitated by hippocampal representations.

## 2 | SPATIAL AND NON-SPATIAL ROLES OF HPC

### 2.1 | The rodent hippocampal formation in spatial navigation

The substantial body of work in rodent spatial navigation suggests that the HPC wears many hats. During free foraging, some cells in the rodent HPC preferentially fire at specific locations in space, constituting a place code (O'Keefe, 1976; O'Keefe & Nadel, 1978; Figure 1). Place fields become more robust with prolonged exposure to an environment (Wilson & McNaughton, 1993), while changes to the environmental cues result in partial or complete place field remapping (Fyhn et al., 2007; Jeffery, 2011; Muller & Kubie, 1987). On the other hand, cells in the medial entorhinal cortex (EC) were found to exhibit multiple firing fields that tessellate space in a regular hexagonal grid (Hafting et al., 2005; Figure 1). In addition, experiments have found head direction cells in the postsubiculum (Taube, 2007), allocentric boundary cells in subiculum (Lever et al., 2009), and egocentric boundary cells in the retrosplenial (Alexander et al., 2020, 2023) and postrhinal (LaChance et al., 2019) cortices. These striking discoveries have supported the notion that the hippocampal formation constructs a cognitive map to facilitate navigation (Hartley et al., 2014).

Furthermore, the HPC generates sequences to order memories and concepts in space and time (Buzsáki & Tingley, 2018). Sequential firing of place cells in rodents has been shown to encode spatial locations ahead of the animal (Diba & Buzsáki, 2007; Johnson & Redish, 2007; Pfeiffer & Foster, 2013), locations behind the animal (Diba & Buzsáki, 2007; Foster & Wilson, 2006; Gupta et al., 2012), and remote locations (Karlsson & Frank, 2009; Lee & Wilson, 2002). This suggests that the hippocampal code is a flexible representation that can be called upon to construct plans and make meaning out of experience and for the formation of cognitive maps. Interestingly, spatial properties have now been encountered in multiple brain areas beyond the hippocampal formation (Maisson et al., 2022) and conversely, hippocampal activation is also seen during nonspatial

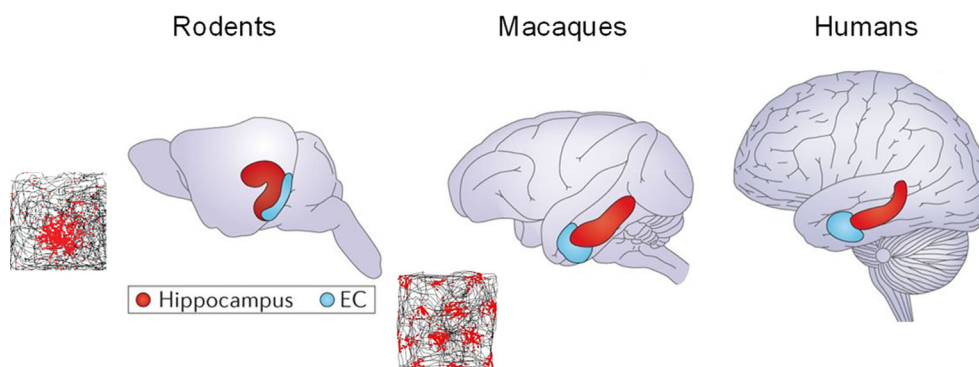
sequential decision tasks (Aronov et al., 2017; Sun et al., 2020). These diverse findings from rodent work have led to multiple computational theories of the hippocampal function.

### 2.2 | Computational theories about the hippocampal formation

An emerging computational framework for interpreting the function of the hippocampal formation is reinforcement learning (RL). Navigation can be cast as a Markov decision process, where a state can be a location (or abstract concept), and an agent (animal or artificial being) can move between states by taking actions (Behrens et al., 2018; Gershman & Daw, 2017; Sosa & Giocomo, 2021). To the extent that the goal of navigation (or any task) is to maximize future rewards, RL provides one possible way to predict and interpret hippocampal representations governing the animal's policy, that is, actions chosen in each state (Tessereau et al., 2021), and can explain why the HPC is engaged in nonspatial tasks. A comprehensive primer on the RL framework as it pertains to the hippocampal formation is provided by Whittington et al., 2022.

Many new and old theories of hippocampal function can be interpreted using the RL framework. The classic *cognitive map* theory (O'Keefe & Nadel, 1978; Tolman, 1948) posits that hippocampal formation represents a precise internal model of the spatial relationships between the states of the environment. According to this theory, navigation is model-based such that actions are chosen by planning using the internal model, and place cells and grid cells constitute the neural substrates of this model.

However, planning is computationally demanding especially in large environments with numerous states. This prompted a recent wave of studies that provide empirical support for a more computationally efficient representational theory for sequential decision-making tasks in humans—the *successor representation* (Momennejad et al., 2017; Russek et al., 2017). This theory also explains many empirical findings regarding hippocampal activity such as the



**FIGURE 1** Differences in the orientation and relative sizes of hippocampus (red) and entorhinal cortex (EC, cyan) in rodents, macaques, and humans. In rodents, emphasis is on spatial location during real-world navigation (Fyhn et al., 2004; Hafting et al., 2005; O'Keefe & Dostrovsky, 1971). Due to restrictions in clinical settings, human studies have almost exclusively used virtual navigation in patients (Ekstrom et al., 2003; Jacobs et al., 2013). Borrowed from Strange et al. (2014).

skewness of place fields, remapping, and the geometric structure of grid fields (Stachenfeld et al., 2017). Under this framework, the core function of the HPC is prediction, as place cell firing rates are posited to be proportional to the probability of visiting the corresponding place field, given the agent's current position. Such probabilities are learned through experience, and are thus policy-dependent. Successor representation place fields are sensitive to the environment topology (Muller & Kubie, 1987) and skew backward from the direction of travel (Mehta et al., 2000), in agreement with experimental evidence. A low dimensional eigen-decomposition of the successor representation exhibits many qualities of entorhinal grid cells, including their alignment to environmental boundaries (Krupic et al., 2015). This theory suggests that grid cells highlight bottlenecks which partition the world, as well as smoothen updates to predictive representations (Stachenfeld et al., 2017).

