

Neurocognitive basis of navigation in children

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Key points

- Late behavioral competence in spatial navigation may be dissociable from early-functioning cognitive processes.
- Children exhibit spatial memory abilities from infancy.
- Different types of information are utilized for various aspects of spatial navigation.
- Neuroscience and comparative research provide important insights for understanding early spatial cognitive development.
- Uniquely-human spatial abilities such as map-use and abstract geometry may emerge through the use of episodic simulation and symbolic representations.

Abstract

Spatial navigation and its underlying neurocognitive mechanisms are challenging to study in early development given children's late-emerging ability to navigate on their own. Nevertheless, over the past few decades, developmental researchers have gained much insight into the rich set of cognitive mechanisms for encoding spatial locations in infants and young children. Moreover, by drawing parallels with studies of the neural correlates of navigation in nonhuman animals, it has been possible to get a deeper understanding into the why children's spatial memory and behavior differs from that of adults. Still, uniquely human abstract spatial abilities must be studied directly with respect to developmental changes in children's brain function and the corresponding changes in their spatial competence.

Introduction

The scientific study of our earliest spatial abilities and how we learn to find our way around different environments is crucial to a full understanding of human cognition and how it changes across the course of our lives. Characterizing cognitive development is a tricky business, particularly when investigating navigational mechanisms in an altricial species like our own. Human babies take months to develop sufficient motor control to interact with their surroundings in a coordinated manner and take an entire year to walk around on their own two feet. Due to this protracted maturation process, philosophers and early developmental psychologists believed that, during those early days of life, infants transition from being in a state devoid of any cognitive representation to gradual learning about the physical world around them (e.g., James, 1890; Piaget and Inhelder, 1967). Opposing views emphasized the necessity of prior conceptualization of space and time in order for our learning to occur in the first place (Kant, 1781), historically positioning spatial cognition at the center of decades of heated debates over nature vs. nurture (Spelke, 2022; Cheng et al., 2013; Newcombe and Ratliff, 2007).

Over the years, biologists brought us the revelation that our traits cannot be dissociated from the environmental conditions under which they evolved. Normal expression of genes and the emergence of "experience expectant" phenotypes make development much more complex and nuanced than the simplistic question of whether something is driven by nature or nurture (Greenough et al., 1987). We now understand that infants, like other animals, are born with early cognitive mechanisms that actually guide their learning about the world (Carey, 2009; Spelke, 2022). Nevertheless, despite this view of infant development from a biological, evolutionary, neurocognitive perspective, researchers still struggle with the mainstream interest on the question of what is innate and learned. This is particularly difficult to study in the case of early navigational mechanisms due to challenges in identifying

behavioral measures of spatial competency in children. Fortunately, neuroscientific studies of navigational mechanisms in animal models have brought much insight into the hippocampal representations that underlie spatial cognition and behavior, even in the earliest stages of development.

The scientific study of spatial navigation

Spatial navigation research has played a critical role in providing us with scientific insight into how the “black box” of the mind works and that there are inherent biases and regularities in behavior that cannot be explained by simple outcomes associated between stimulus and response. Historically, the observation that rats navigate using novel shortcuts based on environmental cues led to the proposal of a cognitive “map,” which can be defined as a set of mental representations of the external world beyond just a trained set of stimuli and responses (Tolman, 1948). Early discoveries that animals spontaneously compute novel spatial trajectories (see Fig. 1), and take shortcuts in their navigation behavior, set the stage for decades of research on the cognitive mechanisms underlying the storage, retrieval, recognition, and computation of spatial information. Research in the field of brain and cognitive sciences followed suit in gathering evidence, mostly from rodents but confirmed later in humans, that the hippocampus provided the neural basis for the spatial maps that underlie navigation behavior (O’Keefe and Nadel, 1978).

