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2.11   Human Spatial Memory and Navigation

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2.11.1   Introduction

Effective navigation abilities are crucial for the survival of almost every living mobile species. They are essential, for instance, for finding the way back to a previously discovered source of food or water, for safely returning home after a sudden change of weather, and for not getting lost in a complex environment such as a cave. For most modern humans, effective navigation skills have become less critical for daily survival, but many common activities, such as getting to work and back home, are nevertheless still characterized by the need to navigate successfully between places.

Successful navigation relies on two capabilities. First, the organism needs to be able to construct enduring internal representations of the locations and identities of significant objects or landmarks in the environment. Second, the organism needs to be able to stay oriented with respect to these represented elements. As the organism moves, the spatial relations between the organism and the elements in the environment constantly change. To remain oriented and to avoid getting lost, spatial updating processes need to be invoked to compensate for those changes.

The goal of this chapter is to review empirical and theoretical advancements in the scientific understanding of human spatial memory and navigation. Our focus is on memories acquired from direct experience, such as vision and locomotion, and on spaces sufficiently large to afford movement, such as translation and rotation, although we also refer to some findings obtained from studies investigating memories of tabletop-sized environments. We are especially interested in the ways memories of familiar environments are used to guide locomotion, reorientation, and wayfinding. Our decision to focus on these topics should not be interpreted to imply that we believe that other types of spatial memories,

such as those obtained from language or indirect sources such as maps, are not important or not interesting. Indeed, for modern humans, navigation based on maps and written works, such as guidebooks, may be at least as important as navigation using one's sense of direction and knowledge of the relations between visible and invisible parts of an environment. Because of space limitations, we were forced to trade breadth against depth of coverage and opted to explore a smaller set of topics in detail, at the expense of several topics equal in importance to those covered here (for reviews of greater scope, see Golledge, 1999; Montello, 2005).

This chapter is divided into nine primary sections. We begin by discussing the elemental types of spatial knowledge: object identity, routes, environmental shape, and survey knowledge. In the second section, we investigate classical and current theories of the acquisition of spatial knowledge. The third section discusses properties of spatial knowledge, such as its hierarchical structure and orientation dependence. In the fourth section, we examine the concept of spatial reference systems and the nature of the spatial reference systems used in spatial memory and navigation. We then turn our attention to the processes and representations that underlie the abilities to guide locomotion and to avoid getting lost. In the sixth section of the chapter, we review contemporary theories of spatial memory and navigation, with an eye for similarities. The seventh section examines the development of spatial memory and navigational capabilities. The eighth and penultimate section looks at the brain networks underlying spatial memory abilities. We close the chapter with a summary and prospectus for future research on human spatial memory and navigation.

2.11.2   Types of Spatial Knowledge

2.11.2.1   Object Identity

The most elemental type of spatial knowledge may be knowledge of the identities and appearances of objects or environmental features (a hill, an intersection of paths, etc.). We use the term object identity to refer to this type of knowledge, recognizing that many entities in an environment that are important for navigation may not be objects in the narrow sense of the term (e.g., path intersection, saddle between two hills). This type of knowledge is sometimes referred to as landmark knowledge (e.g., Siegel and White, 1975), although landmark knowledge is a special case of

object knowledge. People know the identities of many objects in their environments that may not serve as landmarks. Landmarks are objects of special significance to spatial memory and navigation (e.g., Couclelis et al., 1987): They are used to indicate the locations of other objects (e.g., the restaurant is in the basement of the Maxwell House Hotel); they may be the goals of navigation (e.g., I am going to Ryman Auditorium); they mark the locations of changes of direction (e.g., turn right at the Gaylord Entertainment Center); and they are used to maintain course (e.g., you will pass Tootsies Orchid Lounge on your right). According to Siegel and White's (1975) theory of the acquisition of spatial knowledge (discussed in the section titled 'Microgenesis of spatial knowledge'), landmark knowledge is the first to be acquired and is the building block of other types of spatial knowledge.

2.11.2.2   Route Knowledge

Route knowledge consists of knowledge of sequences of landmarks and associated decisions and actions. Actions specify the steps needed to get to the next landmark on the route (e.g., turn right at the post office and drive three blocks to the Laundromat). According to Siegel and White's theory, route knowledge does not represent distance, temporal duration, or turning angles early in acquisition. Such metric properties are acquired gradually with experience in an environment.

2.11.2.3   Environmental Shape

The importance of knowledge of environmental shape was discovered relatively recently. Cheng (1986) found that when rats searched for the known location of food in rectangular enclosures they often committed rotational errors in which they searched the correct location and the incorrect location differing from the correct one by 180° of rotation. For instance, if the correct location was in one of the corners, the rotational error would be the corner diagonally opposite to the correct corner. These errors occurred even when nongeometric featural cues, such as visual or tactile patterns, were available that would allow the rat to distinguish the correct location from the rotational error. Similar findings have been observed in many species, including humans (for a review, see Cheng and Newcombe, 2005). There is ample evidence that people are sensitive to environmental geometry when they learn a new environment (e.g., Shelton and McNamara, 2001;

Schmidt and Lee, 2006) and when they reorient and navigate (e.g., Sandstrom et al., 1998; Hartley et al., 2004; Ruddle and Péruch, 2004).

2.11.2.4 Survey Knowledge

Knowledge of the overall configuration of an environment, including knowledge of Euclidean (straight-line) distances and of interpoint directions, defined in a common reference system, makes up survey knowledge. A key feature of survey knowledge is that the spatial relations between locations can be retrieved or inferred even if the organism has never traveled between the locations. Survey knowledge of an environment is often referred to as a cognitive map (a term coined by Tolman, 1948) and likened to physical maps, although such language and parallels imply isomorphisms between the mental and the physical that do not exit. Survey knowledge is considered to be the most sophisticated type of knowledge obtained about an environment (e.g., Siegel and White, 1975). Behaviors taken to be the signature of survey knowledge include the abilities to create efficient routes (e.g., taking shortcuts), to point directly to unseen locations, and to estimate Euclidean distances.

2.11.3 Microgenesis of Spatial Knowledge

The process of the acquisition of spatial knowledge of a new environment has been referred to as microgenesis. The classical theory of the microgenesis of spatial knowledge was proposed by Siegel and White (1975) and it remains the dominant theory in the field (Montello, 1998). According to this theory, the identities and appearances of landmarks are learned first, followed by routes between landmarks. Route knowledge is primarily nonmetric early in acquisition, consisting of the order of landmarks and the appropriate actions to be taken at each one in the sequence. Through experience, route knowledge can acquire metric, or at least approximately metric, properties, such as distance, temporal duration, and turning angles. The most sophisticated form of spatial knowledge is survey knowledge, which is assumed to be derived from accumulated route knowledge (e.g., Thorndyke and Hayes-Roth, 1982).

Although this theoretical framework has been enormously influential, it has not received a great deal of empirical support (for reviews, see Montello, 1998;

Ishikawa and Montello, 2006). The limitations of the classical theory are apparent in the findings of a recent study published by Ishikawa and Montello (2006). Participants in this experiment were passively transported by automobile along two routes in a private residential area. The routes passed around and over many hills, and afforded few views of distant landmarks. Learning took place over 10 days (once a week for 10 weeks); on the fourth and subsequent days, participants were transported along a connecting route between the two routes and encouraged to learn the spatial relation between them. Participants' knowledge of the routes and their interrelations was tested using landmark recall, direction estimates, route and Euclidean distance estimates, and map drawing.

Performance was above chance on all tasks after the first session, and near perfect on some, such as landmark sequence recall and route distance estimation. Direction estimates and more difficult distance estimates (e.g., Euclidean estimates within the more complex route) were only moderately accurate and improved modestly over the course of learning. However, substantial individual differences were observed. Some participants performed very well after only one or two sessions and maintained high performance levels on all tasks across all sessions. Another subgroup of participants performed poorly throughout the experiment and showed very little learning on the more challenging tasks, even after 12–14 h of exposure to the routes. Only about half of the participants improved monotonically over the course of learning, and those gains were not large.

