Neural systems analysis of decision making during goal-directed navigation

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ABSTRACT

The ability to make adaptive decisions during goal-directed navigation is a fundamental and highly evolved behavior that requires continual coordination of perceptions, learning and memory processes, and the planning of behaviors. Here, a neurobiological account for such coordination is provided by integrating current literatures on spatial context analysis and decision-making. This integration includes discussions of our current understanding of the role of the hippocampal system in experience-dependent navigation, how hippocampal information comes to impact midbrain and striatal decision making systems, and finally the role of the striatum in the implementation of behaviors based on recent decisions. These discussions extend across cellular to neural systems levels of analysis. Not only are key findings described, but also fundamental organizing principles within and across neural systems, as well as between neural systems functions and behavior, are emphasized. It is suggested that studying decision making during goal-directed navigation is a powerful model for studying interactive brain systems and their mediation of complex behaviors.

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1. Introduction

Nearly all cognitive processes utilize or include some aspect of spatial information processing. An animal's ability to find its way around its world is critical for survival; it is crucial for obtaining food, avoiding prey and finding mates. Research into spatial information processing over many decades not only continues to define the mechanisms that contribute to spatial information processing, but these efforts have also provided significant insight into the fundamental mechanisms that underlie learning and memory more generally.

Within the laboratory, goal-directed spatial navigation, in particular, is an immensely useful behavior to study because in many ways it reflects ethologically relevant learning challenges, and provides opportunities to examine dynamic features of neural function that are otherwise not afforded by more simple behavioral paradigms and tasks. Goal-directed navigation is a complex behavior, requiring the subject to perceive its environment, learn about the significance of the environment, and then select where to go next based upon what has been learned. Thus, navigation-based tasks can be used to investigate behavioral and neural aspects of external and internal sensory perception, learning and decision making, memory consolidation and updating, and planned movement. Goal-directed navigation, then, is a powerful model by which to study dynamic neural systems interactions during a fundamental and complex natural behavior.

As a whole, efforts to understand the neurobiology of navigational behavior have focused mainly on the nature and mechanisms of spatial representation in limbic brain structures that are known to be important for spatial learning. As a result, there have been important revelations regarding the physiological mechanisms that control limbic spatial representations. Relating such representations, however, to limbic-mediated learning or memory has been indirect and correlational at best (as discussed in Mizumori et al., 2007a). Here, we suggest that careful application of reinforcement learning theory to an understanding of how decisions are made during goal-directed navigation can identify a fundamental and essential process that likely underlies navigation-related perception, learning, memory or response selection. That is, in order to understand how spatial representations are related to learning, it is necessary to understand how decisions are made during navigation from both neural and behavioral perspectives. Without the ability to make adaptive decisions,

animals will not acquire the efficient learning strategies necessary for adaptive behaviors. It should be noted that the suggestion to link reinforcement learning ideas with navigation dates back decades, although the terminology may be different (e.g., cost–benefit analysis of foraging behavior vs. value-based decision making). By investigating this link in freely navigating animals, we may be able to uncover the mechanisms that underlie naturalistic motivated behaviors.

2. Navigation and foraging behavior

The natural foraging environments on which laboratory navigational tasks are based are tremendously complex. The forager's challenge is to acquire sufficient food stores to prevent starvation, produce viable offspring, and avoid predators. A natural tendency for many animals, including rodents, is to hoard small amounts of food in a scattered distribution within their home range or nest (Stephens, 1986). The caching of food requires careful route planning to and from the source of food, the cache, and the home nest. Moreover, because animals acquire food during times when it is abundant, and recover it when food sources are scarce, the animal must retain knowledge of where the food has been cached. This behavior, a naturally occurring spatially directed behavior, is evident in many species, including rodents, birds, spiders, honeybees, and humans (e.g., Anderson, 1984; Davies, 1977; Diaz-Fleischer, 2005; Goss-Custard, 1977; Hawkes et al., 1982; Waddington and Holden, 1979).

The development of mathematical models that formally defined naturally occurring foraging behaviors led to *optimal foraging theory* which describes the foraging behavior of an animal in relation to the metabolic payoff it receives when using different foraging options. Most animals are adapted structurally and physiologically to feed on a limited range of food and to gather this food in specific ways (e.g., caching of food during times of abundance). Some food may contain more energy but be harder to capture or be further away, while food that is close at hand may not be considered as nutritionally profitable. According to optimal foraging theory, an 'optimal forager' will make decisions that maximize energy gain and minimize energy expenditure (Krebs and McCleery, 1984; Stephens, 1986). Two foraging models are of note: the 'prey model' proposed by MacArthur and Pianka (1966), and the 'patch model' proposed by Charnov (1976). The prey model seeks to define the criteria that determine whether prey items will