Extending neural systems for navigation to hunting behavior

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Abstract

For decades, a central question in neuroscience has been: How does the brain support navigation? Recent research on navigation has explored how brain regions support the capacity to adapt to changes in the environment and track the distance and direction to goal locations. Here, we provide a brief review of this literature and speculate how these neural systems may be involved in another, parallel behavior—hunting. Hunting shares many of the same challenges as navigation. Like navigation, hunting requires the hunter to orient towards a goal while minimizing their distance from it while traveling. Likewise, hunting may require the accommodation of detours to locate prey or the exploitation of shortcuts for a quicker capture. Recent research suggests that neurons in the periaqueductal gray, hypothalamus, and dorsal anterior cingulate play key roles in such hunting behavior. In this review, we speculate on how these regions may operate functionally with other key brain regions involved in navigation, such as the hippocampus, to support hunting. Additionally, we posit that hunting in a group presents an additional set of challenges, where success relies on multicentric tracking and prediction of prey position as well as the position of co-hunters.

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Movement on our planet is a unifying feature for a vast number of animals. For much of our history, humans have been nomadic, moving in search of locations where food can be gathered or hunted. Our capacity to flexibly navigate—accommodating unexpected obstacles—has been a key to our success as a species. This is also true for many other species who have adapted to navigate a wide variety of challenging terrains. How the brain supports such behavior has been and continues to be an important question in neuroscience.

Research over the last decades has provided an impressive level of understanding for how different brain regions may support navigation, with a network of brain regions now known to be important for different aspects of navigation [13]. This brain network includes the striatum, hippocampus, parahippocampal regions, retrosplenial cortex, posterior parietal cortex, and the anterior thalamus [13,12,46,4]. Neurons in the hippocampus and other structures express activity associated with self-position within an environment (e.g. place cells), whereas other neurons appear to encode heading direction within an environment [16]. Pioneering discoveries in this area led to the proposal that the hippocampus provides a cognitive map to support flexible navigation, allowing the navigator to overcome detours and exploit shortcuts by the activity of cells coding for the structure of the environment and the direction to the goal [31]. Recent work has shown how such place and direction coding neurons may be modulated by the distance and direction to the goal [13]. For example, population activity in the dorsal CA1 region of the rodent hippocampus can depict the direction of future trajectories before the onset of goal-directed navigation [37], or code the distance to the goal [53]. Some neurons in the dorsal CA1 of flying bats have been found to be tuned to the specific distances to a goal location (e.g. maximally active at 2 m from the goal), while others have been reported as tuned to the egocentric direction to the goal (e.g. maximally active when a goal is 45° to the right), and others a combination of distance and direction [42].

Neuroimaging research with humans has also explored how brain regions in the wider network might contribute to coding information during navigation. A number of studies have reported distance to goal (within newly learned environments) to be correlated with activity in the hippocampus or entorhinal cortex [2,8,18,35,47,52,56]. More specifically, activity in the posterior hippocampus has been found to track path distance to the goal and entorhinal activity to track distance along the Euclidean vector to the goal [18,52]. Activity in the entorhinal cortex/

subiculum has also been found to be modulated with the allocentric direction to goal locations, for example, 45° north [7,48], thus consistent with the entorhinal/ subicular regions coding for an allocentric vector to goal locations. In addition to identifying the involvement of "classic" navigation brain regions in flexible navigation – that is, the hippocampus and entorhinal cortex – recent research suggests a role for another set of brain regions to include the dorsal striatum, anterior cingulate, and posterior parietal regions. The posterior parietal cortex appears to code for the egocentric (one's heading) direction to a goal [7,18,52]. And, despite the traditional role of the striatum as a "habit" structure, recent evidence suggests the dorsal striatum may be important for updating and representing the transition structure of possible routes through an environment [14,49]. This line of evidence further suggests the dorsal striatum may coordinate with the hippocampus to guide flexible navigation of recently learned environments [15].

In addition to brain regions involved in tracking the distance, direction, and routes to a goal, regions in the prefrontal cortex appear important when adapting to unexpected forced detours (see Figure 1a) and subsequently planning over possible paths [19,21,22, 28,36,40,59]. Within the prefrontal cortex, the dorsal anterior cingulate (dACC) has been found to be a key region, implicated in adjudicating between routes [24], tracking the distance to the goal [18], and underlying the decision to abandon the current route and subsequently back-track along one's route [23*]. Such patterns of activity are consistent with the dACC playing an important role in the monitoring and control of actions [41] or representing task-state variables for planning [17].