These findings largely validate the theoretical distinction between route and survey knowledge, as tasks sensitive to route information, such as landmark sequence recall and route distance estimation, produced similar patterns of results, and tasks sensitive to the layout of the routes, such as Euclidean distance estimation, direction estimates, and map drawing, produced results similar to each other but different from the route tasks. However, these results contradict several key predictions of the classical theory. Landmark knowledge and route knowledge were acquired almost simultaneously. Route knowledge seemed to contain some quantitative information from the very beginning. Even at the earliest stages of learning, participants had some knowledge of the spatial layout of the routes. Finally, although some participants gained more accurate knowledge of the layouts of the routes over the course of learning, few of them could be characterized as having gained accurate survey knowledge of the environments (see also, Gärling et al., 1981; Golledge, 1993).

The evidence on spatial knowledge acquisition is most consistent with Montello's theoretical framework (Montello, 1998; Ishikawa and Montello, 2006). According to this theory, the process of acquiring knowledge of the spatial structure of large-scale environments consists of incremental accumulation of metric knowledge, instead of stage-wise transitions between qualitatively distinct types of spatial knowledge. Spatial knowledge is never limited solely to nonmetric information. This theory emphasizes the importance of knowledge integration – combining knowledge about separately learned places into more complex hierarchically organized representations – in spatial knowledge acquisition. However, even this theoretical framework does not predict or explain the large individual differences observed by Ishikawa and Montello.

2.11.4   Nature of Spatial Knowledge

2.11.4.1   Fragmented

Spatial knowledge is typically fragmented, in the sense that it consists of a patchwork of detailed knowledge of some areas and only sparse knowledge of other, possibly neighboring, areas (e.g., Lynch, 1960; Appleyard, 1970). Survey knowledge never has the property of being of uniformly high fidelity for all familiar areas.

2.11.4.2   Distorted

A second key property of spatial knowledge is that memories of spatial relations, such as distances, angles, and orientation, often differ from the physical values in systematic and predictable ways (e.g., Tversky, 1992, 2000). As discussed in several sections of this chapter, such distortions have played a prominent role in the development of theories of spatial memory.

Estimates of Euclidean distances are greater when locations are separated by a barrier or boundary (e.g., Kosslyn et al., 1974; Newcombe and Liben, 1982; McNamara, 1986) and tend to increase with the clutter between the locations (e.g., Thorndyke, 1981). Boundary effects occur even when the boundaries are subjective (e.g., McNamara et al., 1989; Carbon and Leder, 2005). Estimates of route distance increase with the number of turns (e.g., Byrne, 1979; Sadalla and Magel, 1980) and the number of intersections (e.g., Sadalla and Staplin, 1980). Distance estimates are also asymmetric under certain circumstances (e.g., Sadalla et al., 1980; McNamara and Diwadkar, 1997; Newcombe et al., 1999). In particular, distances from less salient locations or objects to more salient locations or objects (i.e., landmarks or reference points) are underestimated relative to the reverse. Angles of intersection between roads are remembered as being closer to 90° than they are in reality (e.g., Byrne, 1979; Tversky, 1981; Moar and Bower, 1983; Sadalla and Montello, 1989). Disparate regions of space, such as states or continents, are remembered as being aligned with each other, and individual regions of space are remembered as being oriented with canonical reference axes (e.g., Stevens and Coupe, 1978; Tversky, 1981). For instance, people believe that North America and South America are vertically aligned, even though the east coast of the U.S. is roughly aligned with the west coast of South America, and that the Bay Area of Northern California is oriented north-south, even though it actually is oriented along a north-west/south-east axis (Tversky, 1981). These biases produce systematic errors in judgments of the relative directions between objects and cities.

2.11.4.3   Hierarchical

There is strong evidence that memories of the locations of objects in the environment are organized categorically and hierarchically, such that a region of space may be represented as a whole, containing other regions and locations, and as a part, contained in larger regions. One indication that spatial memories are hierarchical is that judgments of the spatial relations between cities or objects are affected by the spatial relations between superordinate regions (e.g., Stevens and Coupe, 1978; Tversky, 1981; McNamara, 1986). For instance, in Stevens and Coupe's (1978) experiments, Reno was judged to be northeast of San Diego, even though it is actually northwest. According to hierarchical models of spatial memory, this error occurs, at least in part, because people represent Reno in Nevada, San Diego in California, and Nevada east of California. These spatial relations imply that Reno should be east of San Diego. Other evidence consistent with the hierarchical representation of space includes the effects of boundaries on distance estimations (cited previously), the effects of region membership on judgments of orientation (e.g., Wilton, 1979; Maki, 1981) and proximity (e.g., Allen, 1981), and errors in estimates of latitude, bearing, and distance at global scales (e.g., Friedman and Brown, 2000; Friedman et al., 2002; Friedman and Montello, 2006).

Even stronger evidence for hierarchical representations can found in studies in which task performance is shown to depend on the structure of explicit hierarchical models of spatial memory (e.g., Hirtle and Jonides, 1985; Huttenlocher et al., 1991; McNamara, 1986; McNamara et al., 1989). For instance, McNamara et al. (1989, Experiment 1) required subjects to learn the locations of objects in a large room; the objects were unrelated, and there were no physical or perceptual boundaries in the space. After learning, subjects were asked to recall all of the objects several times, to estimate distances between pairs of objects, and to take part in an item recognition test in which the measure of interest was spatial priming (e.g., McNamara et al., 1984). The latent hierarchical structure in each subject's recall protocols was modeled with the ordered-tree algorithm (e.g., Reitman and Rueter, 1980). An example is illustrated in **Figure 1**. Distance estimations and spatial priming were conditionalized on whether pairs of objects were in the same or different subtrees (e.g., ruler–coin vs. envelope–truck), controlling for Euclidean distance. Different subtrees were assumed to correspond to different subjective regions of space. Subjects underestimated distances between pairs of objects in the same subjective region relative to pairs of objects in different subjective regions, and spatial priming was greater between pairs in the same subjective region than between pairs in different subjective regions. Additional analyses showed that spatial priming increased with the depth at which object pairs were clustered (e.g., ruler–coin vs. ruler–pen vs. ruler–screw). These findings provide strong evidence that spatial memories are organized hierarchically, even when the layout lacks explicit perceptual organization.

The hierarchical structure of spatial memory affects navigation behavior, at least in virtual environments. Wiener and Mallot (2003) found that people minimized the number of region boundaries
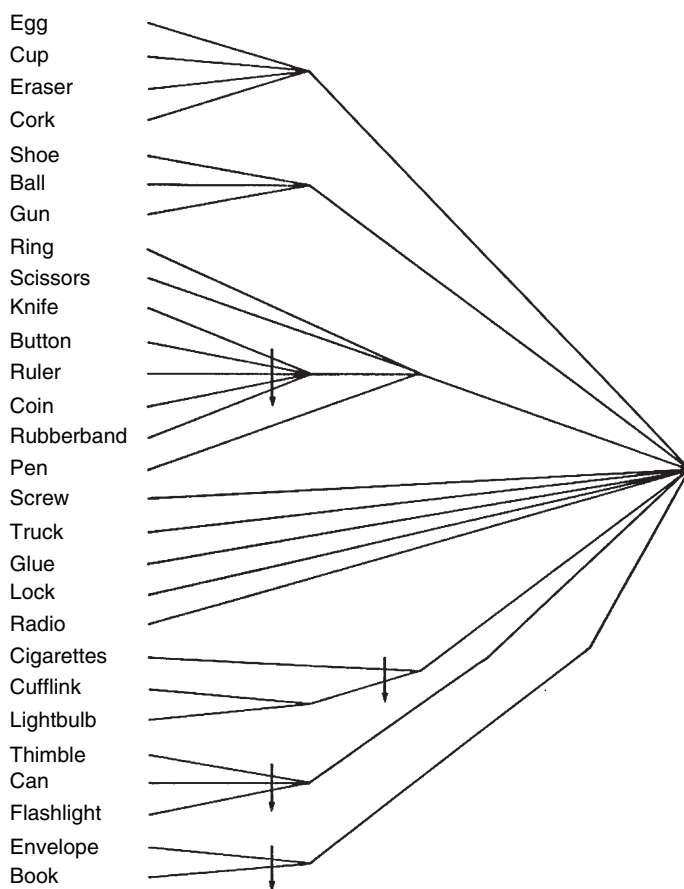

