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Review

Of mice and men: Building blocks in cognitive mapping

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ABSTRACT

Of mice and men: Building blocks in cognitive mapping. NEUROSCI BIOBEHAV REV XX(X) XXX-XXX—Exploration is the process by which humans and other animals gather spatial information and construct some representation of unfamiliar environments, and then utilize this information for traveling in those environments. This survey presents similarities in the travel paths of rodents and humans, suggesting that these constitute an expression of similar underlying biobehavioral mechanisms. Emphasis is given to exploration in dark or large environments, which one cannot encompass at a glance, necessitating a gradual sector-by-sector exploration. This is compared with exploration of the relatively small laboratory testing environments, where a condensed form of exploration dominates. In both rodents and humans, exploration culminates in free traveling, which is mainly determined by the physical environment. For this phase, some principles of urban design in humans and a reminiscent impact of landmarks in test environments in animals are compared. Finally, it is suggested that animal spatial behavior could provide insights into the way that humans perceive and conceive urban environments, and that spatial cognition in different animals, including humans, rests on an evolutionary analogy (or even homology).
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Contents

I dreamed a thousand new paths . . .. I woke and walked my old one (Chinese proverb)

1. Prolog

Humans and other animals explore, learn, and find their way around the environment using some form of internal representation, controversially termed *cognitive map*. This term was coined by Edward Tolman (1886–1959), an experimental psychologist who, based on the remarkable navigational abilities of rats in spatial problem-solving tasks, suggested that rats, and by analogy humans, construct an internal spatial representation of the environment: "... in the course of learning, something like a field map of the environment gets established in the rat's brain ... the incoming impulses are usually worked over and elaborated into a tentative cognitive-like map of the environment" (Tolman, 1948). Tolman, furthermore, suggested to view the performance of rats in mazes in relation to the "God-given maze which is our human world" (Tolman, 1948). Ever since Tolman's seminal studies, cognitive maps have been studied in various fields, such as psychology, ethology, neurobiology, computer science, and geography. From yet another perspective, the urban planner Kevin Lynch

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(1918–1984) suggested that people construct a workable spatial representation of the cities they live in and use this representation to find their way around (Lynch, 1960). This representation (or city image) constitutes a generalized mental picture of the exterior physical world held by the individual, and is constructed of specific urban elements (see Golledge, 1991; Portugali, 2011 for review on spatial concepts and classification of environment elements). The combined perspectives of Tolman and of Lynch suggest that humans and other animals gather information about the surrounding environment and implement this information to establish, maintain, and dynamically update their spatial representation of the environment (Menzel, 1973). They then use this representation to determine a heading direction (Gallistel, 1990), aware of their direction in the environment (Cheng and Newcombe, 2005). In other words, once environment representation is gained, it is possible to switch to path-planning, which is based on identifying the origin of paths, on destinations, directions, and distances (Golledge, 1999a). While humans and other animals differ in their cognitive capacities, they share some similar mechanisms and strategies for spatial orientation. One such mechanism is that of updating position and orientation by *path-integration* (also known as *dead-reckoning*; Etienne and Jeffery, 2004; Mittelstaedt and Mittelstaedt, 1982; Mittelstaedt and Mittelstaedt, 1980; Müller and Wehner, 1988). As detailed below, by virtue of this mechanism, a navigator may turn back and return on a short straightforward route to the start point without the need to rely on environmental cues or retrace unnecessary sections of its outbound journey. Another shared mechanism is *wall-following* or *thigmotaxis* behavior, which is considered a strategy for acquiring the size and shape of the environment (Avni and Eilam, 2008; Kallai et al., 2007). Indeed, path-integration and wall-following exemplify some of the striking similarities in spatial behavior of humans and other animals, even those as "simple" as ants. Intensive research has adopted the concepts of Tolman and Lynch and the perceived similarity in the biobehavioral control mechanisms of spatial behavior between humans and other animals. However, less attention has been paid to how mechanisms like path integration, wall-following etc., are integrated and manifested when an individual is introduced into an unfamiliar environment and becomes oriented there. This integration and its manifestation constitute the focus of the present article. Specifically, (i) the behavior of humans and animals (primarily rodents) upon being introduced into an unfamiliar environment is described first, and the elementary spatial biobehavioral mechanisms that could be utilized for cognitive mapping (or acquiring declarative spatial knowledge) are discussed; and (ii) second, the impact of physical elements in the surrounding environment on cognitive mapping is compared between humans and other animals.

