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From peripersonal space to cognitive maps: An evolutionary perspective

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ABSTRACT

Our brains support at least two major spatial representations: an egocentric, short-horizon representation of peripersonal space (PPS), and an allocentric, longer-horizon cognitive map system. Here, we speculate on their relationship from an evolutionary perspective. We argue that an ancient proto-PPS system for contact prediction likely emerged early in vertebrate evolution as a fight-or-flight mechanism for managing imminent threats, supported by evolutionarily conserved midbrain circuits such as the optic tectum (superior colliculus in mammals). The subsequent transition of many species from aquatic to terrestrial environments dramatically expanded sensory ranges and environmental complexity, arguably creating selective pressures for longer-horizon navigation, prediction, and planning. These pressures likely contributed to the emergence of hippocampal and entorhinal systems supporting allocentric spatial representations. Next, as navigation and foraging behaviors became more sophisticated and required dexterous multi-joint movements, it is possible that a cortical PPS system emerged within neocortical networks, including posterior parietal and ventral premotor cortices. Rather than mediating coarse fight-or-flight responses, we suggest this cortical PPS system now supports fine-grained hierarchical sensorimotor control, reference-frame transformations, tool use, and social interactions. In parallel, the allocentric mapping systems seemingly expanded beyond spatial navigation to support relational, conceptual, and abstract cognitive structures. We suggest that PPS and cognitive maps instantiate shared computational principles operating at different spatial and temporal scales and in different reference frames; a view supported by recent reinforcement-learning frameworks linking body-centered and allocentric predictive value. Together, this perspective points to a putative scaffolded evolutionary trajectory in which cognition may have expanded from near-body safety to a multiscale predictive architecture supporting flexible, goal-directed behavior across space and time.

1. Introduction

Space is a primary ecological currency. The spatial structure of our environments determines access to food, mates, and shelter while simultaneously shaping exposure to predation and other threats. Across species, evolutionary fitness depends on balancing these opportunities and risks across spatio-temporal scales, as captured by ethological and ecological frameworks such as “flight initiation distance“, “refuge use“, and “dynamic landscapes of fear“ (Ydenberg and Dill, 1986; Lima and Dill, 1990; Brown et al., 1999; Kavaliers and Choleris, 2001). These frameworks highlight that the value of a given location is not fixed but varies with distance to dynamic threats and resources, time to contact, and the actions available (i.e., affordances) at different spatial and temporal scales.

Neural systems that encode space must therefore support behaviors across a diversity of spatiotemporal horizons (Maisson et al., 2022). One concerns the space immediately surrounding and adjacent to the body, where threats and afforded opportunities unfold within milliseconds and where action must often be reflexive. The other concerns the broader environment, which extends far beyond reach, where relevant events may be minutes or hours away, and where fitness depends on remembering locations, predicting future states, and evaluating alternative

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routes. Interestingly, these different spatial regimes seemingly have corresponding neural architectures: an egocentric, short-horizon encoding of peripersonal space (PPS) immediately adjacent to and surrounding the body (Rizzolatti et al., 1997; Graziano and Cooke, 2006), and an allocentric, longer-horizon, world-centered cognitive map supporting navigation, memory, and planning (Tolman, 1948; O'Keefe and Nadel, 1978). In other words, PPS governs the "*here and now*," whereas para-hippocampal allocentric maps enable animals to reason about the "*there and then*".

Although these systems are often studied separately—PPS in classic macaque neurophysiology (e.g., Rizzolatti et al., 1997) and current cognitive neuroscience (e.g., Noel et al., 2021), and cognitive maps most commonly within rodent systems neuroscience (Behrens et al., 2018)—here we argue that they may be best understood together. We do not aim to provide a comprehensive review of either the PPS (Serino, 2019) or cognitive maps (Behrens et al., 2018) literature. Instead, the novelty of this contribution is adapting an evolutionary lens in both these sub-fields, and examining how they may relate to one another. Indeed, throughout this piece, we develop an evolutionary argument to speculate on if and how these systems may share common principles and could reflect a scaffolded relationship. Importantly, the distinction between peri-personal versus extra-personal space on one hand, and egocentric versus allocentric reference frames on the other, are conceptually related but not equivalent. Indeed, distance from our bodies (i.e., peri- versus extra-personal space) is inherently sensed and defined in egocentric terms, such that egocentric coding spans both near and far spaces. By contrast, allocentric representations encode relationships between elements in the environment independent of the observer. As such, allocentric coding is not necessarily tied to a particular distance regime, but is most often particularly advantageous in extra-personal space, where evaluating distal, non-immediate, or counterfactual interactions between environmental elements becomes necessary. In what follows, we therefore may use the shorthand of linking allocentric coding with extra-personal space and egocentric coding with peri-personal space to describe dominant functional roles, but we must emphasize that this mapping is neither exclusive nor exhaustive.

2. A Potentially scaffolded evolutionary trajectory: from bilateral symmetry to cognitive maps

The neural architecture for spatial cognition likely emerged through a series of cumulative evolutionary innovations, each transforming how animals represent and interact with space. Here we outline four major evolutionary transitions that putatively scaffolded the evolution of both the PPS and the cognitive map systems. Subsequent sections develop this proposal in further detail.