Figure 1 Ordered tree generated from recall protocols for a single participant. Reprinted with permission from McNamara TP, Hardy JK, and Hirtle SC (1989) Subjective hierarchies in spatial memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 15(2): 211–227.

crossed when navigating to a goal location and that they tended to choose paths that permitted the quickest access to the region containing the goal location. Wiener et al. (2004) showed further that subjects learned environments faster and searched more efficiently when environments were divided into regions than when they were not. This improvement was on the order of a factor of 2. Their results also revealed that navigation strategies seemed to depend on the alignment of the dominant reference directions between different levels of the hierarchical mental representation (see also, Werner and Long, 2003; Werner and Schindler, 2004). (The concept of spatial reference directions and axes will be explored in detail in the section 'Spatial reference systems'.)

2.11.4.4 Orientation Dependent

It is well documented that long-term spatial memory is orientation-dependent (see McNamara, 2003, for a review). People recall and recognize interobject spatial relations more efficiently from some perspectives than from others. These privileged perspectives are usually aligned with (parallel or orthogonal to) experienced points of view (e.g., Shelton and McNamara, 2001) but also may be aligned with salient intrinsic axes of the array of objects (e.g., Mou and McNamara, 2002; Mou et al., 2007). Typical results are illustrated in Figure 2. There is evidence that spatial memories also may be viewpoint-dependent (e.g., Easton and Sholl, 1995; Waller, 2006; Valiquette and McNamara, 2007). Behaviorally this means that performance is better when the test perspective matches the location of the observer at the time of learning in addition to his or her orientation.

Orientation-independent performance has been observed in several published investigations of spatial memory (e.g., Evans and Pezdek, 1980; Presson and Hazelrigg, 1984; Presson et al., 1989; Sholl and Nolin, 1997, Experiments 3 and 4; Richardson et al., 1999, real-walk condition). McNamara (2003) discusses possible limitations of these studies in some detail. One important feature of those studies (with the exception of Evans and Pezdek's) is that only two orientation conditions were compared: The perspective parallel to and in the same direction as the learning view (0°) and the perspective differing by 180°. This fact may be important because task performance for the imagined heading of 180° is often much better than performance for other novel headings, and can be nearly as good as that for the learning view (e.g., Hintzman et al., 1981; Mou and
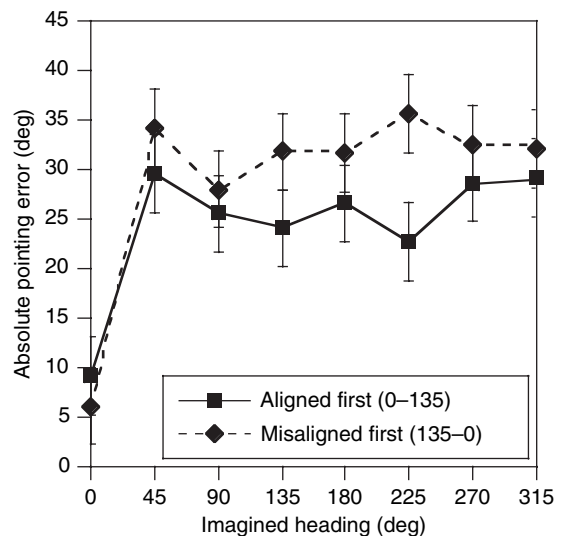

Figure 2 Results of Shelton and McNamara's (2001) third experiment. Participants learned the layout of seven objects in a room from two points of view (counterbalanced across participants): One view (0°) was aligned with salient environmental reference frames (e.g., walls of the room, square mat on which the objects were placed), and the other (135°) was misaligned with these features. Absolute pointing error in subsequent judgments of relative direction is plotted as a function of imagined heading, separately for the two learning-order groups. Results show that participants represented the layout using a single reference direction parallel to the aligned view and demonstrate the importance of environmental frames of reference in the selection of reference directions in memory. From Shelton AL and McNamara TP (2001) Systems of spatial reference in human memory. *Cogn. Psychol.* 43(4): 274–310.

McNamara, 2002). The cause of this effect is not known, but people may sometimes represent, at least partially, the spatial structure of the layout in the direction opposite to the learning view (Mou et al., 2004). It is also possible that people are able to capitalize, under certain conditions, on the fact that arrays of objects may have high self-similarity under rotations of 180° (e.g., Vetter et al., 1994). Investigations of the orientation dependence of spatial memories are at a distinct disadvantage if only the learning view and its opposite are compared.

2.11.5 Spatial Reference Systems

Spatial reference systems are essential for the specification of location and orientation in space. The location of Murfreesboro, Tennessee, for example,

can be specified by describing its position with respect to the boundaries of the state (e.g., Murfreesboro is in the center of Tennessee), by providing coordinates of latitude and longitude on the surface of the earth (e.g., Murfreesboro is located at 35°55′ N and 86°22′ W), or by describing its position relative to an observer (e.g., Murfreesboro is 31 miles to the first author's left as he writes this paragraph). People represent in memory the spatial properties of many familiar environments. Just as spatial reference systems are required to specify the locations of objects in physical space, so too spatial reference systems must be used by human memory systems to represent the remembered locations of objects in the environment.

A spatial reference system is a relational system consisting of reference objects, located objects, and the spatial relations that may exist among them (e.g., Rock, 1973, 1992; Talmy, 1983). The reference objects may be any objects whose positions are known or established as a standard and may include the observer, other objects in the environment, abstract coordinate axes, and so forth. Note that, according to this definition, a reference frame consisting of orthogonal axes is just one of many types of spatial reference systems. Many schemes for classifying spatial reference systems have been proposed (e.g., Hart and Moore, 1973; Paillard, 1991; Pani and Dupree, 1994; Levinson, 1996; Tversky et al., 1999). For the purposes of understanding the use of spatial memories in navigation and other actions in space, it is useful to distinguish egocentric and environmental reference systems (e.g., Klatzky, 1998). In this chapter, we consider environmental and allocentric reference systems to be equivalent.

Egocentric reference systems specify location and orientation with respect to the organism, and include eye-, head-, and body-based coordinate systems (e.g., Andersen et al., 1997). Returning to the previous example, the description of Murfreesboro's location relative the first author of this chapter uses an egocentric reference system.

Environmental reference systems define spatial relations with respect to elements of the environment, such as the perceived direction of gravity, the sun's azimuth, landmarks, or the walls of a room (e.g., Wehner et al., 1996). Abstract reference systems, such as coordinates of latitude and longitude, also qualify as environmental reference systems. An important subcategory of environmental reference systems are intrinsic reference systems. Intrinsic reference systems can be centered on an object (e.g., Rock, 1973;

Marr, 1982). In such cases, the objects usually have inherent facets, such as natural fronts, backs, tops or bottoms, that can be used to define reference axes. The human body is a paradigmatic example. Intrinsic reference systems can also be defined by features of a collection of objects (e.g., Tversky, 1981; Mou and McNamara, 2002). The rows and columns formed by chairs in a classroom constitute an intrinsic reference system. Intrinsic reference systems also may be defined by less explicit perceptual organization, such as an axis of bilateral symmetry or the mutual alignment of several objects (e.g., Mou et al., 2007). An example is illustrated in **Figure 3**.