Given that basic hippocampal function is shared across a wide range of distantly-related species, spatial cognition—and perhaps even abstract representations of space and time—may be biologically founded upon evolutionarily ancient navigational mechanisms that we share with other animals (Lee, 2023). A young animal without the basic ability to return to the safety of its nest, who must acquire such abilities gradually and slowly, would not stand a chance in nature. Thus, the selection pressure would have certainly been strong for any self-locomoting animal, even in early development, to track its spatial movements and remember important places and contexts. It may not be so surprising, then, that some animals are able to navigate very soon after birth and that head direction cells and place cells are mature in their basic function in a baby rat from its very first exploration outside of the nest (Muessig et al., 2016; Wills et al., 2014). Although human babies may not be able to physically move about on their own, they may nevertheless be equipped with early information-processing mechanisms that are present in precocial animals (Wang and Spelke, 2002).

Although the ability to navigate is necessary for daily function and survival, it is obvious that not all spatial behaviors should be innately specified, particularly with respect to information that is widely variable across individual experiences, seasons, and environments (Dehaene, 2020). For instance, although the representation of spatial geometry may be advantageous to all navigating animals, a child born and raised in the desert may grow up to be attuned to different perceptual properties of the environment from one that is born and raised in the jungle; and a long-time sailor may learn to navigate by different cues from a city-dweller. This is not true only for humans but also for animals who inhabit and forage around a diverse range of environments. This individual variability is why experience-based learning plays a critical role in our survival. Nevertheless, there may also be basic properties of physical environments such as large landmarks and terrain structures that provide a framework upon which our representation of places and routes can be built (Gallistel, 1990).

The development of spatial abilities in children

Jean Piaget’s approach to developmental research was critical in giving rise to the modern scientific study of spatial competency in infants and children. However, because he mainly relied on documentation of behavioral changes in the early stages of life, he characterized an infant’s conception of space as extremely limited and consisting mostly of categorical distinctions such as in/out or near/far (Piaget and Inhelder, 1967). According to his views, mental representations of three-dimensional space, distances and

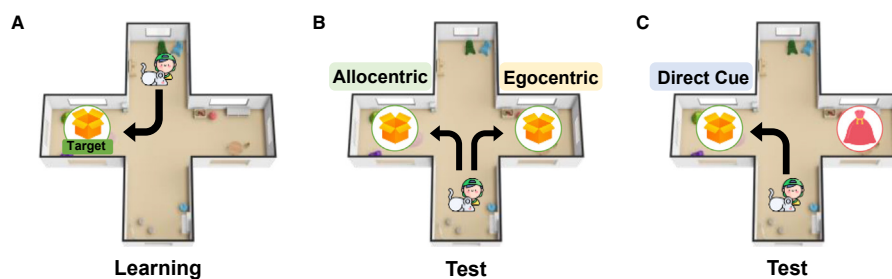


Fig. 1 Experimental paradigm for distinguishing between egocentric and allocentric spatial coding. (A) The subject first learns to navigate to a target location in the room. (B) At test, the subject searches from the opposite side of the room, putting the allocentric (world-based) and egocentric (self-based) reference frames against one another. Tolman (1948) and Acredolo (1978) used such experimental designs to test spatial cognition in rats and young children, respectively. Acredolo found an egocentric bias in infancy that gradually shifts across development. (C) Drastic differences in the features of the two targets presents a challenge in interpreting that a *spatial* representation underlies behavioral response.

directions between locations in the world were to be constructed slowly over time, through direct interactions with the physical world. From a perspective that focused on observations of infant behavior, this was entirely logical and not at all surprising, as human babies are born prematurely—an evolutionary balance between the survival of the mother through childbirth and the survival of a baby who is incapable of surviving on its own.

Behavioral competence in a young infant in a particular task does not fully reveal the underlying cognitive mechanisms that may eventually expose itself under different circumstances or through the process of maturation. In fact, even in experiments similar to Piaget's, once researchers explored different behavioral measures such as looking time, or provided slightly varied task conditions, such as those that did not require too much inhibitory control—they began to unveil a surprisingly rich mental world of babies. For instance, despite Piaget's famous demonstration of the A-not-B error, in which infants search for an object at the previously found location of an object following its displacement to a new location (Piaget and Inhelder, 1967), this error is only seen when the two locations are close together or visually identical and when there is a similar reaching action required (Smith et al., 1999). In other words, infants' overt actions may not always reflect their implicit expectations and early learning mechanisms that they innately possess to guide their interactions with the physical world (Spelke, 2022). In the case of spatial navigation, this means that the fact that babies are unskillful navigators—or that they are not navigators at all for a good part of their infancy—does not necessarily mean that they do not already possess the fundamental spatial representations and cognitive mechanisms that guide their memory in infancy and their eventual navigation behavior (Newcombe, 2019).

