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Human spatial navigation: representations across dimensions and scales

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Humans, like many other species, employ three fundamental forms of strategies to navigate: allocentric, egocentric, and beacon. Here, we review each of these different forms of navigation with a particular focus on how our high-resolution visual system contributes to their unique properties. We also consider how we might employ allocentric and egocentric representations, in particular, across different spatial dimensions, such as 1-D versus 2-D. Our high acuity visual system also leads to important considerations regarding the scale of space we are navigating (e.g. smaller, room-sized 'vista' spaces or larger city-sized 'environmental' spaces). We conclude that a hallmark of human spatial navigation is our ability to employ these representations systems in a parallel and flexible manner, which differ both as a function of dimension and spatial scale.

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Introduction

Much of our knowledge about navigation, particularly its neural basis, derives from studies in rodents [1]. How we navigate, however, differs fundamentally from these mammals in that we are highly visual creatures, and vision, under normal situations, forms a critical foundation for how we represent space compared to rodents [2•]. At the same time, like rodents, we possess many similarities in terms of the basic strategies and access to similar forms of representations that we employ to navigate. In this review, we will focus on the cognitive and behavioral basis of human spatial navigation. We will base much of our discussion on the idea that, like the rodent, we use three fundamental strategies to get to our goal: allocentric, egocentric, and beacon. Because of the advantages that our high acuity visual system confers to navigating, we will also consider how this impacts our ability to represent different dimensions (1D–3D) and scales of space, such as room versus city-sized environments.

Tolman first argued for the importance of an allocentric representation to navigation in the rodent in the context of the cognitive map [3]. As elaborated on later by many others [4–8], an allocentric representation is referenced outside of one's current body position, most often to multiple landmarks external to the navigator (Figure 1a). In 2-D space (e.g. Figure 2), mathematically at least, this involves a minimum of three such landmarks because these are needed to define a plane in X–Y space (alternatively, a boundary and landmark will also suffice because a line and a point can also define a 2-D plane) [7]. The 'purest' form of an allocentric representation emerges when we draw a cartographic map of an environment because these are not possible without detailed knowledge of the relative directions and distances of stationary landmarks [9–10,11,12•,13]. Other tasks, such as the widely used judgments of relative direction (JRD) task [12•,14,15,16••], also involve some use of an allocentric representation because the task requires referencing to the positions of landmarks relative to each other [17]. Specifically, in this task, participants imagine themselves standing at one location, facing a second, and point to a third location. Thus, two primary assays to determine whether participants employ allocentric coordinates are map drawing and the JRD task.

Landmarks themselves, however, are not necessary for an allocentric representation. The surrounding spatial geometry, like a square or rectangle shape defined by the boundaries of an environment, can also serve as a powerful cue for organizing externally referenced knowledge [15,18–21]. For example, when participants perform the JRD task, they tend to point more accurately when they are aligned (parallel) with the major axis of the surrounding environmental boundaries, like a rectangle, compared to when they are misaligned with these axes. Numerous studies have replicated this advantage in pointing accuracy when aligned with the spatial boundaries, which have held across a variety of testing conditions [15,18–23]. Thus, while past theoretical proposals have conceptualized allocentric representations as largely dependent on multiple landmarks [4,7], decades of work in human spatial navigation have demonstrated that the surrounding spatial geometry defined by environment boundaries

Glossary

*Allocentric***:** A representation of a spatial environment referenced to an external coordinate system that is not dependent on the view or direction navigated.

*Cognitive map***:** A representation of a spatial environment that contains information about metric and directional relationships of objects in that environment. By definition, these representations are allocentric.

*Egocentric***:** A representation of a spatial environment tied to a self or body centered coordinate system.