The primate brain represents the locations of objects in space using egocentric and environmental reference systems (e.g., Andersen et al., 1997; Snyder et al., 1998; Matsumura et al., 1999), and human navigation depends on both egocentric and environmental representations of the environment. Actions such as walking through doorways and other apertures, staying on paths, and avoiding obstacles require the computation of precise self-to-object spatial relations to guide locomotion (e.g., Rieser and Pick, 2006). But planning a route to a distant goal, and maintaining a sense of orientation in large-scale environments, would seem to require enduring representations of the locations of objects relative to other objects (e.g., Loomis and Beall, 1998). Contemporary theories of human spatial memory and navigation specify roles for both egocentric and environmental representations of space, and will be reviewed in detail in the section titled 'Models of spatial memory and navigation'.
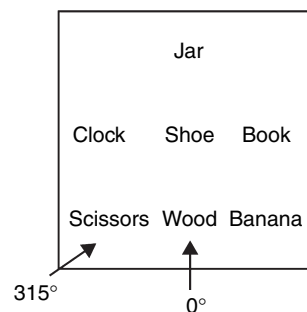
Figure 3 Layout used by Mou and McNamara (2002). Zero degrees is an axis of bilateral symmetry, increasing the salience of that axis and therefore the probability that it will be selected as a reference direction, even if participants study the layout from a different direction such as 315°. Reprinted with permission from Mou W and McNamara TP (2002) Intrinsic frames of reference in spatial memory. *J. Exp. Psychol. Learn. Mem. Cogn.* 28(1): 162–170.

The concept of spatial reference systems proves useful for accounting for two key properties of spatial knowledge. The orientation dependence of spatial memories indicates that the spatial layout of an environment is mentally represented using a dominant reference direction (e.g., Shelton and McNamara, 2001). Interobject spatial relations that are specified with respect to this reference direction can be retrieved, whereas other spatial relations must be inferred (e.g., Klatzky, 1998), introducing costs in latency and errors. The preferred directions in judgments of relative direction, for example, correspond to intrinsic directions in the layout that are experienced or are highlighted by instructions or layout geometry (e.g., Shelton and McNamara, 2001; Mou and McNamara, 2002; Mou et al., 2007). These preferred directions correspond to the dominant reference directions. A simple model of this form that accounts for orientation dependence in judgments of relative direction is illustrated in **Figure 4**.
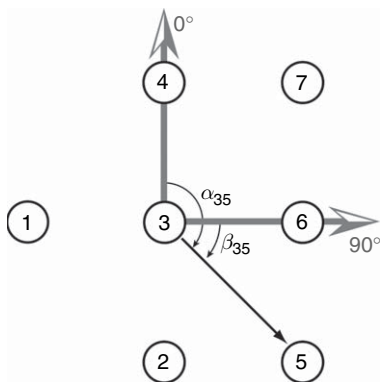

Figure 4   Schematic depiction of an orientation dependent model of enduring spatial memory. Circles symbolize the represented objects. Interobject spatial relations are symbolized by vectors; for simplicity, only the spatial relation between objects 3 and 5 is represented. Grey arrows symbolize reference directions in the representation. The angular relation from object 3 to object 5 is represented with respect to the 0° (α_{35}) and the 90° (β_{35}) reference directions. Because the direction from object 3 to object 5 relative to 0° is explicitly represented in memory, a task such as "Imagine you are standing at 3 and facing 4. Point to 5" is relatively easy, because that direction can be retrieved from memory. A task such as "Imagine you are standing at 3 and facing 7. Point to 5" in contrast, is relatively difficult, because the spatial relation between objects 3 and 5 is not represented relative to 45° and, therefore, must be inferred, which produces measurable performance costs. An important feature of the model is that it uses an environmental reference system, yet produces orientation-dependent performance.

The second key property explained by spatial reference systems is the hierarchical structure of spatial knowledge. This property may result from the use of spatial reference systems at multiple scales (e.g., Poucet, 1993). A region of space that can be viewed in its entirety from a single vantage point with minimal locomotion (vista scale as defined by Montello and Golledge, 1999) may be represented in a locally defined spatial reference system. Spatial reference systems used in neighboring regions of space may be interrelated in higher-order reference systems in which the local reference systems serve as elements. For instance, the spatial layout of each of the rooms in a house may be specified in a spatial reference system unique to the room. These spatial reference systems may serve as elements in a higher-order reference system defining the spatial relations among the rooms.

Reference systems within the same level and between levels of the hierarchy need not use common reference directions; that is, conceptual north in one region may or may not correspond to conceptual north in a neighboring region. The acquisition of skills attributed to the possession of survey knowledge, such as pointing accurately to unseen targets, may occur when the reference directions in such locally defined reference systems become integrated in such a way that all are aligned (Montello and Pick, 1993). Werner and colleagues (Werner and Long, 2003; Werner and Schindler, 2004) have shown that misalignment of reference directions in such a reference system hierarchy impairs way-finding performance and produces less accurate knowledge of interobject directions. Experiments reported by Wang and Brockmole (2003a) provide evidence that people maintain orientation with respect to a single reference system as they navigate. They had participants walk from a room in a building on a college campus to the outdoors and then back inside to the room. When oriented with respect to the room, participants lost track of their orientation with respect to the campus, and when oriented with respect to the campus, they lost track of their orientation with respect to the room (see also, Wang and Brockmole, 2003b).

2.11.6   Navigation and Spatial Updating

The processes and representations used in human navigation can be divided into three categories. Navigation that depends solely on the organism's

history of self-movement is referred to as path integration, or dead reckoning. By integrating velocity or double integrating acceleration with respect to time, an organism can estimate its displacement from a starting location (e.g., Gallistel, 1990). Cues to velocity or acceleration can be internal (e.g., proprioception, efference copy, vestibular cues) or external (e.g., optic or acoustic flow); however, to the extent that external cues are used, path integration is limited to situations in which external cues do not provide information about the organism's position in the environment (Philbeck et al., 2001). Wayfinding (or piloting), by contrast, refers to navigation that depends jointly on an enduring external or internal spatial representation (a map or cognitive map, respectively) and the observation of objects whose locations are specified in the spatial representation (e.g., Gallistel, 1990). The key feature of wayfinding is that the organism uses a representation of the layout of an environment and its perception of objects in that environment to find or orient with respect to objects that cannot be observed. Both path integration and wayfinding may require the organism to pass through apertures (e.g., doorways), follow paths, avoid obstacles and hazards, and so forth. This form of navigation has been referred to as steering (e.g., Rieser and Pick, 2006). Steering requires an organism to guide locomotion in relation to the perceived locations of objects but does not rely on an enduring external or internal spatial representation of the environment.

In general, as an organism locomotes through an environment, it must keep track of its location with respect to objects in the immediate environment and to unseen portions of the environment, to avoid obstacles, to remain oriented, and to navigate to distant goals (Loomis and Beall, 1998; Montello, 2005). These processes are referred to as spatial updating. Experimental research on human navigation has typically been aimed at trying to uncover the mental representations and processes used in spatial updating more broadly, and with the exception of work on path integration, does not divide neatly into categories corresponding to the three types of navigation.

Path integration is often investigated with triangle completion, or return-to-home tasks. An illustrative study was reported by Klatzky et al. (1990). Blindfolded participants were guided along paths of varying complexity and then required to walk back to the starting points. The paths consisted of one to three linear segments, separated by turns. The dependent variables were the angular turn participants made toward the origin and the distance they walked toward it. Participants' errors on both measures were low for the one-leg path and increased with the increasing number of segments. In general, path integration in humans is only moderately accurate and becomes less so as path complexity increases (e.g., Loomis et al., 1993, 1999; Cornell and Heth, 2004; Foo et al., 2005).