The challenges of studying how spatial information is processed in the developing brain highlight the advantages of an interdisciplinary approach that brings together both behavioral and neuroscientific knowledge about the brain's navigational system. Researchers have unveiled thus far that even infants and toddlers remember locations and approach their spatial goals in a directed manner. Their spatial behaviors are not the same as an adult's, nevertheless, and perhaps limited in the types of information and computations they perform over them. The question, therefore, is whether we can explain observed behaviors and their changes over development by characterizing them in terms of cognitive processes and their neural correlates, sometimes drawing parallels from what we know about spatial representations in other animals.

Spatial navigation benefits from a mental representation that is distinguishable from simply recognizing a goal because the final destination is often either hidden from view or perceptually inaccessible from one's current location or perspective. To paraphrase Richard Morris, space is a construct of the mind which requires but is logically independent of the multimodal sensory information used to identify it. For example, it is precisely in situations in which a goal is out of view, whether it is acorns cached by a squirrel or food in a kitchen cupboard, that *spatial* memory becomes so useful—the exact opposite of the situation that applies to normal object *recognition* memory (Morris, 2007). In addition to associating goals and objects to locations, the computational problem that the brain must deal with in spatial navigation include tracking of one's own body through space and remembering various locations and their spatial relations. This process of mapping space involves the discrimination of featural cues and landmarks associated with various locations, the calculation of the geometric layout such as distances and directions between locations, and the planning of a route between one's own location and the intended destination at that moment in time (Gallistel, 1990).

Infants are, in fact, impressively adept at forming associations between the perceptual properties of a location and a target object. This ability to learn the cues that directly mark a goal's location has been demonstrated in infants in many tasks of spatial memory. Even in the absence of training, young children will successfully navigate to and search for a hidden target hidden directly at or near a distinctive feature in the room. For instance, if a toy is hidden under a featurally distinguishable pillow, behind a distinctively colored wall, or in a uniquely-shaped container, they will remember its location even after a delay or after inertial disorientation (Bushnell et al., 1995; Wang et al., 1999; Gouteux and Spelke, 2001; Lee et al., 2006). This cognitive ability is not only apparent in children who can walk on their own; even infants exhibit predictive-looking behaviors toward such remembered target locations in the room (Acredolo, 1978; Garrad-Cole et al., 2001). However, in cases like these in which the presence of certain features is directly associated with a target location or region of space (e.g., box near the window), it is debatable whether the computations underlying behavior in such tasks require a cognitive representation of the *space* or whether they could simply be guided by a stimulus-response learning process (see Fig. 1C).

Even younger infants display a recognition of "place" in their association of a context (e.g., particular features of a room) with a particular event. Studies showed that infants who learn that kicking their leg activates a hanging mobile above them (via a string tied to their ankle) retain this memory up to two weeks and kick their leg again the next time they are placed in the same crib with the same hanging mobile above them. Interestingly, they will show this memory in contexts not only under the exact same circumstances in which they acquired the knowledge but also in contexts that are similar to the original ones (showing a generalization of their spatial memory) but not in environments that are drastically different (Borovsky and Rovee-Collier, 1990). These results suggest that the reactivation of the original memory of the mobile activation is not dependent on the mere presence of the mobile, the string around the ankle, the identity of the researchers, and so on, but rather on the spatial context. Even for infants, using features as a marker of location or reward may not solely be based on a response to a stimulus but perhaps on their recognition of environmental contexts. Nevertheless, it may be important to note that the recognition of a context also does not always require the representation of the spatial layout or "map" of locations within that environment.