We argue that the first evolutionary transition occurred approximately 600 million years ago, with the origin of bilateral symmetry (Evans et al., 2020). This new body plan established directional locomotion. Organisms now had a clear front and back, enabling forward movement through space. We argue, this newly developed bilateral symmetry necessitated the first egocentric reference frames, as animals needed to distinguish "ahead" from "behind", and "left" from "right" relative to their body axis. This fundamental coordinate system likely enabled near-sensing forward models that anticipated imminent encounters with objects and conspecifics during locomotion. We suggest these early sensorimotor circuits, computing variables such as time-to-contact (Shang et al., 2015) for objects in the animal's path, putatively formed the evolutionary scaffold for what would later become the PPS system. Importantly, at this evolutionary stage, spatial representation was purely egocentric and short-range—there was no "far space" to encode.

The second and perhaps most consequential transition occurred approximately 380 million years ago, when vertebrates moved from water to land (Clack, 2002; MacIver et al., 2017). This transition may have restructured spatial cognition in two fundamental ways. First, it must have vastly expanded sensory horizons. While aquatic environments restrict visual range to a few body lengths due to turbidity and light scattering (Nilsson et al., 2014), the move to land increased visual range by orders of magnitude (MacIver and Finlay, 2022). Early animals evolved enlarged eyes and altered eye orbit geometry before fully developing terrestrial limbs (MacIver et al., 2017), likely driven by scanning behavior from the water's surface into air. This would have enabled detection of objects tens and hundreds of meters away, transforming ecological interactions from millisecond reflexes into tens-of-seconds deliberations. For the first time in vertebrate evolution, sensory information extended far beyond the animal's immediate surroundings. Second, terrestrial habitats introduced structured spatial complexity—a patchwork of cover, obstacles, and open areas that permitted multiple potential future scenarios and favored planning across spatial scales (Mugan and MacIver, 2020). We argue that this combination of expanded sensory ranges and environmental heterogeneity could have created selective pressures for allocentric spatial representations and early hippocampal planning mechanisms capable of integrating information across longer horizons. An intriguing corollary of this transition is that what may have begun as a true near-sensory horizon—the physical limit of perception in murky water— arguably became a computational "boundary" that persists in modern vertebrates today, even when sensory limitations no longer apply. Indeed, contemporary mammals, including humans, maintain distinct neural encodings of peri- versus extra-personal space (Rizzolatti et al., 1997; Graziano and Cooke, 2006), yet this distinction largely lacks phenomenological salience. We do not consciously experience visual space near our hands as qualitatively different from distant visual space, even though our brains process them differently. This suggests that PPS representations, potentially initially shaped by genuine perceptual constraints in aquatic environments, may have been retained and elaborated as a functional computational architecture even as perceptual and environmental constraints dissolved on land.

A third evolutionary transition may have occurred in early amniotes approximately 320 million years ago, marked by major expansion of the forebrain, including precursors of the mammalian hippocampus and parietal cortex (Rodríguez et al., 2002; Murray et al., 2017). This neural expansion may have provided the substrate for more stable allocentric mapping and longer-horizon spatial memory, enabling animals to maintain persistent world-centered representations even when displaced from familiar locations. Arguably, neocortical PPS systems may have concurrently emerged, particularly within posterior parietal and ventral premotor regions. Rather than mediating coarse fight-or-flight responses like their midbrain precursors, these cortical PPS representations may support finer-grained hierarchical sensorimotor control, reference-frame transformations across different end-effectors, and flexible action selection (Andersen and Cui, 2009; Serino, 2019). Indeed, it is possible that this transition reflected a shift in the nature of contact prediction. Midbrain-guided proto-PPS systems appear well suited to detecting looming stimuli and encoding time-to-contact based on retinal expansion signals (Shang et al., 2015), potentially operating in predominantly retinocentric coordinates. By contrast, an evolutionarily newer cortical PPS system may support more flexible, body-centered predictions of future contact, including situations in which objects are on a collision course with body parts not directly aligned with the current retinal image. Taken together, the putative elaboration of cortical PPS networks alongside hippocampal cognitive maps could suggest a co-evolutionary relationship between near-body action control and far-space planning systems. We must emphasize that this account is necessarily speculative and intended to generate hypotheses (e.g., time horizons and reference-frame dependance of SC vs. cortical PPS time-to-contact neurons), rather than to assert a definitive evolutionary sequence.

Lastly, we argue a fourth transition impacting neural spatial codes occurred in primates approximately 55 million years ago, with the evolution of stereoscopic vision and fine-grained manual dexterity.