Nonvisual spatial updating has also been investigated in tasks that require the participant to keep track of multiple objects simultaneously. For example, Rieser et al. (1986) asked participants to study the locations of five objects in a room and then point to them while blindfolded. Participants were subsequently escorted to a novel position from which they had to point to the objects again. Locomotion resulted in small, nonsignificant updating costs relative to baseline (e.g., Rieser, 1989).

The results from these and similar paradigms suggest that humans are capable of relatively efficient updating when they move without vision, provided that the movement trajectory is not very complex. The increase in error for more prolonged movement is compatible with the assumption of an updating process that does not operate with perfect accuracy and accumulates error over the course of movement.

Spatial updating necessarily involves computations that compensate for the changes in observer–environment relations caused by locomotion. A number of studies have been conducted to identify which of the cues that are normally associated with physical locomotion are sufficient for efficient spatial updating. Purely imaginary locomotion typically produces inefficient spatial updating (e.g., Rieser et al., 1986; Rieser, 1989; but see, Wraga, 2003). Optic flow appears to be insufficient for efficient spatial updating (e.g., Chance et al., 1998; Klatzky et al., 1998; Péruch et al., 1997; but see Kearns et al., 2002; Riecke et al., 2002). A prerequisite for efficient updating seems to be that the person's physical position changes (Ruddle and Lessels, 2006). Whether this position change is accomplished through passive transport, which primarily provides vestibular cues, or through active movement, which provides additional proprioceptive and efferent cues, does not matter in many circumstances (e.g., Wang and Simons, 1999; Wraga et al., 2004). There is, however, evidence that those additional cues become beneficial when the movement trajectory is more complex (e.g., Sholl, 1989; Yardley and Higgins, 1998; Waller et al., 2004).

Evidence indicates that spatial updating during physical locomotion has two properties commonly attributed to automatic processes. First, it seems to require little attentional effort (e.g., Amorim et al.,

1997; Wang, 2004). Second, the changes in observer–environment spatial relations produced by physical locomotion are difficult to ignore (e.g., Farrell and Robertson, 1998; Farrell and Thomson, 1998; Wang and Simons, 1999; May and Klatzky, 2000; Waller et al., 2002). For example, in Farrell and Robertson's experiment, participants were required to rotate to a novel orientation, but point to objects as if they were still facing their initial orientation. Performance was as poor in this ignore-rotation condition as in the imagined rotation condition, indicating that participants were unable to voluntarily refrain from updating.

Another important property of automatic processes is their relative insensitivity to processing load. The evidence on the capacity limits of spatial updating is mixed. Results of at least one study indicate that spatial updating deteriorates in accuracy as the number of objects increases (Wang et al., 2006), whereas findings from other studies indicate that spatial updating is capacity-free (Rieser and Rider, 1991; Hodgson and Waller, 2006). This pattern of results has led some researchers to distinguish two forms of updating, one that occurs on-line and relies on working memory and another that occurs off-line and relies on long-term memory (e.g., Amorim et al., 1997; Cornell and Greidanus, 2006; Hodgson and Waller, 2006). This distinction is embodied in several theories of spatial memory and navigation (discussed in the section titled 'Models of spatial memory and navigation').

A common interpretation of the advantage in spatial updating produced by physical locomotion in the absence of vision (e.g., walking while blindfolded) relative to imagined locomotion is that body-based information facilitates the transformations needed to update observer–environment spatial relations (e.g., Rieser, 1989; Chance et al., 1998; Farrell and Robertson, 1998). This facilitation may result from the transfer of learned relationships between action and perception to relationships between action and representations (e.g., Rieser et al., 1995; Pick et al., 1999; Rieser, 1999; Rieser and Pick, 2006). The idea is that people learn the consistent covariations between their actions and the resulting changes in the appearance of the environment. This tight coupling of action and perception is proposed to be the basis for a coupling of action and representation. When a person moves without vision, he or she can use the learned covariation between biomechanical cues from locomotion and the changes in environmental flow to update the self-to-object relations at a representational level. It is argued that, by utilizing this learned covariation during locomotion, people can access the changing self-to-object relations directly rather than having to go through effortful cognitive computations.

An alternate account posits that the difficulty of updating after imagined movements results from interference that is caused by a conflict between the awareness of one's physical position in an environment and the discrepant position one has to adopt in imagination (e.g., May, 1996, 2004). May (2004) has proposed that interference arises from conflicts between object location codes at the sensorimotor level, which are specified relative to the physical position, and object location codes at the cognitive level, which are specified relative to the imagined position. Consistent with this hypothesis, pointing to objects from imagined facing directions is worse when people are oriented than when they are disoriented (e.g., May, 1996; Waller et al., 2002). The interference hypothesis is also supported by the finding that performance in both imagined rotations and imagined translations degrades monotonically as a function of object-direction disparity (May, 2004), which is defined as the magnitude of the difference between (1) the direction of the to-be-retrieved object relative to the imagined position and (2) the direction of the to-be-retrieved object relative to the physical position. To account for the finding that imagined rotations are more difficult than imagined translations (e.g., Rieser, 1989; Presson and Montello, 1994), even when object direction disparity is equated, May (2004) proposed a second source of interference that only applies to imagined rotations. This second source of interference, referred to as head-direction disparity, reflects conflicts that arise from having to specify an object direction relative to an imagined heading that is different from one's physical heading (e.g., Mou et al., 2004).

May (2004) has also shown that providing participants with additional time between the presentation of the to-be-imagined position and the presentation of the target object improved overall performance, but did not mitigate the effect of object-direction disparity in either imagined rotations or imagined translations. This finding indicates that the spatial transformations required for effective spatial updating cannot be performed efficiently in working memory, even if they are somehow facilitated by physical locomotion.

In summary, extant findings indicate that spatial updating during imagined locomotion is difficult in part because knowledge of object locations relative to the actual position interferes with knowledge of object locations relative to the imagined position.

But in addition, imagined spatial updating does not benefit from facilitative transformations provided by physical locomotion.

2.11.7 Models of Spatial Memory and Navigation

Cognitive models of spatial memory and navigation attempt to explain how the spatial structure of an environment is represented in memory and how memories of familiar environments are used to guide navigation. All of the models employ both egocentric and environmental representations of space, and although there are important differences between models in the nature of those representations and in the ways they are used to maintain orientation and guide navigation, the models are fundamentally quite similar.

These models include an egocentric system that computes and represents self-to-object spatial relations needed for spatially directed motor activity, such as walking, reaching, and grasping. In the models proposed by Burgess and colleagues (e.g., Burgess, 2002; Burgess et al., 2001; Byrne et al., 2007), Mou and colleagues (Mou et al., 2004, 2006) and Waller and Hodgson (2006), spatial relations represented in this system are transient and decay rapidly in the absence of perceptual support or deliberate rehearsal. In Sholl's model (Sholl and Nolin, 1997; Sholl, 2001; Holmes and Sholl, 2005) and in Wang and Spelke's model (2002), this system is dynamic but can represent more enduring egocentric self-to-object spatial relations. Recent evidence implicates the role of a transient egocentric system in spatial updating, but this evidence is far from definitive (Mou et al., 2006; Waller and Hodgson, 2006).

The second major system in all of the models is an environmental (allocentric) system. Wang and Spelke's model is perhaps the most unusual, in that the environmental system in this model only represents environmental shape. It is difficult to reconcile this aspect of the model with the abilities of people to judge interobject distances and directions using long-term memories of the layouts of environments. The other major difference among models, at least among those which specify the nature of the reference systems used in the environmental system, is whether the spatial reference system is orientation-dependent or -independent. Mou and McNamara argue that the environmental system uses an intrinsic reference system (as discussed in the section titled 'Spatial

reference systems'). Sholl, in contrast, claims that an orientation-independent reference system is used, at least in well-learned environments. Sholl's model would seem to have difficulty accounting for the large body of evidence demonstrating orientation-dependent performance in spatial memory tasks, even for well-learned environments, as reviewed previously.