Exploration is the process by which humans and other animals become organized in time and space and gain a spatial representation or image of their living space. O'Keefe and Nadel (1978, p. 242) consider exploration as follows: "The hippocampal locale system is assumed to form the substrate for maps of environments an animal has experienced; these maps are established in the hippocampus during exploration, a species-specific behavior pattern concerned with the gathering of information". Exploration, or becoming organized in time and space, rests on: (i) continuously integrating and updating the current position in reference to a fixed location such as the starting point of travel (Alyan, 1996); and (ii) the perception of the direction and distance between landmarks and self (Guazzelli et al., 1998). Landmarks are external cues in the layout of the environment, in reference to which the navigator may locate itself (Collett, 1996; Etienne et al., 2000; Golledge, 1999a,b). Navigators may also use internal cues generated by their self-movement (e.g. vestibular and kinesthetic cues). Together, external and internal cues are utilized in navigating and constructing spatial representation (Etienne et al., 1996, 1999; Shettleworth, 2009; Shettleworth and Sutton, 2005; Sovrano et al., 2005). Regarding external cues (landmarks), it should be noted that environment novelty can comprise an unfamiliar context or unfamiliar configuration of familiar landmarks, and not necessarily a new physical environment. This is illustrated in the following anecdotal example: "Few items or places are completely novel; novelty typically consists in new configuration of familiar elements... the novelty of the wife in the best friend's bed lies neither in the wife, nor the friend, but in the unfamiliar conjunction of the three" (O'Keefe and Nadel, 1978). Finally, behavior in the context of exploration is also a factor in shaping the external environment, such as in the obvious case of a mole rat constructing its living space by digging a burrow system (Zuri and Terkel, 1996) or a spider spinning its web (Portugali, 2002). Indeed: "It (space) is marked physically, with objects forming borders, walls and fences. The marker (wall, road, line, border, post, and sign) is static, dull, and cold. But space is marked, and shaped, in other ways as well. When lived (encountered, manipulated, touched, voiced, glanced at) it radiates a milieu, a field of force, a shape of space" (Wise, 2000). Cognitive mapping during exploration can thus be viewed as a gradual integration of internal and external representations (Golledge, 1991; Haken and Portugali, 1996). Here we discuss how the organization of spatial behavior is shaped by endogenous mechanisms together with the influence of the geometric and physical properties of the environment.

2. Returning to the origin: An initial strategy for exploring an unfamiliar environment

Following introduction into an unfamiliar environment, exploration usually takes one of the following basic forms: (i) home-base as a terminal for roundtrips in the environment; (ii) looping back to the start point or to a recently visited location; (iii) wall-following (or perimeter walk). In an aversive environment where animals are initially stressed, freezing may precede the above behaviors. Alternatively, the animal may try to remove itself from an aversive environment by moving further away (fleeing) or settling in a location perceived as safer. These behavioral phases are first described in their order of performance, and then the possible underling mechanisms involved in them are suggested.

2.1. Home-base behavior

Upon being introduced into an unfamiliar environment, rats cling to a conspicuous landmark and commence traveling in relation to this landmark (Eilam, 2003; Nemati and Whishaw, 2007). This behavior, in which a specific location is a terminal for roundtrips in the environment, has been termed *home-base behavior* (Eilam and Golani, 1989). Roundtrips to the home base have a characteristic structure: their outbound segment is slow and interrupted with stops, while the inbound segment is fast with fewer if any stops, and the number of stops typically have an upper limit of 8–10 (Golani et al., 1993). At the home-base location, rats also display typical behavior: grooming is almost exclusively home-base behavior, and extensive bouts of grooming follow relatively long roundtrips or long crouching periods. The location of the home base is also characterized by a high incidence of rearing and the rats tend to stop there more than in other locations. Most conspicuously, rats spend extended periods at the home base, usually crouching only there (Eilam and Golani, 1989). Overall, exploration based on home-base behavior is conceived of as a set of roundtrips that are anchored to one specific location—the home base.

Although home-base behavior was implicit in early studies, indicating that rats displayed a tendency to frequently return to the same location, typically a corner (Chance and Mead, 1955; Flicker

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