These newly acquired capacities must have imposed strong computational demands on near-space representation, putatively driving further elaboration of cortical PPS circuits to support reaching, grasping, and ultimately tool use (Iriki et al., 1996). The development of semi-upright and fully upright postures, along with terrestrial bipedalism, freed the hands from locomotor constraints and enabled specialized manipulation within PPS. Indeed, the primate brain hosts extensive parietal-frontal networks with multisensory-to-motor functions underlying reaching (middle intraparietal sulcus, MIP-F2), reaching-to-grasp and grasping (anterior intraparietal sulcus, AIP-F5), and the PPS system itself (VIP-F4). In parallel, these species developed complex social structures, and PPS systems may have expanded to encode social interactions unfolding within shared PPS (Caggiano et al., 2009; Ishida et al., 2010; Brozzoli et al., 2014; Noel et al., 2020, 2022). Meanwhile, it is possible the hippocampal and entorhinal systems generalized beyond spatial navigation to support relational, conceptual, and abstract cognitive structures (see Eichenbaum and Cohen, 2014 and Behrens et al., 2018 for arguments suggesting the involvement of the para-hippocampal system in higher-order cognition, although this is still an active area of research).

Synthesizing across these transitions, we speculatively propose a scaffolded evolutionary trajectory with four broad stages. First, early vertebrates relied primarily on a primitive proto-PPS system computing time-to-contact and supporting near-instant defensive behaviors, mediated by evolutionarily conserved midbrain circuits such as the optic tectum (superior colliculus in mammals). Indeed, classic work demonstrates neural sensitivity to looming stimuli and collision-course trajectories in birds and non-mammalian species (Wang and Frost, 1992; Frost and Sun, 2004; see Shang et al., 2015, 2018 for evidence in rodents), and similar computations are widespread in aquatic species where rapid approach detection is critical for survival. Second, the water-to-land transition could have catalyzed the emergence of hippocampal allocentric representations (O'Keefe and Dostrovsky, 1971; Moser et al., 2008), as expanded sensory ranges and environmental complexity made planning computationally advantageous. Third, egocentric and allocentric systems began to co-evolve, each scaffolding the other. This co-evolution could explain commonalities between the systems—for instance, both showing velocity-dependent modulations (Geisler et al., 2007; Gupta et al., 2012; Fogassi et al., 1996; Noel et al., 2018), and both putatively sharing computational underpinnings in reinforcement learning (see below; Stachenfeld et al., 2017; Bufacchi and Iannetti, 2018; Bufacchi et al., 2025). Fourth, the putative co-evolution between the cortical PPS system and the cognitive map para-hippocampal system may have imbued each of these systems with additional "non-spatial" capacities, such as their roles in social cognition or even the subjective sense of self-location and the broader coding of bodily self-consciousness (Ionta et al., 2011; Petkova et al., 2011; Guterstam et al., 2015; Noel et al., 2015, 2019; Bertoni et al., 2026). Together, this perspective reveals that spatial cognition could have expanded from near-body sensing and safety to a multiscale predictive architecture supporting flexible, goal-directed behavior across time, space, reference frames, and conceptual landscapes.

The subsequent sections detail the putative neural and computational properties of PPS and cognitive maps, building on this proposed evolutionary foundation.

3. Peripersonal space: the egocentric short-horizon safety margin

Peripersonal space (PPS) refers to the depth-limited region of space surrounding the body in which events can lead to physical contact and therefore require rapid detection and action (Fig. 1**A**). Seminal studies in macaques described neurons, most prominently in ventral premotor cortex (area F4) and posterior parietal cortex (notably ventral intraparietal area, VIP), but also in the putamen and related structures, that respond both to tactile stimulation on the body, as well as to visual or auditory stimuli presented near the same body part (Rizzolatti et al., 1981; Graziano and Gross, 1993; Graziano et al., 1997). These neurons exhibit several properties that have since become defining features of PPS representations. First, their receptive fields are anchored to specific body parts: movements of the head or limbs (but not the eyes) shift the visual or auditory receptive fields so that they remain aligned with the same skin region (Graziano et al., 1994; Duhamel et al., 1998; di Pellegrino et al., 1997). Second, these neurons respond more vigorously to dynamic rather than static stimuli, and preferentially to approaching rather than receding objects (Graziano et al., 1997; Serino et al., 2015a). Third, their depth-limited three-dimensional receptive fields expand as a function of stimulus velocity, such that faster-approaching objects are represented at greater distances (Fogassi et al., 1996; Noel et al., 2018). Stimulation of PPS-related regions can elicit defensive behaviors, including ducking, arm withdrawal, or protective postures (Cooke and Graziano, 2004), and stimuli presented within PPS selectively activate