Egocentric and allocentric representations in children

There are several ways in which spatial navigation mechanisms can be categorized, but they largely group into two types based on the sources of input and the computations that may be performed on them. One common approach to understanding such computations is by distinguishing between route-based navigation, involving an egocentric or body-based frame of reference (e.g., “go right from the subway exit and turn left at the flagpole to cross the bridge”), and map-based navigation, involving an allocentric or world-based frame of reference (e.g., “go uphill from the subway exit and cross the bridge to the west side of the river”). Although both mechanisms take input from perceptual representations and combine their outputs to guide behavior (Burgess, 2006; Starrett and Ekstrom, 2018), the neurocognitive computations that are performed over those inputs are dissociable. For instance, in egocentric navigation, a path may be represented by a set of movements—the distance traversed and direction and degree of the turns along the way. Vestibular cues from our inner ear and proprioceptive cues from the mechanical movements of our body are translated by our brain into an estimation of how fast and far we have moved and turned. Using that information, the navigator can calculate a direct vector to get to a previously visited location of interest, through a process also known as path integration. However, under any normal circumstances, behaviors requiring a sense of direction and estimation of distance will be influenced by both body-centered and world-centered representations of space.

There is ample evidence that both egocentric and allocentric cues can be detected and utilized by a baby’s brain, albeit at a lower level of precision. Like adults, infants and young children are able to triangulate their way back to their starting point while blindfolded (Rieser and Rider, 1991). In fact, one study showed that a congenitally blind child can do it, suggesting that such path integration processes are functional even without vision, based on internal representations (Landau et al., 1984). If we solely rely on internal cues, there would be a heavy memory load and error that accumulates with each movement; hence, effective learning of routes involves positional corrections using external positional cues, such as local landmarks, geometry, and directional anchors, such as distal landmarks or celestial cues (Etienne, 2004; Maurer and Seguinot, 1996; Zhang and Mou, 2017).

A representation of space that is not tied to one’s own stimulus-response based bodily movements would require the building of a spatial representation based on locations in the external world. Tolman’s original formulation of the “cognitive map theory” was based on a rich set of evidence showing that rats can produce a set of novel movements or compute a shortcut that it has never traveled before in order to reach a goal location. Such behaviors would necessitate the existence of a mental representation of external space that can function independently, even when it is sometimes at odds with the previously executed body movements (i.e., egocentric representations). Nevertheless, early developmental researchers like Piaget believed that children ought to possess an egocentric representation of space first and, incrementally build an allocentric representation through their physical experience of navigating (Piaget and Inhelder, 1967; Siegel and White, 1975). According to an egocentric starting point for spatial navigation, however, there should be an egocentric bias in children’s organization of spatial information. Several studies have demonstrated this egocentric behavior in certain situations, with infants and younger children showing a tendency to search for objects based on the same side of their body from whether they first saw it, relying heavily on their self-motion (Acredolo, 1978; Bremner, 1978; Fernandez-Baizan et al., 2020; Nardini et al., 2006).

Although the utilization of an allocentric strategy has been demonstrated later in development (Lehning et al., 1998; Nardini et al., 2009), it is possible that the findings are confounded by children’s preference to repeat an action sequence that has been rewarding in the past. Some studies demonstrate that children actually are quite adept at an allocentric representation of space (Lew et al., 2004) and sometimes show a bias in the other direction (Montello, 1998); in other words, despite—or perhaps in addition to—children’s proficiency in using local cues and egocentric representations, they also have the capacity to consider the world as stable and invariant, rather than one’s own position and viewpoint. For instance, children’s ability to keep track of spatial location is more greatly disturbed by a transformation in the environmental structures (e.g., an “unstable” world in which the environment rotated around the child) than by a transformation of their own position in the room (e.g., a “stable” world in which children are moved to a new orientation in the environment) (Lourenco et al., 2005; Nardini et al., 2006). This allocentric bias is also true in adults: people are more accurate in their memory of relative locations and directions when the world remains stable (and they change their own viewpoints and positions within it), rather than when parts of the external world are changed (Wraga et al., 2004).