Successor representation models account for the spatial structure of hippocampal activity, but do not explain the striking temporal structures such as sequential firing patterns and replays. An RL-based computational theory of *prioritized memory access* has recently been proposed to account for these robust temporal dynamics (Liu et al., 2021; Mattar & Daw, 2018). According to this theory, sequences and replays help improve the efficiency of learning and planning algorithms and may be interpreted as mental simulations (Erdem & Hasselmo, 2012; Erdem & Hasselmo, 2014; Hasselmo & Eichenbaum, 2005; Kubie & Fenton, 2012) that are restricted to specific regions of the state space based on their relevance to the navigation problem.

These RL-based theories were mainly geared toward explaining data from rodents performing spatial navigation tasks. However, research in primates and humans had revealed that the role of hippocampal formation extends to nonspatial domains. A new framework of relational inference, called the *Tolman-Eichenbaum machine* proposes that HPC and EC are involved in structural abstraction and generalization in spatial and relational memory tasks (Whittington et al., 2020). This theory accounts for the conjunctive nature of hippocampal responses whereby neurons respond to both structural and sensory variables inherited from the medial and lateral EC, respectively. Such mechanistically grounded theories are helpful in generating precise predictions and can accelerate progress by informing experimental design. For example, *attractor dynamics* in the hippocampal formation was previously theorized as a possible mechanism of path integration (Burak & Fiete, 2009; McNaughton et al., 2006; Rolls, 2007), and has subsequently been supported by experiments (Agmon & Burak, 2020; Yoon et al., 2013). Another recent theory based on the *Bayesian inference* framework posits that the distortions induced in the response fields of grid cells due to changes in environmental geometry reflect the animal's uncertainty in representing their spatial location from noisy visual input (Kang et al., 2023).

In general, the above theories and other computational accounts of the hippocampal formation begin to address its role in *integration, inference, learning, planning, and remapping*, computations that manifest diverse behavioral and neural signatures depending on the task and context. These theories, although fragmented at the outset, are

likely to be directly linked. Since natural behaviors are interactive, expanding the above theories to incorporate the role of information gathering can help unify them. Information gathering is typically performed through whisking or visual exploration. Although rodent studies have only recently begun to consider the role of visual exploration (Mallory et al., 2021; Michaiel et al., 2020; Payne & Raymond, 2017), the above perspective enjoys experimental support from experiments in primates, which we describe below.

### 2.3 | Eye movement signals strongly infuse the primate hippocampal formation

The neurophysiology of the primate hippocampal formation has been explored less well compared to rodents, and previous studies had focused on a limited range of variables (Doeller et al., 2010; Ekstrom et al., 2003; Jacobs et al., 2013; Figure 1), almost exclusively with head-fixed monkeys either performing cart navigation (Matsumura et al., 1999; O'Mara et al., 1994) or moving through a virtual environment (Furuya et al., 2014; Gulli et al., 2020; Wirth et al., 2017). In general, macaque hippocampal neurons show some location-specific hippocampal activity, reminiscent of rodent place cells, albeit more dispersed and less prevalent (Courellis et al., 2019; Hazama & Tamura, 2019; Ludvig et al., 2004). Similar to the results of rodent studies, lesions of the monkey HPC impair allocentric, but not egocentric, navigation (Lavenex et al., 2006; Rueckemann & Buffalo, 2017).

Perhaps, the most provocative finding distinguishing the primate hippocampal formation from that of the rodent is that the former is strongly modulated by vision (Nau et al., 2018; Rolls, 2021). Some of the earliest recordings in monkeys aimed at disentangling representations of place from spatial view (Feigenbaum & Rolls, 1991; Georges-François et al., 1999; Robertson et al., 1998; Rolls, 1999; Rolls et al., 1997; Rolls & O'Mara, 1995), found that the primate HPC seems to encode views of particular regions of space, rather than the position of the monkey in the environment. Since then, there has been growing evidence for the existence of gaze-centered spatial representations in the hippocampal formation of head-fixed macaques (Killian et al., 2012; Meister & Buffalo, 2018; Wirth et al., 2017).