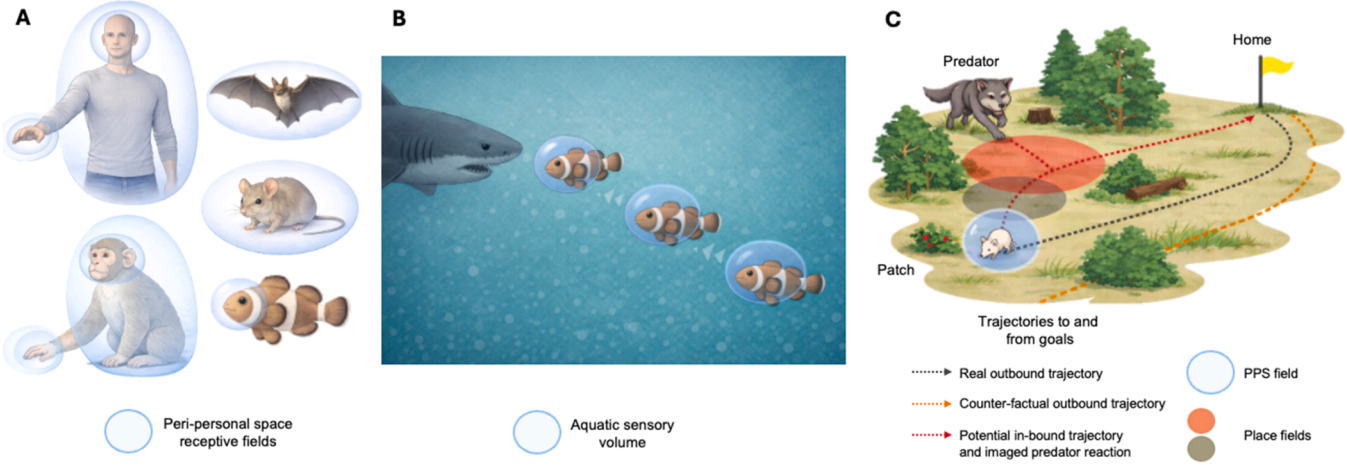

Fig. 1. Peri-personal space, sensing horizons, and cognitive maps. (A). Peri-personal fields (blue) schematized around a human and non-human primate hand, face, and trunk. We also speculatively draw peri-personal space receptive fields around bats, mice, and fish, though this has not been demonstrated empirically. This panel renders homage to the classic Graziano and Cooke diagram (Figure 4 in Graziano and Cooke, 2006). (B) The aquatic sensory volume (i.e., what is perceivable) is small and only allows for near sensing and immediate reactions. Inspired by figure 7 A in MacIver & Finlay, 2021. (C) On land, sensory volumes are larger and environments are more complex, rending planning adaptive. Here we show the PPS field (blue) still around the animal (mouse), but also allocentric place-cell codes, which may tile different potential trajectories and allow for spatio-temporally more extended cognition. Inspired by figure 7E in MacIver & Finlay, 2021.

corticospinal pathways (Makin et al., 2009), underscoring the tight coupling between perception and action in this near space. Together, these properties suggest that PPS networks implement a mechanism for predicting imminent contact and initiating appropriate defensive or avoidance responses. Consistent with this view, Cléry and colleagues demonstrated using neuroimaging and psychophysics that primate PPS networks encode both spatial and temporal predictions of impending touch (Cléry et al., 2015, 2017). To our knowledge, however, a single-neuron correlate demonstrating that PPS neurons perform spatio-temporal contact prediction is still lacking.

Although PPS has been most thoroughly characterized in humans and in non-human primates (Fig. 1**A,** left column), behavioral signatures consistent with PPS-like functions appear across a wide range of species, suggesting that a more primitive proto-PPS system may predate its canonical cortical implementations. For instance, many animals maintain well-defined safety zones surrounding the body (Hall, 1966). For example, insects rapidly withdraw or initiate escape when objects breach a minimal surrounding airspace (Card and Dickinson, 2008; Card, 2012; Dürr and Schilling, 2018); cockroaches rely on wind-sensitive cercal hairs to detect airflow perturbations and trigger evasive responses (Camhi and Tom, 1978); fish execute Mauthner-cell-mediated C-starts when the retinal image of a looming stimulus reaches a critical angular threshold (Preuss et al., 2006); and cephalopods transition from freezing to inking or jetting when threats cross specific distance boundaries (York and Bartol, 2016). Similarly, rodents seemingly make predictions regarding the future position of visual stimuli, with looming stimuli eliciting escape behavior while overhead sweeping trajectories elicit freeze behavior (Yilmaz and Meister, 2013; De Franceschi et al., 2016). These responses imply an internal representation of near space that is egocentric, rapidly updated, and tightly coupled to the animal's action repertoire.

Beyond behavioral correlates, there is emerging neural evidence for PPS-like representations in distantly related vertebrates, though this work is rarely interpreted through the lens of PPS. For example, neurons in the SC of rodents encode variables related to time-to-contact and collision trajectories (Shang et al., 2015, 2018; Dean et al., 1989; Wang and Frost, 1992; Frost and Sun, 2004; Campagner et al., 2023). These responses are most often observed in the intermediate and deep layers of the SC, which are multisensory and sensorimotor, rather than in the superficial layers that primarily receive direct retinal input and encode visual features in retinotopic coordinates (Meredith and Stein, 1986; May, 2006; Basso and May, 2017). Nonetheless, these SC neurons encoding time-to-contact are highly sensitive to the spatiotemporal pattern of retinal image expansion associated with looming stimuli, rather than to object speed or size in isolation (Shang et al., 2015; Yang et al., 2020). This stands in contrast to cortical PPS representations described in primates, which appear to encode impending contact in more flexible, body-centered coordinates that generalize beyond purely retinocentric visual signals. In a related vein, Krishna et al., (2025) recently reported hippocampal neurons in bats tuned to egocentric auditory distance, with a strong bias toward very near distances. Echolocation call patterns exhibited abrupt transitions at specific distances, with call rates increasing sharply as objects approached, mimicking a PPS boundary. Notably, call rate modulated the decodability of object distance from neural activity, mirroring the enhanced sensitivity to approaching stimuli observed in cortical PPS systems. These findings suggest that such neurons may encode not only distance, but also the likelihood of imminent contact, consistent with normative formulations of PPS as a contact-prediction system (Straka et al., 2022; see also Guterstam et al., 2015 for evidence of human hippocampal engagement during manipulations of self-location).