The dACC has also recently been implicated in another dynamic goal-directed task—hunting [61**]. Hunting inherently involves many of the same behavioral and computational challenges as spatial navigation. This is

Figure 1
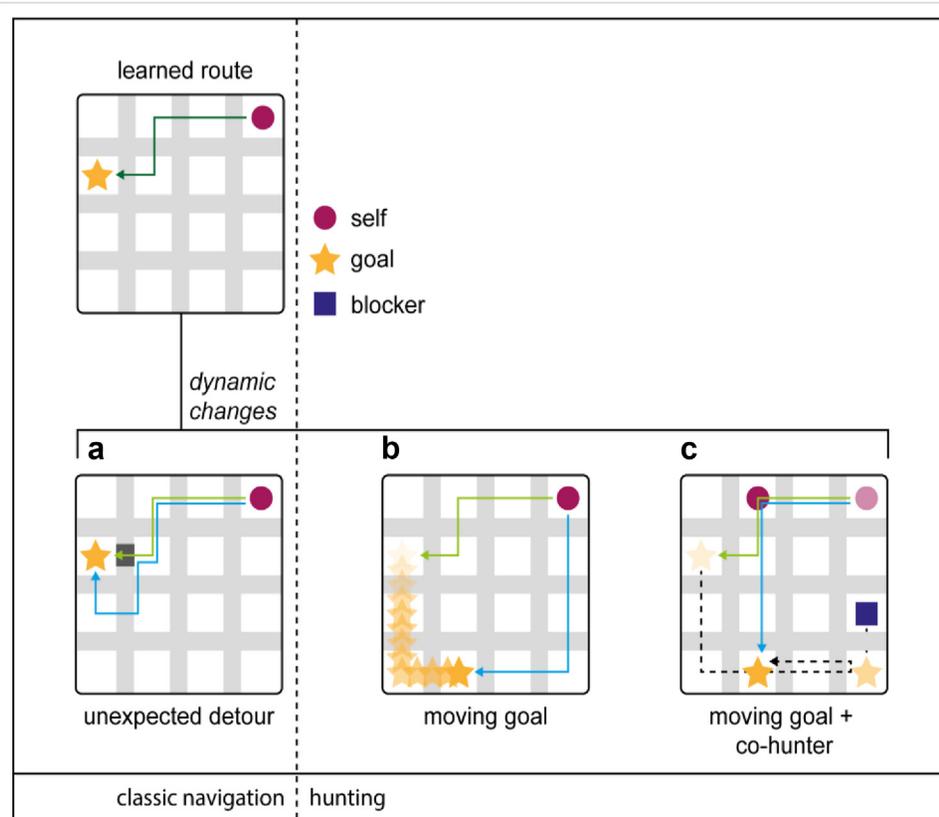
Current Opinion in Neurobiology

Dynamic route navigation in a grid world. Schematic portrays three variations from simple goal-directed route navigation and hunting from a top-down perspective. Each scenario varies from a learned route in a familiar environment (top). (**a**) The learned route is blocked, requiring updating from the learned route to a novel route to the goal. (**b**) The goal position has changed due to the goal agent moving within the environment, requiring updating from the learned route and prediction of future goal position. (**c**) A co-hunter "blocker" agent is introduced into the environment, changing the movement direction of the goal upon encounter, requiring updating of both learned route and future goal position.

particularly the case when chasing prey from a distance across a terrain—as opposed to within the final moments of capture, when the prey is visible and within strike. It is this process, of chasing through the environment when the prey may not be visible, that is relevant to the scope of this review. Akin to navigation, hunting involves minimizing the distance to a goal location to obtain reward. However, hunting behavior commonly differs from navigation in that the goal (prey) is capable of moving (Figure 1). While the process of hunting over distances in terrain has been studied extensively in ethological settings across species (e.g. the studies by Boesch et al., Muro et al., Pitman et al., Watts et al.[3,30,38,57], the neural correlates of this behavior remain unclear. Successful hunting over terrain may require exploitation of the environment's layout to find efficient detours around obstacles or to spot useful shortcuts when they present themselves [54], see Figure 1. Thus, it seems plausible that to succeed at hunting many of the same brain regions necessary for navigation would be needed. This can be true in a trivial sense. To reach a location where the prey may be located, the hunter may need to navigate to that remembered location. In this scenario, there is little or no difference between the standard, classical navigation experience and the experience of hunting, albeit a potential local chase at the target location (Figure 1). However, we speculate here that some of the mechanisms involved in tracking movement towards hidden goal locations during navigation may also be in operation for the hunting of moving prey. The posterior parietal cortex in non-human primates and rodents has been found to contain neurons that can represent the location of objects relative to the body's axis [50,1,43,58]. The posterior parietal cortex of humans has been found to encode the angle between the current heading (from the midline) and the egocentric angle to a fixed hidden goal during navigation activity [7,18,52]. It seems likely such regions of the parietal cortex would also track the estimated location of moving prey beyond the field of view, given posterior parietal regions have also been reported during the tracking of moving visible objects [9,1].