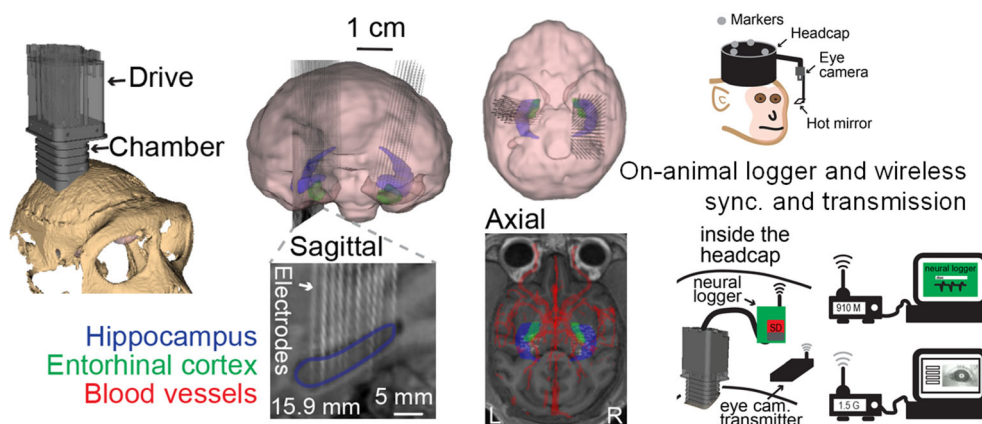
Flexible head movements are a critical component of natural behavior since they afford the opportunity to control one's spatial view. Until recently, this phenomenon had not been interrogated by monitoring both 3D eye and head movements in truly freely moving primates. Electrophysiological studies which reported the canonical place code in monkeys during free movement (Courellis et al., 2019) or virtual navigation (Furuya et al., 2014) and in humans during virtual games (Ekstrom et al., 2003; Miller et al., 2013) did not dissociate 3D head facing location from 3D spatial view, head movements, eye movements, nor body orientation. However, 3D head-facing location (the location of the arena toward which the head faces) and 3D spatial view (the location of the arena that is gazed upon) can be easily confounded when eye movements are not considered but they can be disambiguated by combining eye-in-head movement and 3D head orientation. We have recently disambiguated these variables in the study

of the macaque hippocampal formation by analyzing simultaneously tracked head and eye positions during head-unrestrained foraging (Mao et al., 2021; Figure 2). By combining head tracking, wireless eye tracking, and telemetric recordings across multiple regions—the HPC, EC, and subicular complex (SUB)—in freely foraging macaques with a multimodal modeling approach to characterize the neural encoding of spatial variables, we have provided a quantitatively rigorous characterization of how the macaque HF encodes space under ethological conditions.

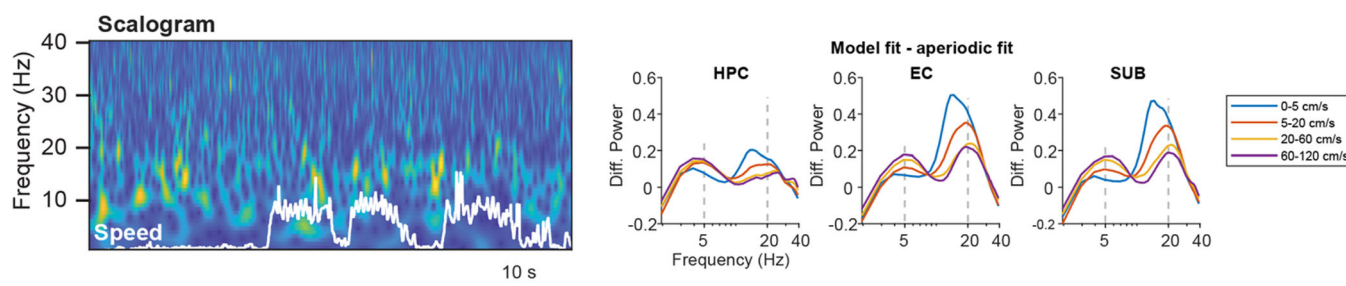
In contrast to rodents, and in line with previous primate studies (Courellis et al., 2019; Ekstrom et al., 2005; Talakoub et al., 2019; Watrous et al., 2013), we found that the theta rhythm is discontinuous in primates (Figure 3). Interestingly, despite low power theta oscillations in macaques, theta phase coding is conserved: a significant fraction of neurons were phase-locked to low theta (56%) and theta (25%). Nevertheless, theta phase precession existed only in a very small number of random-foraging macaque hippocampal neurons, in contrast to its abundance among rodent place cells (Mizuseki et al., 2009). In this respect, the primate HPC has more in common with the bat place coding system (Eliav et al., 2018). It remains to be

determined whether theta phase precession becomes more prominent when macaques engage in cognitively demanding memory consolidation and decision-making tasks (Zhang & Jacobs, 2015), as well as whether and how distinct theta bands and theta phase precession are tied to specific aspects of a task.

By using a multimodal modeling approach, Mao et al. (2021) found that many neurons that were responsive to animal position in the world also encoded other variables (Figure 4), in alignment with the high dimensional coding in the HPC reported by previous studies (Bernardi et al., 2020; Gulli et al., 2020; Wirth et al., 2017). Perhaps, the most unexpected finding was that the representation of head facing location and head tilt were more dominant than position. In fact, head facing location was consistently the best predictor for single neuron activity across regions and animals (Mao et al., 2021). These results expand upon the neural responses described previously in macaques in the form of “spatial view” cells (Rolls et al., 1997), and indicate the importance of using naturalistic foraging tasks in which head-centered versus eye-centered reference frames are naturally decoupled. While the strong head tilt correlates in the HPC may appear surprising, tilt tuning has nevertheless been shown to be



**FIGURE 2** Large-scale recordings across the entire hippocampal formation of freely moving macaques. From left to right: Recording drive and skull models. Segmented models of the brain, hippocampus (blue), entorhinal cortex (green), and blood vessels (red). Electrodes are visible as tracks in the co-registered images. Animals were instrumented to wear an eye tracker. Neural logger recordings and wireless transmission. Adapted from Mao et al. (2021).