The above studies suggest that, in some cases, both young children and adults relied more heavily on a spatial representation of the goal locations, independent of their egocentric positions or local cues. Moreover, in contrast to the prediction that egocentric spatial concepts may be intuitive for young children, it is not trivial for children to learn body-centered spatial words such as left or right. When children are taught an ambiguous spatial label, they tend to map it onto world-based or landmark-based directions (e.g., north/south) rather egocentric direction (e.g., left/right) (Shusterman and Li, 2016). In other words, despite the possibility that representing a location as “the lamp that is to my right when I am facing the couch,” a more readily available representation may be something like “the lamp that is to the east of the couch.” Although the exact neural correlates of such readily available world-based coding of space is unknown, this phenomenon may be related to mechanisms in which representations of spatial cues guide place and head direction in the rodent brain (Muller and Kubie, 1987; Taube et al., 1990).

Spatial navigation by environmental boundaries

Separate from the question of what spatial frame of reference is dominant over navigation behavior is the question of which computations are performed over the input representations. Under normal circumstances, it is difficult to dissociate the multiple processes

that together contribute to spatial behavior. Therefore, many studies of spatial cue representation have placed cues in conflict with one another by transforming the environment (e.g., the placement of a landmark with respect to the geometry of the room) between training and test (Cheng and Newcombe, 2005). However, because it is not easy to decouple the behavioral effects of egocentric representations from the use of allocentric reference points, some studies have implemented a disorientation paradigm in which subjects are inertially rotated while the external cues are made perceptually inaccessible (e.g., using a blindfold or enclosed box in the case of small animals) (e.g., Cheng, 1986; Hermer and Spelke, 1994). Disorientation is a useful experimental manipulation because tracking one's own exact movements and heading direction is rendered useless in such situations. Under such conditions, disoriented navigation must rely on recognizing targets based on external cues and involve realigning one's spatial representation with respect to allocentric orientation cues.

Research across various fields of brain and cognitive sciences has investigated allocentric spatial representations using disorientation tasks, but the simplicity of this procedure, along with the fortunate fact that most little children enjoy being spun around, has made it particularly popular among developmental scientists. The past three decades of research has resulted in a wealth of knowledge about the developmental origins of the representations underlying navigation and the capacities and limitations of early spatial cognition (Spelke, 2022). One of the most fruitful lines of cross-disciplinary research and scientific debate is the strong influence of extended boundaries or terrain structures on navigation and spatial memory (Lee, 2017).

When children as young as 18 months old are shown a toy being hidden in one corner of a rectangular testing arena and then are disoriented, they split their subsequent searches for the toy between the correct corner and its geometrically equivalent diagonal corner, indicating their sensitivity to the rectangular layout of the room (Hermer and Spelke, 1994; Learmonth et al., 2002) (see Fig. 2A). This representation of environmental geometry is not limited to just walls or rectangles, as even 2 to 3-year-old children are capable of using a variety of 3D terrain layouts, or "boundaries", such as an array of short, truncated surfaces or even curved speed-bump-like structures on the floor or walls of an otherwise symmetrical space (Wang et al., 1999; Lee and Spelke, 2008, 2010a, 2011).

Studies have shown that the spatial inputs to this representation of the environment are specific to extended boundaries and do not apply to relative positions of freestanding objects or 2D lines; for instance, children under the age of about 5 or 6 search randomly in geometric arrays of identical objects (in the middle of a larger cylindrical room), even when they are connected by 2D lines or a thin cord (Gouteux and Spelke, 2001; Lee and Spelke, 2008, 2011; Mastroguseppe et al., 2023). Interestingly, infants and toddlers incorporate the array of objects into the environmental geometry when they are placed at the periphery, continuous with the boundaries of the enclosure (Garrad-Cole et al., 2001; Lew et al., 2006). Similarly, while children fail to use a freestanding object on one side of a room to distinguish between geometrically symmetric corners (Hermer and Spelke, 1994), they succeed when there is a three-dimensional structural bulge on one of the walls of the room (Wang et al., 1999).