Finally, Wang and Spelke's model includes a third system in which the appearances of familiar landmarks and scenes are represented. These representations are viewpoint-dependent and can be conceived of as visual-spatial snapshots of the environment (e.g., Diwadkar and McNamara, 1997; Wang and Simons, 1999; Burgess et al., 2004). Valiquette and McNamara (2007) recently attempted to find evidence for such a system and to determine whether it could be distinguished from an environmental system. They asked participants to learn the locations of objects in a room from two points of view, one of which was aligned with salient environmental frames of reference (the mat on which the objects were placed and the walls of the room), and the other of which was misaligned with those same frames of reference (i.e., a view from the corner of the room). Participants then took part in judgments of relative direction (e.g., 'Imagine you are standing at the shoe, facing the lamp; point to the banana') and old–new scene recognition. Performance in judgments of relative direction was best for the imagined heading parallel to the aligned learning view and no better for the imagined heading parallel to the misaligned learning view than for unfamiliar headings. This pattern of orientation-dependent performance replicates previous findings (e.g., Shelton and McNamara, 2001; Valiquette et al., 2007). Performance in scene recognition, however, was equally good for the two familiar views and better for familiar than for novel views (see also Waller, 2006). These findings are consistent with a model in which interobject spatial relations are represented in an environmental system using intrinsic reference systems, as specified in Mou and McNamara's model, and visual memories of landmarks and scenes are stored in a viewpoint-dependent system, as specified in Wang and Spelke's model.

This viewpoint-dependent system may account for the effectiveness of the look-back strategy in wilderness navigation (e.g., Cornell et al., 1992). Routes often look quite different coming and going, leading to navigational errors on the return trip. The look-back strategy involves occasionally stopping and turning around to view one's route in the opposite direction while navigating in unfamiliar wilderness environments. These look-back views

may be stored in the viewpoint-dependent system and support place recognition when returning.

Spatial updating in these models takes place at two levels. Self-to-object spatial relations are continuously and efficiently updated in the egocentric system as a navigator locomotes through an environment. This updating process supports steering and interactions with objects in the environment. At the same time, the navigator must update a representation of his or her position in the environment, to remain oriented and to locate distant goals. This updating process takes place in the environmental system. According to Mou and McNamara, navigators update their position with respect to the intrinsic reference system used to represent the spatial structure of the local environment. Sholl's model is the most explicit about the environmental updating process. In this model, the egocentric system is referred to as the self-reference system, and it codes self-to-object spatial relations in body-centered coordinates, using the body axes of front–back, right–left, and up–down (e.g., Franklin and Tversky, 1990; Bryant and Tversky, 1999). The engagement of the self-reference system with the physical environment determines the position of a representation of the self-reference system in the environmental system. As a person moves in the environment, the axes of the representational self-reference system are moved to the corresponding new position in the environmental system representation.

To a significant degree, these models primarily describe the perceptual-cognitive architecture of the human spatial memory and navigation system. For this reason, they have varying amounts to say about the various topics covered previously in this chapter. All are intimately concerned with object location, survey knowledge, spatial reference systems, and spatial updating. But none of these models has much to say about route knowledge, the microgenesis of spatial knowledge, or the nature of spatial knowledge (e.g., distortions). An important direction for future research will be to extend these models to account for a broader array of findings in the spatial memory and navigation literature.

2.11.8   The Developmental Foundations of Navigation

Decades of research have revealed a host of burgeoning spatial abilities during the first few years of life. These developments are most likely intimately coupled with changing motor abilities (for discussion, see Campos et al., 2000) and, toward the end of infancy, symbolic capabilities such as language. In this section, we focus on the development of rudimentary abilities necessary for navigation (for a recent and more comprehensive review, see Newcombe and Huttenlocher, 2006). Specifically, we discuss the development of two of the elemental types of spatial knowledge: object location (including landmarks) and environmental shape. Route and survey knowledge follow later in development (e.g., Allen et al., 1979) and most likely depend on these earlier abilities. In addition, we consider what children's responses in various situations reveal about early use of egocentric and environmental spatial frames of reference.

2.11.8.1   How Children Use Objects and Landmarks

In the first months of life, infants can locate objects through response learning, which involves learning the association between a bodily response (e.g., an eye movement or a reach) and a particular position in space. For example, an infant may learn that lying in her crib she can turn her head to the left to see a colorful toy. Response learning illustrates a very simplistic egocentric reference system – one that does not take self-movement into account. In order to locate objects after movement through space, infants must be capable of what Rieser (2000) has called dynamic spatial orientation, which requires awareness of one's changing orientation with respect to the world.

Early studies have suggested limitations on the infants' ability to keep track of an object's location during self-movement. Acredolo (1978) examined 6-, 11-, and 16-month-olds in the following task. Infants first learned that an auditory cue signaled an interesting event in one of two windows (either on the left side of the room or on the right side of the room for each infant). Infants were then carried on a semicircular path to the opposite side of the room. Only 16-month-olds looked toward the correct window when the cue sounded, whereas younger infants continued to look toward the egocentric side on which the event had occurred earlier. Similar results were obtained by Bremner and Bryant (1977), who found that 9-month-olds continued to search for an object on the egocentric side of a table after being moved to the opposite side of the table.

These initial studies seemed to suggest that sometime during the second year there is a transition from response learning (not taking movement into account) to spatial updating (taking movement into account). However, it is likely that even very young infants use spatial updating when simple forms of movement, such as rotation about the trunk or tilting with respect to gravity, are involved (e.g., Rieser, 1979; Landau and Spelke, 1988). Furthermore, Newcombe and Huttenlocher (2000) have argued that spatial development is most likely characterized by an increased weighting of relevant cues rather than by the appearance of wholly new abilities (for evidence in older children, see Hund and Spencer, 2003). As infants become more mobile and can perform more complex actions in larger environments, cues such as self-movement and landmarks become increasingly relevant.

Early studies have also examined infants' ability to use landmarks as direct cues to locating objects. A direct landmark is one that is either contiguous with or adjacent to some target, thus serving as a beacon for the target location. (Because no coding of distance or angular information is necessary, use of direct landmarks is technically associative rather than spatial in nature.) In contrast is an indirect landmark, which is distant enough from a target that both are not visually available at the same time; consequently, in order to use an indirect landmark a viewer must represent the spatial relations between it and the target location. Acredolo and Evans (1980) explored the landmark use of 6-, 9-, and 11-month-olds. The task was similar to that used by Acredolo (1978) in that infants were carried to the opposite side of the room before searching for an event in a left or right window. Nine- and 11-month-olds clearly benefited from the presence of a landmark that surrounded the correct window, whereas 6-month-olds did not. A consistent finding was that of Bremner (1978), who found that 9-month-olds who moved to the opposite side of the table were more likely to search on the correct side for an object if the left and right hiding places were noted by a black cover and a white cover. Such findings seemed to indicate that, before they are capable of spatial updating, infants are able to use direct landmarks to locate targets. Additionally, when landmarks are highly salient, even 6-month-olds sometimes use them in locating target objects or events (Rieser, 1979; Lew et al., 2004).

Toward late infancy, humans show evidence of using landmarks in the surrounding environment in complex ways. Newcombe et al. (1998) examined children between the ages of 16 and 36 months in a task that required them to locate a toy in a long rectangular sandbox. Success required distance coding (in the continuous space of the sandbox) rather than the categorical coding involved in many earlier studies (e.g., at the left or right window). The children searched either with a circular curtain surrounding them (thus, with no indirect landmarks visible) or without the curtain (thus, in full view of surrounding landmarks in the room). After children watched an experimenter hide a toy in the sand, they moved to the opposite side of the box to perform the search. Children older than 22 months were more accurate when indirect landmarks were visible, whereas the youngest children performed the same whether the landmarks were visible or not. These data suggested that toward the end of infancy children begin to use indirect landmarks to guide navigation (see also DeLoache and Brown, 1983; Bushnell et al., 1995).