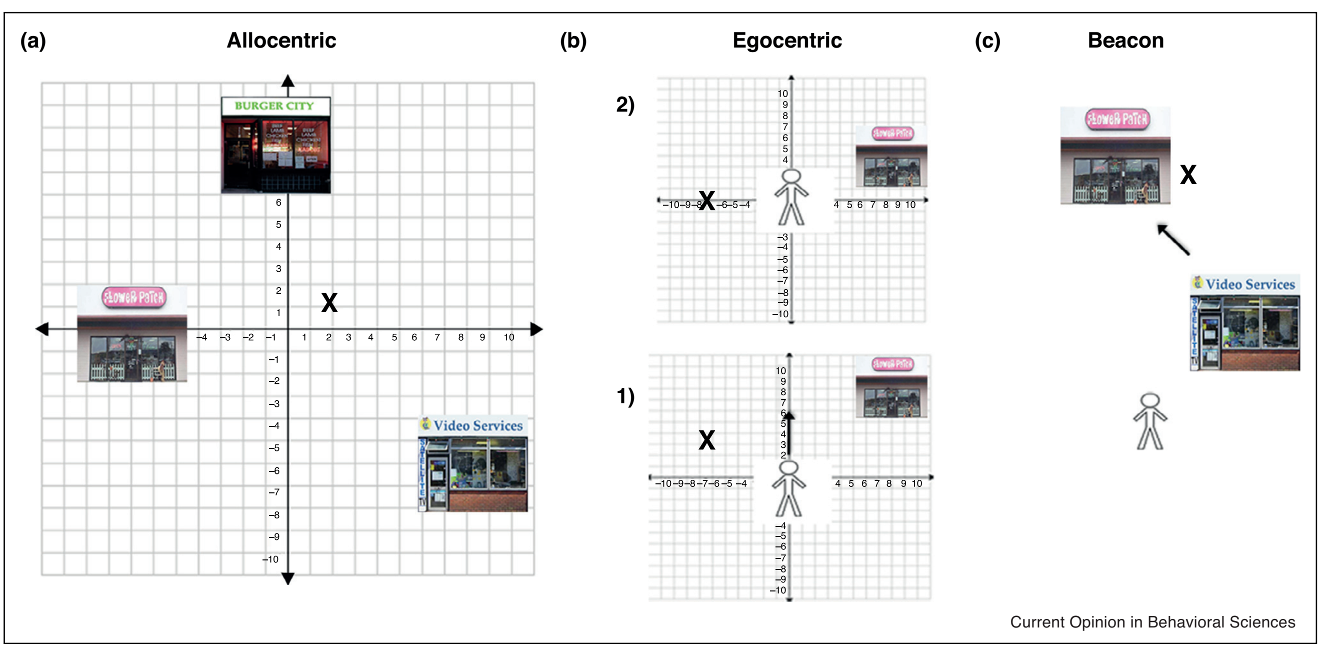
*Path-integration***:** Computation of the optimal, or shortest, path to a location based on previous paths. Based primarily on egocentric representation.

can also serve as a powerful cue for organizing an allocentric coordinate system.

Another form of spatial representation, arguably more commonly used in everyday situations like reaching for an object or remembering where a chair is in the room, is the egocentric representation [7]. Egocentric representations involve reference to our current body position, such as that a chair is located 30 ft in front of us about 10 degrees off from our current facing direction (Figure 1b). As suggested in numerous studies of human spatial cognition [16••,24,25], we often employ egocentric forms of representation for avoiding collisions with objects and navigating our immediate, peripersonal space. Consistent with this notion, several studies suggest that egocentric representations tend to be high-resolution visual 'snapshots' linked to our current bearing [16••,24]. By taking a series of these high-resolution, static, body-referenced snap-shots, we can integrate them together to form a single coherent egocentric representation linked to our current location in space [26•] (Figure 1b). Each of these representations can then be updated as we move throughout an environment (Figure 1b), forming the basis for a system of a vector addition called path integration [17,27]. However, during disorientation [16••,24,28], or moving in large scale environments [29], these representations degrade, necessitating other forms of representation, like an allocentric one.

What conditions emphasize egocentric over allocentric representations? To what extent can the two develop in parallel [30]? In one particular study, Zhang *et al.* compared performance on the JRD task after studying a map and navigating a route with performance on the scene and orientation dependent pointing task (SOP task), commonly used to assay egocentric forms of representation [12•]. In this task, all visual cues (except the target locations) remain and participants use these orienting cues to point to the hidden location (i.e. 'Point to the Supermarket'). Studying a map resulted in rapid, nonlinear improvements in JRD pointing accuracy but slow

Figure 1



(a) Allocentric navigation: The navigator treats the location of the target ('x') as a coordinate on a 2-D plane defined by three landmarks (stores). The coordinates in allocentric space are constant as long as the landmarks remain stable. **(b)** Egocentric navigation: The coordinates of the target location ('x') change continuously with the displacement of navigator from location (1) to (2). In other words, egocentric coordinates change continuously as a function of displacement. c. Beacon/response navigation: The navigator uses the visible locations of stores to find the target. Finding the target is simply based on using its size on the retina to gage the relative distance of the target. Thus, it is not necessary to encode or retrieve a spatial representation or coordinate system when using beacon navigation.