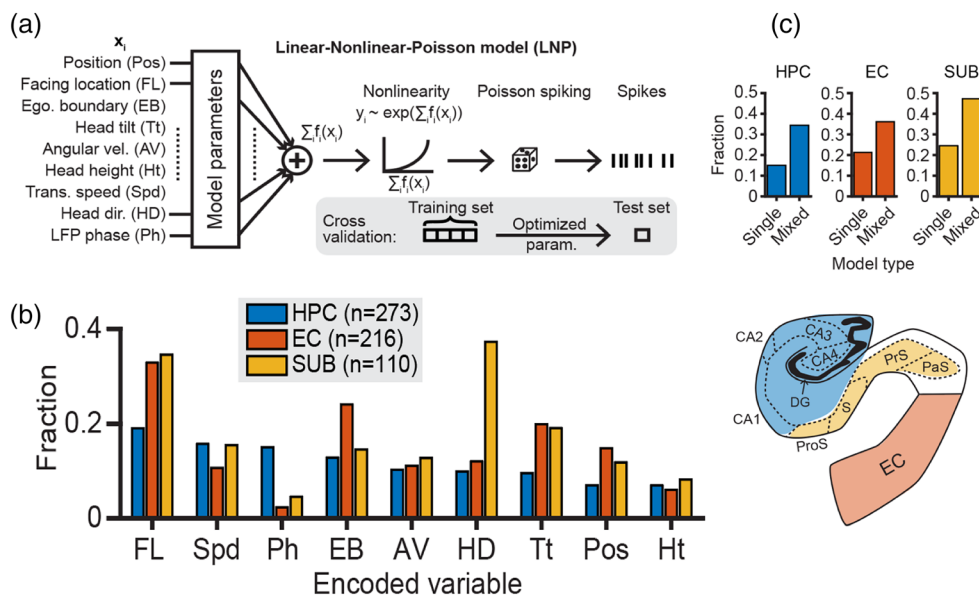


**FIGURE 3** Lack of sustained theta oscillations in freely moving macaques. Left: a short segment of the LFP spectrogram with speed trace overlaid in white: clearly there is no sustained theta during locomotion. Right: power spectrum of the oscillatory component, color-coded by locomotion speed; there is a local maximum around 5 Hz and a broad peak around 20 Hz, and their relative power is modulated by running speed (from Mao et al., 2021).



**FIGURE 4** Model-based approach to quantify simultaneous encoding of multiple variables.

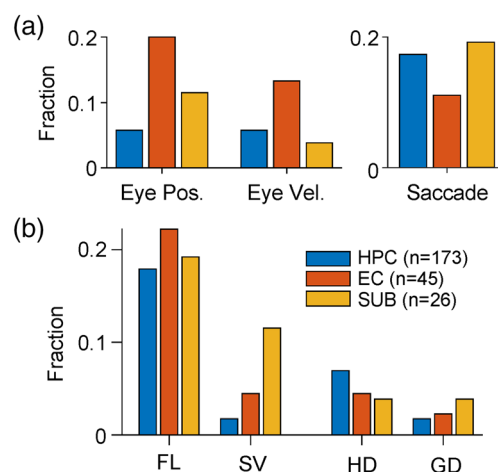
(a) Model schematic (for, see Mao et al., 2021). (b) Left: Fraction of encoding neurons for each variable in each region (defined in the coronal section on the right). HPC: blue; EC: orange; SUB: yellow). The main model included eight variables: 3D position, which was decomposed into horizontal position (Pos) and head height (HH), angular velocity (AV), linear speed (Spd), egocentric boundary (EB), facing location (FL), as well as 3D orientation, which was decomposed into head tilt (HT) and azimuth head direction (HD). (c) Prevalence of mixed selectivity across areas (from Mao et al., 2021).



prevalent in the bat presubiculum (Finkelstein et al., 2014), monkey anterior thalamus (Laurens et al., 2016) and mouse anterior thalamus, and retrosplenial cortex (Angelaki et al., 2020). These results complement earlier findings of hippocampal representation of spatial view along the vertical dimension, independent of head tilt (reviewed in Rolls, 2022). Thus, vertical orientation may be an important component in spatial coding and behavior across species.

Using such a multimodal, model-based analysis, we found that only 7% of the cells recorded in the hippocampal formation were true place cells, which is much lower than the proportion reported by other primate studies using traditional tuning curve analysis (Courellis et al., 2019; Hazama & Tamura, 2019; Ludvig et al., 2004; Matsumura et al., 1999), but consistent with the conclusions drawn from earlier multimodal approaches based on information theory (Georges-François et al., 1999; Robertson et al., 1998). It is important to note that the discrepancy between these findings was not data-driven, but rather analysis-driven: using traditional tuning curve analysis, the proportion of place coding cells (26%) reported by Mao et al. (2021) is not different from the conclusions of previous monkey studies. However, by considering multiple variables simultaneously, activation previously attributed to place coding, due to taking averages to obtain tuning curves, is now assigned to other variables that were not measured in previous experiments. Thus, we emphasize the advantages of taking a multimodal modeling approach, as well as the need to consider all postural variables, when analyzing neurons in the hippocampal formation.

Many neurons in freely moving macaques, particularly in the EC (22%), were tuned to egocentric eye-in-head position and/or velocity (Figure 5a). Similar findings have been reported in head-fixed



**FIGURE 5** Eye movements strongly influence hippocampal formation activity. (a) Fraction of neurons in each region (color-coded bars) encoding eye position, eye velocity, and saccade event. (b) Fraction of neurons in each region encoding FL, spatial view (SV), azimuth head direction (HD), and gaze direction (GD) when fitting all head- and gaze-related variables simultaneously (from Mao et al., 2021).

macaques exploring images on a screen (Killian et al., 2012; Meister & Buffalo, 2018; Nowicka & Ringo, 2000). In addition, we found that many cells, particularly in the HPC and subiculum, were modulated by saccadic eye movements and coupled to the local field potential, as previously reported in head-fixed animals (Doucet et al., 2020; Jutras et al., 2013). Despite strong eye movement-related responses in the hippocampal formation, we found that the macaque EC showed

limited grid tuning for allocentric location and spatial view. Although a slightly greater percentage (11.9%) of EC cells were reported to show grid tuning based on eye movements in head-fixed macaques (Killian et al., 2012), compared to 9% in freely moving macaques (Mao et al., 2021), the tuning of visual grid tuning is far less robust compared to rodent grid cells. Nevertheless, even if visual grid-like tuning is weak, the coding of eye movements within the macaque navigation circuit is robust during both head-fixed and natural behavior.