In contrast to the early-developing and cross-species findings of spatial mapping by environmental boundaries, children's ability to compute relative locations using landmarks (e.g., objects in the environment) or featural cues (e.g., color or texture) is much more varied across species and experimental tasks (Cheng and Newcombe, 2005; Cheng, 2008). For instance, when features, such as a distinctively colored wall, were available in a rectangular space, disoriented children tested in a small experimental space fail to use it to help them discriminate between the two diagonal corners of the room (Hermer and Spelke, 1994; Learmonth et al., 2002). In contrast, children tested in a large room with a distal colored wall are better at incorporating that information into their spatial searches, although they still continue to choose based on boundary geometry (Learmonth et al., 2002). These failures are not

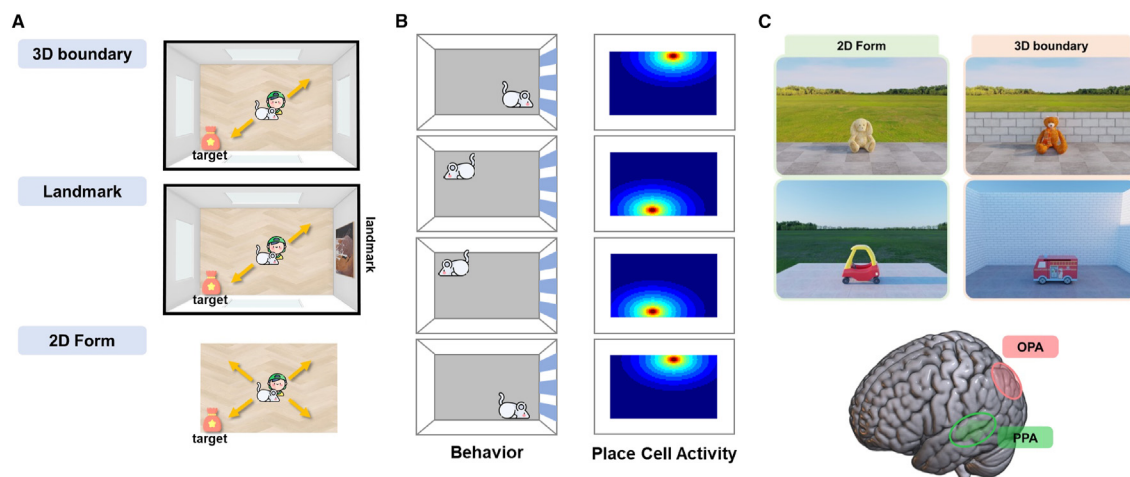


Fig. 2 Boundary-based spatial coding. (A) Disoriented spatial search in a rectangular room (top), a rectangular room with symmetry-breaking feature or object (middle), or a 2D rectangular form (bottom). The 3D boundary layout has been shown to strongly influence spatial navigation behavior. (B) The single-neuron activity of place cells in the rodent hippocampus predicts the boundary-dependent patterns of behavior (Keinath et al., 2017). (C) Scene-selective regions of the cortex in adult fMRI studies respond to 3D boundaries and may provide input to the hippocampus for navigation.

due to a competition between geometry and landmarks in influencing behavior—disoriented children still successfully remember and use objects and features as direct markers to location, even from infancy. Yet, even when there are no informative geometric cues, as in a square or circular room, they still fail to use the relative positions of landmarks to guide spatial mapping and often search completely randomly among possible locations if they do not have local features that distinguish them (Gouteux and Spelke, 2001; Lee et al., 2006; Wang et al., 1999).

Most complex behaviors, especially one as ubiquitous and important as spatial navigation, involve multiple cognitive computations that together influence the resulting behavioral output. It is important to recognize, therefore, that their combined influence on behavior is not the same as their integration at the computational level. The studies on children's spatial memory suggest that their allocentric representation of the environment may not be a coherent, equally represented combination of spatial inputs and, instead, may be more consistent with a view of multiple, dissociable spatial memory systems. In other words, a boundary-based computation of spatial relations among locations in the environment may be independent, at some level, from the representation of landmarks and their features that guide the discrimination of one location from another (Lee and Spelke, 2010b for review).

Insights from neuroscience

The types of spatial cues that children rely on in early development are actually not specific to humans and reveal something more fundamental and general about the nature of spatial representations in the brain. A similar pattern of findings, regarding both the primacy and specificity of boundary representations, has been shown across multiple vertebrate species, including untrained domestic chicks, fish, and rodents (see Lee, 2017 for review). Moreover, controlled-rearing studies with both chicks and fish have suggested that reorientation by environmental boundary geometry does not require any explicit training and experience with boundary-based navigation, supporting the view that these behaviors may indicate an immediately available capacity to process such environmental cues for spatial memory and wayfinding (chicks: Chiandetti and Vallortigara, 2008; fish: Brown et al., 2007).