While Newcombe et al. (1998) argued that the indirect landmarks aided children's search, it is also possible that children were using the shape of the room (see discussion in section titled 'How children use environmental shape'). Consistent with this latter argument is a recent study by Nardini et al. (2006), who found that 3-year-olds were able to use the shape of the room during a search task that involved indirect landmarks, but not until 5 years did children seem to use the actual landmarks. In fact, there is recent evidence to indicate that young children do not represent landmarks in an environmental reference system.

In a series of experiments, Gouteux and Spelke (2001) examined preschoolers' ability to search for a target that was hidden inside one of several identical landmarks within a room. When landmarks were identical, the configuration (a triangle in some experiments and a rectangle in others) was the only available spatial information. The critical trials took place after children were disoriented within the search space. Across all experiments, children failed to use the configuration specified by the arrangement of landmarks. In contrast, when landmarks were differentiated, children were successful in locating the target. Gouteux and Spelke (2001) noted that the landmarks could have served as beacons for the target location rather than as cues to reorientation within the space.

Lee et al. (2006) explored this latter possibility. Four-year-olds searched for an object among three landmarks that formed an equilateral triangle – thus,

the geometric information alone was uninformative; two of the landmarks were identical. As in Gouteux and Spelke's (2001) experiments, children were disoriented before beginning their search. Children successfully retrieved objects that were hidden at the distinctive landmark; however, when objects were hidden at one of the two identical landmarks, children searched at each of those two landmarks with equal frequency. Lee et al. (2006) argue that children can use landmarks as beacons for target locations, but do not use them to reorient to the locations of other landmarks (see also, MacDonald et al., 2004). These findings are consistent with researchers who have argued that humans keep track of discrete objects egocentrically (Wang and Spelke, 2000; Wang et al., 2006). Once these egocentric relations are disrupted, humans cannot use individual objects to reorient to the locations of other objects. The validity of this claim has been a matter of dispute in the adult literature (see discussion in section titled 'Models of spatial memory and navigation'). However, children at least do seem to have difficulties remembering the locations of objects with respect to other objects.

2.11.8.2 How Children Use Environmental Shape

When toddlers and older children see an object hidden in one corner of a rectangular space and then undergo a disorientation procedure, they search equally in the correct corner and in the geometrically equivalent corner (Hermer and Spelke, 1994; Learmonth et al., 2001, 2002; see for a discussion Cheng and Newcombe, 2005). Since there is no spatial information available other than the shape formed by the walls of the room, these data clearly demonstrate that, by the time they can walk, humans use the shape of extended surfaces to reorient when lost and to locate desired objects. Furthermore, children's use of geometric information in extended surfaces generalizes to situations in which they are translated outside of the space before searching (Lourenco et al., 2005) and to spaces that are not rectangular (Huttenlocher and Vasilyeva, 2003; Hupbach and Nadel, 2005). Finally, the knowledge of geometric shape must be stored in an environmental reference system, since the disorientation would have disrupted any self-to-surface representations. The shape of extended surfaces, in contrast to object location, seems readily represented in an environmental reference system early in development.

When geometric information is ambiguous, combining that information with other sources of information can be a powerful tool. One question is whether children can combine information about the shape of a room with featural information, unlike rats and other species, which cannot combine these two sources of information (see discussion in the section titled 'Environmental shape'). Hermer and Spelke (1994) examined 3- and 4-year-old children in the following task. Children watched as an object was hidden in a corner of a rectangular room, were disoriented, and then were allowed to search for the object. The researchers found that when one of the walls was blue, making the correct choice of corner unambiguous, young children did not search with greater frequency in the correct corner. Since adults have no difficulty combining the geometry of the room with landmark information, Hermer and Spelke (1996) hypothesized that humans use language capabilities to solve such a task, a hypothesis supported by Hermer-Vasquez et al. (2001). In this study, adults who performed a verbal shadowing task while searching for an object that was hidden in one of four corners were less likely to use relevant landmarks in the room.

There is some controversy over the claim that geometric shape of space cannot be used in combination with landmarks without the aid of language (Learmonth et al., 2001, 2002; Hupbach and Nadel, 2005; see for a discussion Cheng and Newcombe, 2005). However, there is a considerable amount of support for the claim that geometric information, at least in some situations, is processed independently from other spatial cues. One particularly important variable seems to be the size of the room (Learmonth et al., 2002). In spaces that afford only minimal locomotion, children are more likely to ignore featural information and rely solely on the shape of the room. The reasons for this finding, whether they relate to limited locomotion, the proximity of landmark information, or both, are not yet clear (see for discussion Newcombe and Huttenlocher, 2006).

2.11.9 Cognitive Neuroscience of Spatial Memory

Our goal in this section is to review some of the primary findings that have emerged from decades of research on the neural bases of spatial memory. Recently there has been a growing focus on understanding how egocentric and environmental reference

systems operate in parallel and interact with each other. First we discuss how the hippocampal and parietal cortices subserve spatial memory. Next we turn to a discussion of the parahippocampal cortex, which has been the focus of recent growing interest in its role in navigation and its possible role in hippocampal–parietal interactions.

In now classic research with rats, O'Keefe and Dostrovsky (1971) demonstrated the existence of place cells in the hippocampus, which fire selectively based on the position in the environment that the animal occupies, independently of the animal's facing direction. O'Keefe and Nadel (1978) argued that these cells serve as the basis for an environmental spatial reference system, or the cognitive map. Ekstrom et al. (2003) have provided the first demonstration of place cells in the human hippocampus, confirming what was long hypothesized from several lines of research with humans. This literature has shown that the human hippocampus is involved in performance on a variety of spatial tasks (e.g., Maguire et al., 1997; Holdstock et al., 2000; Kesner and Hopkins, 2001; Stepankova et al., 2004). In particular, the hippocampus seems to be crucial for performance on spatial tasks that require learning the relations among external landmarks, i.e., tasks that cannot be solved using egocentric responding (Astur et al., 2002; Bohbot et al., 2004; Parslow et al., 2004; Shelton and Gabrieli, 2004).

Recently discovered grid cells in adjacent entorhinal cortex (Hafting et al., 2005) may serve a function complementary to place cells. Grid cells respond whenever the animal is in a position that coincides with a vertex in a grid of equilateral triangles that spans the surface of the environment. The grid is initially anchored to landmarks in the environment, although the cells continue to fire even in the dark. Thus, the cells may serve as the neural basis for an environmental reference system, in conjunction with the place cells, and also facilitate path integration within that environment.

In contrast to individuals who have endured damage to hippocampal regions, those with lesions to parietal regions sometimes exhibit severe difficulty navigating through immediate space, often failing to avoid obstacles (e.g., Stark et al., 1996). Such findings have led researchers to postulate that the parietal cortex is critically involved in action and, specifically, in representing self-to-surface relations (see for discussions Andersen et al., 1997; Colby and Goldberg, 1999).

Recently there has been a growing emphasis on how the parahippocampal cortex (PHC) serves spatial functioning. PHC is ideally situated for combining information from parietal and other temporal areas and also projects to entorhinal cortex, a primary input region for the hippocampus. As noted by Epstein:

> . . . the anatomical data suggest that a pathway from parietal cortex to parahippocampal cortex to the hippocampus may be critical for processing navigationally relevant spatial information. (Epstein, 2005: 971)

Neuroimaging studies have shown the PHC to be involved in a wide range of navigation tasks (e.g., Aguirre et al., 1996; Maguire et al., 1996; Mellet et al., 2000; Shelton and Gabrieli, 2002). In addition, humans who have endured damage to this area exhibit impairments in spatial tasks such as route learning and scene recognition (e.g., Bohbot et al., 1998; Aguirre and D'Esposito, 1999; Barrash et al., 2000; Luzzi et al., 2000; Epstein et al., 2001).