Interestingly, the HPC, EC, and subiculum were found to encode both spatial view and head-facing location (Figure 5b). We propose that, because primates saccade continuously to explore their environment, head-anchoring may provide a more stable representation (Mao et al., 2021). Specifically, head facing direction might provide a useful scaffolding for organizing more detailed information contained in the spatial view. Facing direction might itself be, in turn, scaffolded into more abstract variables like the animal's direction of heading in the world. Thus, information in the hippocampal formation might be organized hierarchically, with different levels of representation being appropriate for different tasks that involve navigation and memory retrieval. For instance, navigating in impoverished environments might rely on more abstract representations while feature-rich settings are likely to benefit from information about the spatial view. This perspective might help reconcile discrepancies in the relative proportions of different types of cells found under different experimental paradigms and across different species.

In summary, by disentangling traditionally intertwined variables, Mao et al. (2021) found that eye movements strongly modulate neural responses in the primate hippocampal formation during unconstrained, freely moving behaviors. The prevalence of eye movement representations in the primate hippocampal formation is not surprising, given that the eyes actively interrogate and efficiently gather information. The general consensus is that the reported eye movement encoding in navigation circuits may reflect task-relevant variables: for example, eye movements may reflect internal deliberation and the prioritization of goals in real-time (Gottlieb & Oudeyer, 2018; Yang et al., 2016; Yang et al., 2018), but the functional principles remain poorly explored. Next, we summarize two recent studies showing that eye movements during navigation primarily embody subjects' beliefs generated by their internal model (Lakshminarasimhan et al., 2020) or primarily reflect active sampling for improving their internal model (Zhu et al., 2022).

### 3 | UNDERSTANDING HPC THROUGH EYE MOVEMENTS

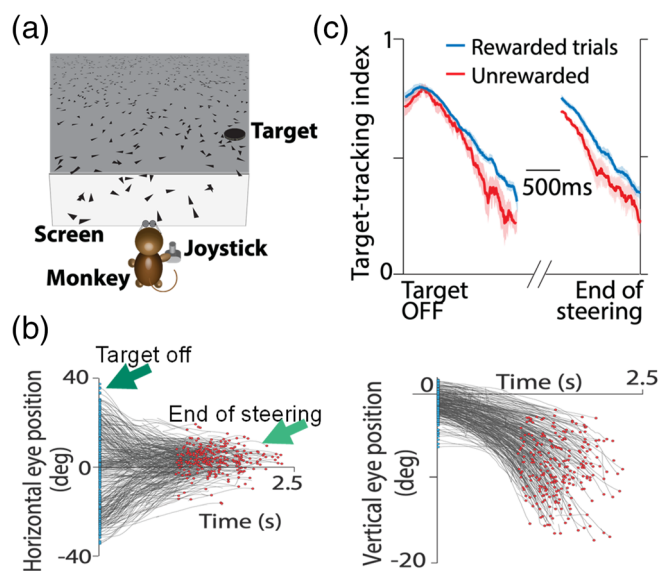
#### 3.1 | Eye movements embody internal beliefs during path integration

That vision facilitates navigation is easy to fathom. Navigators might compute their bearing with respect to a visible landmark, triangulate their allocentric position using combinations of landmarks, or even memorize sequences of landmarks to find their way (Rolls, 2021). But

there is much more to this, particularly in primates. To explore the neural basis of visual path integration, our lab designed a virtual reality task in which participants used a joystick to navigate to the location of a target after it disappeared (Lakshminarasimhan et al., 2018). Only transient visual stimuli, termed optic flow (Warren & Hannon, 1988), and/or vestibular cues conferred by a motion platform (Stavropoulos et al., 2022), were available to guide path integration. This task, reminiscent of "catching fireflies" at night, elicits naturalistic prey capture behaviors (Ngo et al., 2022) and the associated neural computations (Lakshminarasimhan et al., 2022; Noel et al., 2022). Humans and monkeys successfully integrated optic flow to navigate by path integration (Alefantis et al., 2022; Lakshminarasimhan et al., 2018; Stavropoulos et al., 2022).

The most remarkable behavioral finding was that oculomotor circuits contribute to *landmark-free* navigation. Both humans and monkeys track the invisible target with their eyes while performing path integration (Figure 6; Lakshminarasimhan et al., 2020). Navigation errors were correlated with target tracking errors, suggesting that participants' eye movements reflected their evolving internal beliefs about the target location. Accurate goal-tracking by gaze was associated with improved task performance, and inhibiting eye movements impaired navigation precision.