In mice, La Chioma et al., (2019) demonstrated binocular disparity tuning across visual cortex, with the rostro-lateral visual area showing a particular preference for near distances. This higher-order visual area also responds to touch (Olcese et al., 2013), raising the possibility that these visuo-tactile neurons encode a PPS-like representation in rodents. We hypothesize that neurons in the rostro-lateral visual area of rodents may be functionally analogous to PPS neurons in macaque parietal and premotor cortex. If such neurons exist, we would expect them to: (1) encode longer time horizons than SC time-to-contact neurons (which are typically limited to ~1 s or less; Shang et al., 2015), while still prioritizing near over far space; (2) be less dependent on retinal expansion cues and capable of encoding impending contact even in their absence; and (3) exhibit broader context dependence, such as modulation of receptive fields by the velocity of approaching stimuli. It would also be important to characterize areas of convergence and divergence between PPS representations in cortex, the SC, and the para-hippocampal formation, in order to test hypotheses of convergent evolution. While it is likely that most, if not all, animals encode aspects of their immediate surroundings (for example, fish navigating in murky water), the co-variance across animals (i.e., comparative neurophysiology) of the presence and encoding complexity of para-hippocampal and cortical PPS representations across species remain largely unexplored. Mammals possess both a well-developed hippocampus and cortical PPS representations. Birds and reptiles have structures homologous to the mammalian hippocampus, but it is unknown whether they exhibit PPS representations. Fish lack a canonical hippocampus (but see below), and we believe it is likely they may also not possess a cortical-like PPS system. Instead, fish may exhibit a more primitive form of PPS without a clear distinction between peri- and extra-personal space. This remains an open area of research: to our knowledge, classically defined PPS neurons have not yet been formally identified in bats, mice, or other non-primate species (Fig. 1**A**, right column is speculative). The comparative study across species of the SC, para-hippocampal regions, and PPS-like representations will allow testing the herein expressed hypothesis of their co-evolution.

4. The water-to-land transition: a catalyst from reacting to planning

Although bilateral symmetry (~600 million years ago) and a proto-PPS likely provided an early foundation for spatial (re)action, we argue that the transition of many animals from water to land approximately 380 million years ago (MacIver et al., 2017) fundamentally restructured the computational demands placed on brains. The aquatic sensory environment imposes severe limitations: turbidity, light scattering, sound-wave dampening, and water density all restrict visual and auditory ranges to only a few body lengths (Fig. 1**B;** Nilsson et al., 2014). This produces a perpetual fog in which predators and prey are detected only at very short distances. For many fish, the entire interval between detecting a potentially dangerous approaching stimulus and needing to execute an escape maneuver is on the order of a second or less. Under these conditions, the effective temporal and spatial window for decision-making is extremely narrow, favoring rapid, reflexive policies over deliberation. There is little room for exploration, foresight, or evaluating multiple options. Survival depends on reflexive escape maneuvers, learned stimulus-response routines, and short-horizon predictions—precisely the regime wherein PPS-like systems excel.

By contrast, the move to land increased visual range by orders of magnitude (MacIver and Finlay, 2022). Fossil evidence suggests that proto-tetrapods evolved enlarged eyes shortly before they had fully developed limbs capable of terrestrial locomotion. This evolution was likely driven by scanning behavior from the water's surface into air, enabling these animals to detect objects at least tens of meters away and transforming ecological interactions from millisecond reactions into tens-of-seconds deliberations. MacIver and colleagues (2017, 2021) beautifully argue that this sensory expansion was a critical evolutionary event: longer preview time provides the conditions under which planning becomes computationally useful (also see Hunt et al., 2021). In addition to the increased visual ranges, terrestrial environments also introduced structured spatial complexity (Fig. 1**C**). Early land habitats such as Devonian wetlands and Carboniferous forests offered a

patchwork of cover, obstacles, and open areas. Unlike the relatively homogeneous underwater environment, terrestrial space permitted multiple potential future scenarios: a prey animal might freeze behind a rock, circle around a brush, or sprint toward a thicket. A predator might exploit occlusions or approach from different angles. Terrestrial environments are characterized by more frequent and more significant landmarks. In computational terms, the invasion of land effectively expanded the spatiotemporal state-space of survival, creating many more possible future trajectories and making the comparison of alternatives (i.e., counter-factual thinking) evolutionarily advantageous.