More speculatively, we argue it is possible the hippocampus-entorhinal circuit may be involved in tracking the distance and direction to the goal in world-centered, allocentric space. If the hippocampus and entorhinal region can track the distance and direction to a fixed location, it would seem possible that they might also do so for a moving target. Recent neuroimaging work suggests the hippocampus may play a role in learning to generalize across multiple experiences requiring prediction of the information about moving targets on a screen [39]. Moreover, recent studies have shown that place cells (which express spatially localized activity) in bats and rats can show activity modulated by the presence of another conspecific [10,32]. In humans, theta-band oscillations in the hippocampal and parahippocampal regions have been found to be modulated by the spatial locations of another

person navigating to the locations of a hidden goal in a room [55*] Thus, it seems plausible that hippocampal dynamics may extend from tracking distance to fixed goals to tracking the distance to moving goals (see Figure 1). There is less evidence to suggest the entorhinal/subicular region would encode the allocentric direction to a moving goal. However, given evidence that the entorhinal cortex appears to encode directional information in domains beyond space, such as social networks [33] this may also be a feature of neural dynamics during a hunt.

While there has been impressive research exploring the use of sound to track prey in barn owls, alligators, and geckos [5,6] and planned detours to capture prey by spiders and dragonflies [20], it remains unclear how neural dynamics in mammals support hunting behavior requiring memory for prey positions and predictions for future prey positions. However, work in rodents and non-human primates has begun to reveal circuits involved in chasing and catching visible prey (See Figure 1b, c). Studies in mice have shown neurons in the periaqueductal gray and hypothalamus play key roles in driving predatory chase and attack of visible prey [27*,29,34]. Optogenetic stimulation of these circuits will cause mice to act as predators towards potential prey [27]. While these subcortical structures appear essential for mediating an approach and attack, other regions are implicated in guiding predictive pursuit, such as the dACC. Work in non-human primates has explored the neural dynamics associated with hunting in the context of a flat screen display of icons indicating self-location and moving prey [61**] and other hunters [60**]. Movement in this context is controlled by a joystick and juice reward is provided by moving an avatar icon to make contact with the prey icon. In this task the self and other agents are always visible, and thus navigation to the goal is minimally required. However, the task does allow important insight into the neural mechanisms that support hunting behavior. To succeed at hunting, it is critical to estimate not where the prey is currently, but where it will be in the future. dACC neurons were found to show tuning to features of the velocity and future locations of self-location, prey and other hunters [60**]. Thus, such neurons encode task relevant variables needed for predictive pursuit of the prey, and not only track self-location but also the location of other agents necessary for success. Based on recent evidence of dACC activity during back-tracking [23*] it seems likely dACC neurons are also critical for monitoring when the current trajectory should be abandoned and a new direction attempted for pursuit.

Predicting the movements of other agents when hunting can be important not only to avoid other predators, but also coordinate with others helping with a cooperative group hunt. Cooperatively hunting in groups is a behavior humans share with a number of other species such as orcas, wolves, and chimpanzees [25,26,38]. In a group hunt, the

members of the group must not only predict the future location of the prey but the future movements of the members of the hunting group. For chimpanzees, members take on different roles such as "catchers," "chasers," and those who climb trees to block the escape of the prey [25]; see Figure 1c). In such a scenario, it seems likely neurons in the dACC would encode such task relevant variables, and plausibly be joined by other prefrontal regions involved in tracking the intentions of others movements such as the anterior medial prefrontal cortex [51,44].

One avenue for exploring the neural dynamics involved in cooperative group hunting in humans would be to combine neuroimaging with performance in multiplayer first person video games. *Apex Legends* is a useful example of this type of game, as players are required to play in a cooperative "squad" within the game's complex environment. Such video games place high demand on players to plan potential routes through an environment as well as to coordinate with other members of the squad to track the game's objective (e.g., enemies or other players). Players of such games become adept at exploiting the terrain and communicating with other players to track down and corner other teams, not unlike the behaviors shown by chimpanzees in their group hunting (e.g. the study by Klein et al. [25]). Alternatively, it may be useful to simulate virtual hunting tasks in a controlled VR environment. While participants would lack the skill of players of online games, it would be possible to control the scenarios within which the hunting occurred to maximize the variation in variables for analysis. Recent studies of navigation behavior from rodents and humans in dynamic environments have shown the value in modeling the trajectory data and the use of simulated agents to uncover the underlying mechanisms guiding the behavior [45,11]. Such an approach would be beneficial for exploring group hunting.

In summary, we have proposed that brain regions implicated in hunting behavior such as the medial hypothalamus, periaqueductal gray and dACC, are joined by brain regions considered core for navigation such as the hippocampus and entorhinal cortex. We predict this would be particularly the case when the goal cannot be directly observed and the environment negotiated to reach the moving prey. For cooperative group hunting, it seems likely brain regions such as the medial prefrontal cortex would be involved in estimating intentions of other agents.

Conflict of interest statement
Nothing declared.

Acknowledgements

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* of special interest
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