The distinction between boundaries and objects may have its neural foundations in the hippocampus. For instance, single-cell recording studies of rats have identified hippocampal place cells that respond when an animal is in a particular location in space (O'Keefe and Nadel, 1978). While changes in environmental geometry cause changes in place cell firing, changes in texture and material do not (O'Keefe and Burgess, 1996; Lever et al., 2002). Moreover, one study demonstrated that the rotation of hippocampal place cell "maps" that accords with the boundary geometry predicts behavioral search on a trial-by-trial basis (see Fig. 2B). Interestingly, just as in children's behavior, place cells activity is also guided by landmark objects at the periphery of the environment—continuous with the environmental boundaries—to a much greater extent than freestanding objects within the testing arena (Cressant et al., 1997; Zugaro et al., 2001).

Specific neural representation of boundaries that responds to perturbations of the ground surface such as walls, bumps, and drop-offs have been found in the entorhinal cortex and subiculum of rodents (Solstad et al., 2008; Lever et al., 2009). More recently, their correlates have been found in the human brain using direct intracranial recordings of neural activity (Lee et al., 2018; Stangl et al., 2021) or functional neuroimaging (Shine et al., 2019) during navigation in both virtual and real environments. One study suggested a possible dissociation between boundary-based navigation and landmark-use, with boundary use resulting in activation of the hippocampus and landmark-based navigation resulting in activation of the dorsal striatum (Doeller et al., 2008). Behavioral results using the same task showed that while landmark-based navigation might, in some situations, obey the rules of associative learning, boundary-based learning might happen incidentally, occurring even without reinforcement (Doeller and Burgess, 2008). Interestingly, these basic neural representations of boundaries and spatial location develop early in rat pups, showing spatial specificity that resembles that of adult animals right around the time they first open their eyes and start moving about the environment (Bjercknes et al., 2014; Wills et al., 2014). Such insights from animal studies suggest that, contrary to Piaget's views, infants also have such early-functioning neural mechanisms that do not manifest in their behavior until they are able to move around on their own.

One implication of navigation that is supported by multiple, dissociable underlying mechanisms is that there may be a differential developmental trajectory across those mechanisms, as well as specific delays or deficits in a subset of those mechanisms. Evidence from individuals with William's Syndrome (WS), a genetic neurodevelopmental disorder, suggests that their severe deficits in spatial cognition may be associated with an abnormal development in the dorsal stream regions and hippocampal network (Meyer-Lindenberg et al., 2006). Individuals with WS show an interesting pattern of spatial behavior that is distinctive from that of normally developing children. First, they often show an impairment in navigation, both in their use of boundary geometry-based spatial navigation behavior (Lakusta et al., 2010; Ferrara et al., 2019) and spatiotemporal episodic memory (Mastrogiuseppe et al., 2019). In contrast, however, they have been shown to utilize a landmark (e.g., a red wall) to specify one correct corner in a rectangular room (Lakusta et al., 2010) and remember a sequence of objects independent of their spatial location (Mastrogiuseppe et al., 2019). Moreover, their ability to distinguish between different objects based on shape (Landau et al., 2006) and to remember spatial locations based on landmarks is relatively preserved. Recent studies in cognitive neuroscience have partly attributed the navigational deficits in WS to a dysfunction in their boundary-related scene-processing cortical mechanisms (see Fig. 2C) that provide input to hippocampus, which ultimately results in an impairment in their ability to navigate (Ferrara et al., 2019; Julian et al., 2019; Kamps et al., 2023). Such findings are consistent with the existence and development of parallel cognitive mechanisms that inform navigational decisions. In other words, while the spatial boundary representations may be disrupted in WS, their landmark representations may still be intact.