We suggest that the combination of long-range vision and moderate environmental complexity produces a state space in which mentally simulating alternative potential trajectories yields meaningful advantages. Indeed, simulations of predator-prey interactions show that planning produces minimal benefit under short-range aquatic-like conditions but dramatically improves survival under terrestrial-like conditions characterized by expanded sensory horizons and patchy structure (Mugan and MacIver, 2020). Habitual strategies that are effective in water fail under terrestrial uncertainty, whereas agents that simulate future paths outperform reactive ones. Supporting this *in-silico* work, recent empirical work has demonstrated that interactions with a predator in a simple open environment cause ballistic darting behavior in mice, while these same interactions in complex environments elicit increased path diversity, peeking, and even baiting behaviors (Lai et al., 2024). This demonstrates how the complexity of environments may cause a shift in computational balance, from reflexes to planning.

These evolutionary time-scale changes in how organisms may interact with their environment likely placed selective pressure on expanding and refining the hippocampal formation, which already existed in rudimentary form in early vertebrates. Comparative neuroanatomy suggests that in ancestral fish this pallial-hippocampal structure was small and supported only simple spatial functions, whereas early tetrapods and amniotes evolved enlarged forebrains and hippocampal regions commensurate with the demands of terrestrial navigation (Rodríguez et al., 2002; Murray et al., 2017; Ocaña et al., 2017). As spatial ranges expanded, we argue that selection increasingly favored circuits capable of supporting stable, world-centered representations. In mammals, these evolutionary pressures may have yielded hippocampal place cells that fire at specific world-centered locations (O'Keefe and Dostrovsky, 1971), grid cells in the entorhinal cortex forming a metric tiling of space (Hafting et al., 2005), and head-direction cells providing a directional vector (Taube et al., 1990), as long as stable environmental landmarks are present.

Seen in this light, the terrestrial transition shifted the balance from ancient habit-based stimulus-response circuits—likely centered on basal ganglia and SC homologs already present in jawless vertebrates—to slower, hippocampally mediated planning mechanisms capable of simulating alternative future paths. While much of the modern study of spatial codes in hippocampus and entorhinal cortex has still arguably focused on relatively short distances (i.e., on the order of meters; McNaughton et al., 2006; Moser et al., 2008), newer approaches are highlighting how these networks map hundreds and thousands of meters, if not more (Eliav et al., 2021, 2025; Palgi et al., 2025).

Importantly, these (and other) spatial cells do more than encode the animal's current location: they participate in prospective non-local activity. For example, some hippocampal cells encode distance from reward (Gauthier and Tank, 2018), and hippocampal ensembles, particularly during pauses at decision points, generate sweeps ahead along potential paths (Foster and Wilson, 2007; Johnson and Redish, 2007). In large environments, these non-local replay events are fragmented and depict behaviorally relevant events such as bat landings and conspecific interactions (Eliav et al., 2025). Intriguingly, the spatial extent of these sweeps increases with the animal's velocity of approach toward intersections (Gupta et al., 2012). This velocity-dependent look-ahead resembles the velocity-driven receptive field expansion observed in PPS (Fogassi et al., 1996; Noel et al., 2018). Unlike the PPS system, however, place cell sweeps are by definition a population code: the sweeps are defined by the successive activation of many place cells. In contrast, the expansion of PPS with velocity is a single-cell code. This parallelism across spatial systems and potential biological convergence not only suggest the intriguing possibility that PPS and place-cell codes are intertwined but may even suggest a specific neural motif wherein hippocampal populations project onto individual cortical PPS cells. We hypothesize that concurrent recordings of ensembles of place-cells and cortical PPS cells during an animal's approach to an intersection – a decision point – would demonstrate trial-to-trial covariance between hippocampal sweep distance, and the size of PPS receptive fields in depth.

Together, we suggest that the water-to-land transition may have catalyzed a shift from short-horizon PPS-like reactions to longer-horizon predictions. The hippocampus and associated circuitry, likely increasingly interacting with prefrontal cortex, became central to evaluating imagined and counterfactual outcomes, integrating memory with planning and reward, and enabling animals to solve spatial problems that extend far beyond their peri-personal sphere.

4.1. Putative tandem evolution of cognitive maps and expanded PPS affordances: time, social cognition, reference frames, and tool use

As hippocampal representations matured, they may have expanded beyond solely encoding physical space. A similar trajectory may have been followed by PPS neurons: originally encoding an entire umwelt which was necessarily restricted to the near space, to then encoding a boundary between the near and far spaces, and finally now encoding affordances (Gibson, 1979). We argue that the expansion of the encoding repertoire in para-hippocampal and PPS networks was most probably bootstrapped across these two systems, given the dynamic and hierarchical relationship between spatial navigation and object manipulation affordances: e.g., turning a doorknob (PPS) opens new potential navigational paths (hippocampus), while climbing a ladder (hippocampus) enables reaching a new desired object (PPS). This putative tandem evolution between cognitive maps and PPS affordances is a speculation – potentially falsifiable via comparative neurobiology – but one that is consistent with recent empirical work.