One potential explanation for these findings is that looking at the goal might optimize the structure of optic flow fields to facilitate the inference of self-motion (Land & Lee, 1994; Wann & Swapp, 2000). Alternatively, participants' gaze may have embodied the contents of



**FIGURE 6** Eye movements dynamics during virtual navigation using a joystick. (a) Firefly task. (b) Time-course of the horizontal and vertical eye position during a random subset of trials. Red dots denote the end of steering. (c) Accurate target-tracking is associated with increased task performance. Time-course of the target-tracking index shown separately for trials in which monkeys stopped within the reward zone (blue) or outside it (red). Shaded regions denote  $\pm 1$  standard error estimated by bootstrapping (from Lakshminarasimhan et al., 2020).

working memory (Hannula et al., 2010; Luke et al., 2018; Postle et al., 2006; Theeuwes et al., 2009). The latter hypothesis is supported by the observation that when human participants were required to navigate using only vestibular cues (in the dark), they still tracked the invisible target (unpublished observation). Memory offloading is a prime example of *embodied cognition* where the boundaries between perceptual, cognitive, or motor neural systems vanish due to the representations being distributed across neural systems (Bridgeman & Tseng, 2011; Foglia & Wilson, 2013; Shapiro, 2010; Wilson, 2002) and could facilitate observing the contents of the hippocampal memory-activation indirectly through behavior.

While the causal role of HPC in the above task remains to be tested, it is worth noting that spatial view cells outside the CA3 region of the macaque hippocampal formation remain responsive in the dark (Robertson et al., 1998). Furthermore, Wirth et al. (2017) describe a subset of hippocampal neurons that predicts the contents of the upcoming spatial view. This is reminiscent of neurons in the rodent EC predictive of spatial position, which have been implicated in path integration behaviors (Campbell et al., 2018; Campbell et al., 2021). Therefore, one possibility is that the activity of spatial view cells is relayed to oculomotor areas to support embodiment of the spatial location of the goal during path integration.

The virtual environment in the above experiments comprised a featureless ground plane with no structure. Consequently, those studies did not test the extent to which humans could navigate optimally in large state spaces with complex transition structure—a combination that makes sequential decision-making notoriously hard. How do humans perform planning in such settings? This was addressed by another experiment which we address next.

### 3.2 | Eye movements support navigational planning in structured environments

It just so happens that animals often navigate without planning substantially, such as by moving toward a visible beacon (Jain et al., 2017), although in more complex scenarios like driving through a city (Maguire et al., 2000), this strategy would be clearly inefficient. A navigator could also take a route from memory, and thus would not need to wrangle with a model of the environment (Shamash et al., 2021). However, humans have demonstrated flexible, sometimes stratified planning behaviors with impressive planning horizons (Balaguer et al., 2016; Mattar & Lengyel, 2022). Furthermore, humans (Liu et al., 2019) and rodents (Pfeiffer & Foster, 2013) exhibit neural evidence of rehearsing future action sequences never previously taken, which suggests that they skillfully use representations in the hippocampal formation to create their desired future (Erdem & Hasselmo, 2012; Erdem & Hasselmo, 2014; Kubie & Fenton, 2012). In fact, damage to the right HPC impairs allocentric model-based planning in humans (Vikbladh et al., 2019) and detour taking in rodents (Winocur et al., 2010).

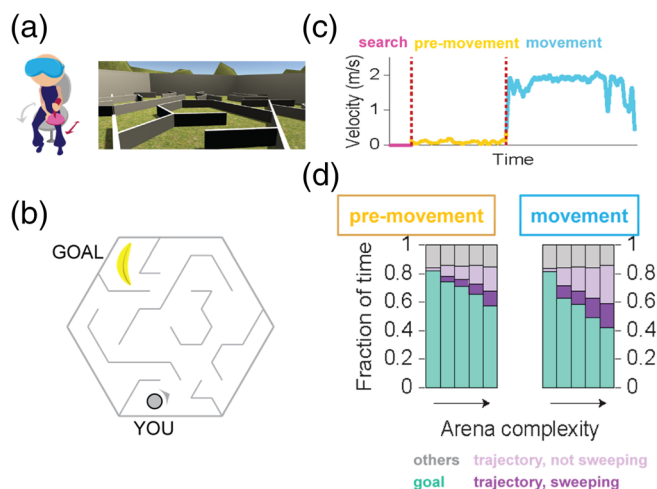
Planning, the evaluation of prospective future actions using a model of the environment, plays a critical role in sequential decision

making (Hunt et al., 2021; Mattar & Lengyel, 2022)—thus, also navigation. Planning might be loosely defined as using knowledge and evidence to make decisions about future actions and can be contrasted with acting out of habit (Hunt et al., 2021). Choosing an optimal sequence of actions requires knowledge of the transition model—a mapping from the current state to the successor state associated with each possible action. This makes sequential decision-making substantially harder particularly in large state spaces. Under unfamiliar or uncertain task conditions, planning may depend upon and occur also in conjunction with active sensing, the cognitively motivated process of gathering information from the environment (Kaplan & Friston, 2018).

In common between the diverse studies of planning (which constitute a subset of a much larger body of work) is the underlying assumption that a model should be well-learned before quality planning can take place. As spatial representations are grounded by sensory stimuli, it might then appear upon first glance that vision best serves planning through allowing for the learning of a cognitive map. But this may not be the whole story: Could it be that vision more directly serves planning (in the absence of a learned cognitive map) such that even forgetful animals in unfamiliar environments could make good plans? To answer this question, we designed a virtual reality navigation task where participants were asked to navigate to transiently visible targets using a joystick in unfamiliar arenas with obstacles of varying degrees of complexity (Zhu et al., 2022). Although the obstacles served as barriers, they were relatively short such that human participants could look beyond them and learn about the structure of the environment at distal locations. The key motivation is that the paradigm used in this study allowed participants to use eye movements to visually sample the environment and learn the transition model in conjunction with planning. What are the principles governing eye movements under these conditions?