Uniquely human spatial cognition

The degree to which outputs of multiple dissociable mechanisms influence spatial cognition may change over experience and across situations. This may explain why, despite the evidence for the initially privileged status of extended three-dimensional boundaries for reorientation, children and nonhuman animals are able to use both boundaries and landmarks to remember locations, especially with repeated experience. Additionally, there may be at least two uniquely human developmental changes that occur in children's navigational capacity. The first is the ability to represent spatiotemporally organized events in the form of episodic memories that emerge with the maturation of the fronto-hippocampal network in middle childhood (Lee et al., 2020). The second, perhaps much more culturally driven than the first, is the acquisition of a symbolic representation of space (Spelke et al., 2010; Uttal, 2000).

Although both episodic memory and spatial navigation involve the hippocampus, the two cognitive functions were historically studied independently, with the former strongly driven by human clinical researchers and the latter by animal behavioral neuroscientists. While some researchers make important distinctions in the navigational and episodic memory function of the hippocampus (e.g., Ekstrom and Hill, 2023), particularly across cerebral hemispheres or anterior-posterior subregions of the hippocampus (Burgess et al., 2002; Kühn and Gallinat, 2014), others have tried to bridge the gap by proposing that hippocampal place mapping provides a spatial framework upon which episodic memories are represented (Maguire and Mullaly, 2013; Miller et al., 2013). According to such accounts, events are recalled as mental reconstructions of the spatial context and the details associated with it. These recreated spatial scenes organized into a temporal sequence may give us the sense of re-experiencing the episode (Kim and Lee, 2023). Because episodic memory requires the concerted activity of the hippocampus along with various cortical networks, particularly with regions of the frontal lobe, it may develop over a protracted period in middle to late childhood (Demaster and Ghetti, 2012). The resulting consequences on children's navigation skills are significant, as even a single experience can later be remembered in detail to guide adaptive spatial behavior. For instance, around the age of about 6, disoriented children begin to reliably find their way back to a target location even when it is defined by a landmark rather than solely by boundary geometry (Hermer-Vazquez et al., 2001; Learmonth et al., 2002). This success may, in part, be supported by a maturing cortico-hippocampal network giving rise to adult-like episodic memories.

At the same time, however, the development of symbolic and linguistic representations may be at play, conceptually changing the way children think about space altogether. There are several ways in which our symbolic capacities allow us to surpass our early, core cognitive representations. One way is by providing us with a variety of flexible ways for organizing space, such as dividing up space into regions (e.g., halves of a sandbox) or categories (e.g., floors of a building) (Newcombe and Huttenlocher, 2000). This allows us to remember a large amount of information by chunking it into meaningful, hierarchical units (e.g., Rah et al., 2022). Second, a linguistic combination of conceptual categories allows us to encode relationships that may not be readily available in early childhood—for example, remembering a target location as “the corner to the left of the red wall” can help children to avoid making a geometry-based symmetric error in a rectangular room (Hermer-Vazquez et al., 2001; Shusterman et al., 2011). Furthermore, the description of both a small-scale object and a large-scale room by the same word (e.g., square) can help children apply their representation of objects to navigable spaces.

Perhaps even more critical to this process might be the use of maps—two-dimensional symbolic depictions of three-dimensional environments from which we must locate ourselves and our trajectories through them. Not only could maps aid in children's survey representations of large-scale spaces (e.g., overhead view) (Uttal, 2000), it could additionally allow them to reason about space using a combination of concepts, such as size and shape, that they already have acquired for reasoning about objects (Spelke et al., 2010). Such changes may allow older children to connect a configuration of separated objects or 2D lines into their representation of environmental boundary-based maps (e.g., Ferrara et al., 2019; Mastrogiuseppe et al., 2023; Shusterman et al., 2008). Importantly, such uniquely-human symbolic representations may extend beyond physical space and serve as a basis for our flexible cognitive manipulation of conceptual spaces.

Conclusion

In this review, I have laid out some basic cognitive mechanisms that underlie children's early spatial navigation and how they might change over the course of development. Some of these changes occur through experience or maturation. But others are a product of human language and culture. Ultimately, such tools can provide children with an abstract representation of space that is qualitatively different from what they started out with in infancy, resulting in a uniquely human way of calculating, remembering, communicating, and optimizing navigational strategies in adulthood. Further research in developmental cognitive neuroscience, using neuroimaging and electrophysiology in combination with navigational tasks, will provide key advances in revealing the neural basis of spatial cognitive change over development.

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