For instance, recent work suggests that hippocampal circuits may not only encode space, but also time: time cells fire at specific moments in behavioral episodes (Eichenbaum, 2014), and even evolutionarily ancient species such as bats possess neurons that code for time, either independently or in conjunction with spatial contexts (Omer et al., 2023). In humans, hippocampal lesions are associated with long-term memory deficits – even more so than navigation deficits (Nadel and Moscovitch, 2001) – and it is believed that the hippocampus largely contributes to self-projection, whether across space or time (Buckner and Carroll, 2007). There is also nascent evidence that the hippocampus may code for the location not only of the self, but also of others (Danjo et al., 2018; Omer et al., 2018) and even their identity, sex, social hierarchy, and affiliation (Ray et al., 2025). Lastly, there is some evidence that in modern mammals hippocampal-entorhinal circuits may encode conceptual and relational spaces using place- and grid-like codes (Constantinescu et al., 2016; Garvert et al., 2017; Aronov et al., 2017). People navigating a graph of social relationships or family trees, for example, seemingly recruit hippocampal signals analogous to those used in physical navigation (Garvert et al., 2017; Tavares et al., 2015; Schafer and Schiller, 2018; Park et al., 2020; Whittington et al., 2022). This convergence suggests that perhaps allocentric spatial maps were exapted into a more general cognitive map that encodes relational knowledge (see Behrens et al., 2018 for a review). Frameworks such as the successor representation (Stachenfeld et al., 2017) formalize this idea: hippocampal cells encode expected future state occupancy under a policy, enabling the brain to combine model-based planning with efficient habit learning.

The putative, expanded, hippocampal functions appear

phylogenetically widespread but unevenly distributed. Hippocampal spatial codes analogous to those in mammals are established in birds (Payne et al., 2021), and the hippocampus of both mammals (including bats) and birds exhibits non-local and/or offline activity believed to be involved in planning. However, whether, for instance, avian or chiropteran hippocampal representations extend to the same degree of abstract relational coding observed in mammals remains unknown. To the best of our knowledge, it is also not known if evolutionarily older, cold-blooded animals such as reptiles or fish show non-local hippocampal activity.

In parallel to the expansion of the computational abilities of the para-hippocampal formation, PPS networks and representations underwent their own expansions, particularly in species with the ability for dexterous manipulation or living in complex social habitats. A key refinement of PPS might have occurred with terradynamics causing the need for multi-joint limbs movement and fine dexterity within the PPS, and with primates consequently developing semi-upright and upright postures and terrestrial bipedalism, allowing hand specialization for manipulation. A canonical example is tool use. In classic experiments, monkeys trained to use a rake to retrieve rewards located in extra-personal space showed expansions of PPS to include the tip of the tool (Iriki et al., 1996). Neurons that previously responded to objects near the hand began responding to objects near the rake's distal end (Iriki et al., 1996; Serino et al., 2015b; see also Miller et al., 2018 for a broader discussion of tool incorporation into the body schema). This flexible incorporation of environmental objects indicates that cortical PPS is not merely a sensory or defensive boundary, but a representation of near-action space that supports goal-directed interactions: the tool literally expands the range of possible actions (i.e., the animal's affordances).

Modern PPS representations also integrate motivational and social information (Teneggi et al., 2013; Bogdanova et al., 2021; Taffou and Viaud-Delmon, 2014; Ferri et al., 2015; de Haan et al., 2016; Heed et al., 2010). For instance, PPS expands or contracts as a function of the quality of social interaction (Teneggi et al., 2013), stress level (Ellena et al., 2022), self-representation (Bertoni et al., 2023; Masson et al., 2021), and the perceived moral character of others (Pellencin et al., 2018). PPS encoding also appears more rigid, with sharper self–other boundaries, in psychiatric and neurodevelopmental conditions such as autism spectrum disorder (Noel et al., 2020, 2022). Consistent with this, humans and other primates adjust interpersonal distance based on emotional state, familiarity, and trust: approaching strangers or sick individuals elicit defensive PPS responses at greater distances than familiar or healthy individuals (Kennedy et al., (2009); Holt et al., (2014); Trabanelli et al., (2025)). Thus, a system originally selected to detect imminent bodily contact and trigger rapid reactions has gained high-level flexibility. It now supports social cognition, interpersonal coordination, and hierarchical affordances. In this sense, PPS may have expanded in parallel with the para-hippocampal network, moving from sensorimotor prediction to more abstract representations of self and other.

This putative tandem evolution suggests that spatial maps and cognitive maps mutually constrain and enrich each other. PPS operates in an egocentric perspective and supports near-immediate interactions. Hippocampal maps are allocentric and represent extended landscapes across longer time scales. Together, these systems likely form a unified predictive architecture integrating body-centered and world-centered information. Indeed, behavior and neural activity may alternate between PPS-driven "here and now" actions and hippocampal "there and then" planning, allowing individuals to exploit immediate surroundings while exploring future opportunities (see Fiebelkorn, Kastner, 2019, for a similar idea in a different domain). In this vein, an intriguing observation is that neurons in the hippocampus oscillate at a theta-frequency between local (ascending phase; trough to peak) and non-local (descending phase; peak to trough) coding (Hasselmo, 2005; Calvin et al., 2025). Thus, a falsifiable hypothesis of our current thesis is that PPS neurons may preferentially fire during hippocampal theta-ascending phases. In order words, if hippocampal and PPS networks bootstrapped one another, we may predict their activity is most aligned when the hippocampal network is in its preferred "here and now" state.