First, Zhu et al. (2022) found that humans took trajectories nearly optimal in length through complex, unfamiliar arenas and they spent more time planning prior to navigation in more complex environments. Using the RL framework, they identified spatial locations in the arenas that are most relevant for planning. Simulations confirmed that agents that prioritize gathering information about the transition structure at the relevant locations substantially outperform other agents achieving near-optimal navigation performance with very few samples.

Second, Zhu et al. (2022) showed that humans can plan optimal trajectories for navigation while simultaneously using eye movements to visually sample the environment and learn the transition dynamics in conjunction with planning. In fact, human participants balanced foveating the hidden reward (i.e., remembered goal) location with viewing highly task-relevant regions of space both prior to and during active navigation, and that environmental complexity mediated a trade-off between the two modes of information sampling (Figure 7). The spatial distribution of gaze was largely concentrated at the hidden goal location in the simplest environments (as in the firefly task of Figure 6), but participants increasingly interrogated the task-relevant

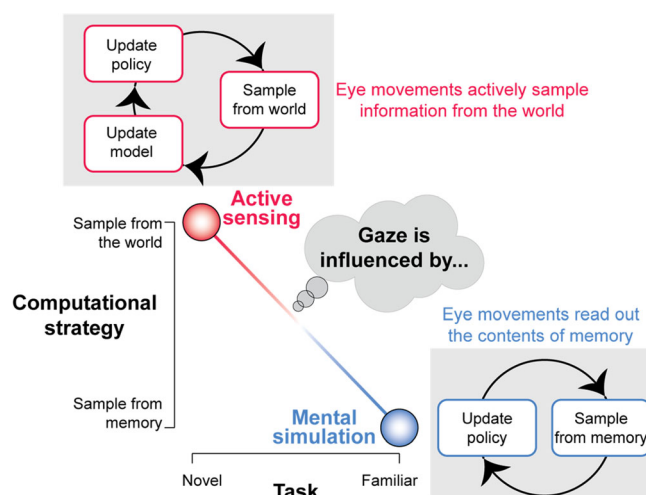


**FIGURE 7** Gaze is split between the remembered goal and chosen trajectory. (a) Human participants wore a VR headset and navigated mazes of varying complexity toward a memorized goal. (b) Overhead view of one of the mazes. (c) The search epoch was defined as the period between goal stimulus appearance and goal stimulus foveation. A threshold applied on the filtered joystick input (movement velocity) was used to delineate the premovement and movement epochs. (d) Fraction of time gaze follows goal (target, green) versus the chosen trajectory (purple). There is a trade-off between gathering information about the relevant aspects of the environmental structure and looking at the remembered goal location based on environmental complexity (from Zhu et al., 2022).

structure of the environment as the arena complexity increased. In the temporal domain, participants often rapidly traced their future trajectory to and from the goal with their eyes (sweeping), and generally concentrated their gaze upon one subgoal (turn) at a time until they reached their destination. In fact, participants made sequential eye movements sweeping forward and/or backward along the future trajectory, reminiscent of sequential neural activity in the rodent HPC.

### 3.3 | Role of HPC in planning

Whether these forward and reverse sweeping sequences relate to hippocampal temporal sequences remains to be explored. We hypothesize that direct or indirect hippocampal projections to higher oculomotor controllers (e.g., the supplemental eye fields through the orbitofrontal cortex) may allow eye movements to embody the underlying activations of state representations (Hannula & Ranganath, 2009; Larson & Loschky, 2009; Wilming et al., 2017). This would allow memory replays to influence eye movements (Figure 8, “mental simulation” or planning). Alternatively, but not mutually exclusive, active sampling could be a result of rapid peripheral vision processing which drives saccade generation, such that the eye movements reflect the outcome of sensory processing rather than prior experience (Figure 8, “active sensing”). Consistent with this idea, past studies have demonstrated that humans can smoothly trace paths through entirely novel 2D mazes (Crowe et al., 2000; Crowe et al., 2004).



**FIGURE 8** Hypothesis of how to model the cognitive factors driving eye movements during navigation. In novel environments, eye movements might be used primarily to sample information from the world to learn a model via active sensing (left). In familiar environments with a good internal model, eye movements might primarily embody mental computations such as internal deliberation or planning, and thus correspond to samples from memory (right).

Planning and active sensing share many similarities. In fact, Hunt et al. (2021) noted that both processes lead to the creation of new policies, although the source of information is one's cognitive map during planning (Callaway et al., 2022), while the source of information is the environment during active sensing (Hunt et al., 2021). However, the actions chosen by planning using an internal model stored in memory (Mattar & Daw, 2018) and those chosen by active sensing to minimize uncertainty in that internal model (Yang et al., 2018) may coincide if the respective state spaces governing the two cognitive processes are aligned, which is likely the case when we go about our lives mindfully, watching where we are going. This is indeed the assumption underlying the active inference theory, which provides a computational and process-level account of how model-based planning and model learning occur simultaneously, serving the general principle of minimizing surprise (Friston et al., 2016; Kaplan & Friston, 2018; Parr & Friston, 2019).

We propose that these principles governing the functional roles of eye movements during visually guided navigation may explain why the contents of gaze have been found to influence activity in the primate HPC and EC (Fotowat et al., 2019; Jun et al., 2016; Liu et al., 2017; Monaco et al., 2014; Ringo et al., 1994; Turk-Browne, 2019). Therefore, it is conceivable that sequential neural activity could emerge partly from consolidating temporally extended eye movements such as sweeps into a map of spatial relationships. Simultaneous recordings from brain areas involved in visual processing, eye movement control, and the hippocampal formation would uncover the mechanisms underlying trajectory sweeping eye movements and their relationship to planning and memory.