The posterior region of the PHC has been the focus of increasing interest due to its dedication to the perception of spatial scenes. In a functional magnetic resonance imaging (fMRI) investigation, Epstein and Kanwisher (1998) found that this area responds more to scenes than to houses, faces, or objects, even during passive viewing. Further experiments revealed that this area responds just as strongly to empty rooms as to scenes with multiple objects. Additionally, this region responds more to coherent scenes than to those in which the component parts are fractured and rearranged. Based on this set of findings, Epstein and Kanwisher called this region of cortex the parahippocampal place area (PPA). Both neuroimaging and lesion studies suggest that the PPA's role is one of encoding (Brewer et al., 1998; Epstein et al., 1999, 2001). Epstein et al. (2003) conducted a study indicating that the region processes geometric information in background elements, in particular. These researchers found that the PPA responds as much to changes in entire scenes as it does to changes in viewpoint of the same scene, suggesting that the PPA processes scene information in a viewpoint-dependent (egocentric) manner. However, there is evidence that over time the way the PPA processes particular scenes may become more viewpoint-independent (Epstein et al., 2005).

One notable finding that has contradicted studies on the PPA was that by Maguire et al. (1998). These

researchers found activations of the right PHC when subjects navigated through and learned a series of rooms with salient objects in a virtual reality environment. However, they did not find any medial temporal involvement when participants performed the same task with a series of empty rooms distinguished from each other only by their different shapes. They hypothesized that the parahippocampal region is involved in object-location binding, not analysis of the geometry of the scene. Consistent with this view is the recent finding that monkeys with lesions to the PHC are impaired in the formation of object–place associations (Malkova and Mishkin, 2003; see also Parkinson et al., 1988) and the finding by Bohbot et al. (1998) that humans with lesions to the right PHC are impaired in a spatial task that requires memory for object locations. The contradictory findings may have to do with functional differentiation within the PHC, with the PPA serving a specialized purpose of geometrical analysis and other regions involved in binding object information to the geometry.

2.11.10   Summary and Prospectus

Learning a new environment typically begins by learning routes from place to place; even in large-scale outdoor environments, navigation usually takes advantage of trails of some kind. People quickly acquire knowledge of the identities of important objects, or landmarks, and the sequential order of landmarks on routes. Route knowledge has at least quasi-metric properties very early during acquisition. Humans and many other organisms seem to be very sensitive to the shape of the immediate environment and to depend on environmental shape to reorient. With extensive experience in an environment, people sometimes acquire knowledge of its overall layout, or survey knowledge. The acquisition of spatial knowledge is best characterized as the incremental accumulation of quantitative spatial relations. Spatial knowledge does not seem to be limited to qualitative, nonmetric information at any point during acquisition.

Humans represent the locations of objects in space using egocentric and environmental (i.e., allocentric) reference systems, and navigation almost certainly depends on both egocentric and environmental representations of the environment. There is evidence that the process of learning a new environment involves interpreting the spatial structure of that environment in terms of an environmental spatial reference system. Interobject spatial relations seem to be specified with respect to a small number of reference directions. This aspect of the mental representation produces one of its key properties, orientation dependence: interobject spatial relations can be utilized more efficiently from perspectives aligned with the dominant reference directions in memory. These reference directions are typically parallel to points of view experienced during learning, but also may be determined by instructions and by properties of the environment, such as the mutual alignment of several objects or geographical slant. The use of spatial reference systems at multiple scales may explain why spatial knowledge is hierarchically organized.

Effective navigation in a familiar environment depends on the abilities to avoid obstacles and stay on course, to use one's history of self-movement to keep track of one's position, and to use mental representations of the layout of the environment to estimate the positions of objects that cannot be observed. Collectively, these abilities – steering, path integration, and wayfinding, respectively – are referred to as spatial updating. A prerequisite for efficient updating seems to be that the navigator's position in space changes. Imagined spatial updating is difficult and error-prone. An important source of this inefficiency seems to be conflicts that are created by having to imagine a position in the environment that is different from one's physical position in that environment. Physical locomotion in the absence of vision mitigates this interference and also seems to benefit from body-based information, which facilitates the transformations needed to update observer–environment spatial relations. But even physical nonvisual updating breaks down with prolonged movement over complex trajectories.

Contemporary models of spatial memory and navigation specify roles for three types of spatial memories: Egocentric self-to-object spatial relations used for steering and path integration, viewpoint-dependent representations of landmarks and scenes used for place recognition, and environmental representations of object-to-object spatial relations used for wayfinding and some forms of path integration. There are differences among the models in the properties of each of these representational systems and in the manner in which they are used in navigation. For instance, in some models, the egocentric system computes and represents transient representations, whereas in other models, these representations are more enduring. In one model, the environmental

system only represents the shape of the environment and is used for reorientation, whereas in the others, it represents object-to-object spatial relations and is used for virtually all locomotion in familiar environments. Despite these differences, however, the models are quite similar in terms of their overall architecture.

The development of these capabilities begins with simple forms of egocentric spatial coding, such as learning the association between a bodily response and a location in space, and of spatial updating, such as compensating for trunk rotation. During the second year of life, children begin to be able to use landmarks in more sophisticated ways and to update after complex movements, developments that are coincident with (and certainly related to) their increased mobility. By the time children can walk, they can use environmental shape, as defined, for example, by the shape of a room, to locate a desired object. This knowledge must be represented in an environmental frame of reference because it survives disorientation, which destroys self-to-object spatial relations. Toddlers appear to have difficulty under some conditions using featural cues or landmarks to find a desired object after having been disoriented. The ability to effectively use such cues does not develop until well into the school-age years.

Research on the neural basis of spatial memory and navigation in humans has isolated the hippocampus, the parietal cortex, and the parahippocampal cortex as especially important brain areas. The hippocampus seems to be critically involved in the formation of long-term representations of the spatial structure of the environment using environmental frames of reference. The parietal cortex is involved in representing the locations of objects in the egocentric reference systems needed for sensorimotor mappings and in coordinating these representations. The parahippocampal cortex is involved in navigation, and its posterior regions seem to play an important role in representing landmarks and scenes.

The scientific understanding of human spatial memory and navigation has advanced enormously since Tolman (1948) presaged the distinction between route and survey knowledge with his categorization of spatial memories into strip maps and comprehensive maps. Significant progress has been made in understanding the nature and acquisition of spatial memories, how remembered spatial relations are used to guide navigation, properties of spatial updating processes, the development of early navigational capabilities, and areas of the brain involved in spatial memory and navigation. But of course much remains to be discovered. Many important avenues of future research are indicated by the findings reviewed in this chapter. A few especially promising ones, to our minds, include the following.

There is abundant evidence of the hierarchical organization of enduring spatial memories, but the processes involved in the formation of such representations are not well understood. Of special interest are the mechanisms used to establish correspondences between representations that use different reference directions and the spatial updating processes used to switch from one hierarchical level to another. The relative importance of egocentric and environmental representations in various spatial tasks, their dynamical properties, and the processes by which egocentric representations in sensorimotor systems are transformed into environmental representations, and vice versa, are largely unknown. Much remains to be learned about how children come to represent spatial relations among landmarks in ways that effectively support navigation. Recent investigations of spatial updating in adults suggest that steering depends on a transient egocentric system, whereas wayfinding depends on an enduring environmental system. Relatively little is known about the nature and the development of these capabilities in children. Finally, research on the neural basis of human spatial memory and navigation has isolated a network encompassing, at minimum, the parietal cortex, the hippocampus, and the parahippocampal cortex. The nature of the representations in these areas and the interactions among them need to be explored in greater depth.

We look forward, with optimism, to seeing the empirical and theoretical fruits of these efforts to understand how people remember where they have been and how they find their way home.

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