5. A unifying reinforcement learning perspective

Recent work suggests that reinforcement learning offers a common computational language through which to understand the interplay between short-horizon egocentric and longer-horizon allocentric maps. For example, Stachenfeld and colleagues (2017) showed that hippocampal place-cell activity can be understood as emerging from a successor representation that predicts future state occupancy. Because the successor representation encodes the expected discounted visitation of all future states, it supports instantaneous inference about transitions between any two states, unconstrained by spatial or temporal adjacency. In this way, the hippocampal code inherits both short-range structure and long-horizon spatial and temporal predictions from the successor representation. In this framework, there is in principle no distinct spatial or temporal horizon, but only selection between spatiotemporal representations.

More recently, Bufacchi and colleagues (2018, 2025) extended this reasoning to egocentric PPS maps. Indeed, when artificial agents were trained to maximize reward by either making or avoiding contact, they spontaneously form body-centered value fields that resemble PPS: akin to the biological PPS fields, these artificial fields expand with stimulus velocity (Fogassi et al., 1996; Noel et al., 2018), encode valence (de Haan et al., 2016), plastically incorporate tools (Iriki et al., 1996; Serino et al., 2015b), and scale with reward magnitude (see Bufacchi et al., 2025). In turn, Bufacchi and colleagues suggest that PPS may be a short-horizon analog to the successor representation studied in the hippocampal formation. Just as the sequence of activity of place cells may suggest a trajectory an agent takes through allocentric space, activity of PPS neurons would suggest a trajectory of an object through egocentric space, coded in terms of the actions that the object affords the organism. The empirical study regarding the function of PPS neurons (e.g., their roles in ecological behaviors and how they coordinate with hippocampal representations) is still very much an open area of research.

This convergence suggests that both PPS and cognitive maps instantiate predictive and complementary mechanisms, shaped by reinforcement learning and operating at different spatiotemporal scales but solving similar problems: anticipating the consequences of actions in dynamic environments. This suggests analogous functions across the PPS and cognitive map systems.

6. Conclusion

We speculatively suggest a four-stage evolutionary progression. First, early animals likely possessed a proto-PPS system that computed extremely near-space contact predictions and mediated transitions between flight, fight, and escape when threats approached contact range. This proto-PPS system likely reflected real sensory horizons. This system relied on egocentric representations and was probably implemented in ancient midbrain structures such as the optic tectum. Second, the transition of many animals from water-to-land may have dramatically expanded sensory horizons and environmental complexity, generating selective pressures for allocentric spatial maps and more mature hippocampal circuits capable of long-horizon planning and model-based evaluation. Third, egocentric and allocentric systems started to co-evolve, each scaffolding the other, and potentially driven by the dynamic and hierarchical nature of terrestrial affordances. Lastly, this co-evolution expanded the coding repertoire of both systems, with nascent evidence suggesting that the PPS and cognitive maps systems are involved in computational challenges beyond physical space. The tandem evolution would explain why we observe commonalities across the systems. For example, the fact that they both seem to encode social

variables (e.g., location of conspecifics), show velocity-dependent modulations, and may share a computational underpinning (i.e., reinforcement learning).

Future studies should better describe what are the structural and functional interactions between the PPS fronto-parietal network and hippocampal maps, and how these putative interactions change across the phylogenetic tree. As stated above, we may generate a number of hypotheses: e.g., (1) evolutionarily older "PPS-systems" putatively in the SC encode shorter time horizons and are more rigidly dependent on retinal expansion dynamics than evolutionarily younger cortical PPS representations, (2) there is a monotonic relationship between the coding repertoire of hippocampal and cortical PPS networks across species, (3) PPS and hippocampal networks are most coupled during theta-frequency ascending phases, when the latter also codes for "here and now." Phenomenologically, the two systems in humans might contribute to self-experience, the PPS to the bodily self and most clearly for the "here and now" (Blanke and Metzinger, 2009), and cognitive hippocampal maps more readily focused on the "narrative self", starting from the self but extending in time (Gallagher, 2000). How these two types of self-experience coexist, switch or interact is still an open question.

The overarching theme is that spatial cognition may have grown outward from a simple near-body safety buffer into a multiscale predictive architecture that enables flexible, goal-directed behavior. We argue that a potential early proto-PPS may have taught animals about the *here-and-now* of bodily interactions. Then, an allocentric map may have taught them about the *there-and-then* of navigation and planning. These modes of functioning seemingly coexist today, and putatively alternate in complex forms within individual-environment interactions. Together, these systems could form the foundations for the complex forms of imagination, foresight, and social coordination that characterizes advanced vertebrate cognition.

CRediT authorship contribution statement

Summbla Anjum: Writing – original draft. **Jean-Paul Noel:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization. **Andrea Serino:** Writing – review & editing. **Sosa Maria:** Writing – original draft.

Declaration of Competing Interest

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