Taken together, we propose that the spatiotemporal dynamics of gaze are significantly shaped by cognitive computations underlying



sequential decision-making tasks like navigation. The neural circuitry governing the oculomotor system optimally schedules and allocates resources to tackle the diverse cognitive demands of navigation, producing efficient eye movements through space and time. Planning is often regarded as a covert computation involving mental simulation which is similar to directing covert attention toward one's memory without the movement of a sensory apparatus. The premotor theory of attention states that premotor circuits covertly orient attention, even if no movement is made during active sensing (Rizzolatti et al., 1987). The theta rhythm may play a major role in this process (Buzsáki, 2002). However, as demonstrated by Zhu et al., 2022, planning may also take place in conjunction with active information search which can be overtly studied through tracking the movements of animals' sensory apparatuses (Hunt et al., 2021).

Eye movements can reveal the dynamics of active sensing during many common tasks like viewing natural images (Noton & Stark, 1971; Yarus, 1967), searching for a target stimulus (Najemnik & Geisler, 2005), and making decisions via visual inference (Orquin & Mueller Loose, 2013). We here recapitulate the definition of active sensing as sensing guided by attention and intent (Schroeder et al., 2010; Wundt, 1902; Zweifel & Hartmann, 2020). Where you direct your fovea in visual space during active sensing is where you direct your spotlight of attention, and this spotlight is moved during saccades to turn visual information into a temporal sequence of samples. Incidentally, RL provides a formal interpretation of active sensing, which can be understood as optimizing information sampling for the purpose of improving knowledge about the environment, allowing for better planning and ultimately greater long-term reward (Yang et al., 2018). Just as a note, although we have been discussing vision and overt active sensing, sensing.

## 4 | CONCLUDING REMARKS

The differences between the signals found in the primate versus the rodent hippocampal formation are consistent with the species' divergent adaptations evolved over time. While rodents might learn a model of the environment mainly through physical experience, primates have evolved highly advanced visual and semantic systems to rapidly gather the most relevant information (Huberman & Niell, 2011; Prusky & Douglas, 2004).

However, these findings do not preclude that the common thread between the mammalian hippocampal formations of different species involves the interplay between a structural code, sensory inputs, and conjunctive binding (Mathis et al., 2015; Whittington et al., 2020), and that these codes serve prediction and is updated through replay. The multiplexed nature of the hippocampal code (Gulli et al., 2020; Mao et al., 2021) supports the previously hypothesized role that it plays in binding information about relational structure to sensory information (Whittington et al., 2020). Replay has been observed in humans (Liu et al., 2019; Schapiro et al., 2018; Schuck & Niv, 2019), and behavioral evidence of replay

has been recorded in monkeys (Shushruth et al., 2022; Zuo et al., 2020). Uncovering neural evidence of replay in monkeys may require the combination of innovative experimental paradigms, advanced computational methods to detect sequential activity from sparse data, and more powerful recording techniques to capture the responses of many spatially tuned neurons in the HPC simultaneously.

On the other hand, spatial place and grid cell tuning is at best weak in monkeys and humans, although grid like firing was exhibited by humans evaluating stimuli along arbitrary dimensions like neck and leg length (Constantinescu et al., 2016), olfactory space (Bao et al., 2019), semantic space (Viganò et al., 2021) and object spaces (Mack et al., 2016). It is conceivable that the structural code in primates is high-dimensional (Mathis et al., 2015) and flexibly modulated by task demands, such that it does not reveal itself as a place/grid during physical navigation, although it becomes effectively low-dimensional when the attended stimulus is on a flat screen (Killian et al., 2012). Nevertheless, hippocampal activation during abstract space navigation has also been described in rodents (Aronov et al., 2017; Sun et al., 2020).

One possibility is that the capacity for abstraction, as conferred by a more advanced neocortex, is accompanied by the capacity for mental travel to locations and concepts outside of the body (Corballis, 2019; Tulving, 1985), and the neural apparatus originally evolved to represent an animal's immediate position in their subjective model of the world now primarily encodes (in species like primates) the locus of attention in an appropriately allocated neural subspace. For example, in a virtual reality study where humans learned about the location and identity of treasures by exploring an arena from an egocentric perspective, but performed spatial recall from an allocentric vantage point, researchers observed that electrophysiological signals in the HPC mainly reflect allocentric goal locations (Tsitsiklis et al., 2020).

Perhaps in primates, most natural behaviors entail mentally traveling through a series of abstract goals and subgoals, and then bridging our bodies to where our minds are. In studies of eye movements during everyday tasks, humans tend to look at the bounce point of balls, the end point of reaches, the principal ingredient in next step of a long procedure like making a sandwich, and so on (Foulsham, 2015; Hayhoe & Ballard, 2005; Land & Hayhoe, 2001). Since the head facing location or gaze of an animal often reflects its object of attention, it makes sense that the contents of vision and eye movements are often reflected in the activity of the hippocampal formation as new spatial relationships are being learned via active sensing (Zhu et al., 2022). On the other hand, eye movements observed during path integration by humans and monkeys suggest a cognitive advantage of embodying through gaze the contents of core cognition (Lakshminarasimhan et al., 2020). Such an embodiment is most likely to occur in familiar environments, reflecting the contents of memory recall or mental simulation and involve information flow in the other direction: from the hippocampal formation to cortical areas controlling eye movements. Developing a comprehensive computational theory of the mechanisms governing learning and planning in primates requires further

empirical studies of bidirectional communication between hippocampal formation and oculomotor centers during naturalistic behaviors.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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