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REVIEW

Two systems of spatial representation underlying navigation

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Abstract We review evidence for two distinct cognitive processes by which humans and animals represent the navigable environment. One process uses the shape of the extended 3D surface layout to specify the navigator's position and orientation. A second process uses objects and patterns as beacons to specify the locations of significant objects. Although much of the evidence for these processes comes from neurophysiological studies of navigating animals and neuroimaging studies of human adults, behavioral studies of navigating children shed light both on the nature of these systems and on their interactions.

Keywords Spatial navigation · Reorientation

Introduction

An animal's ability to find its way around the world is of utmost importance to its survival. Most animals navigate by keeping track of the direction and extent of their own movement with respect to the visual environment by updating their position as they move (Mittelstaedt and Mittelstaedt 1980; Gallistel 1990; Wang and Spelke 2002; Burgess 2006). This process of path integration requires no encoding or memory of environmental features, but it is limited both in precision and in the complexity of the navigation patterns it supports (Etienne 2004; Wang et al. 2006). To overcome these limits, navigating animals and humans encode properties of the environment, including its objects and landscapes, and they use that information both to identify significant locations and to maintain or recover a sense of their own position and orientation. Thus, the spatial representations of the environment that guide navigating animals are best revealed when path integration is pushed beyond its limits or disabled altogether by disorientation.

The present review focuses on behavioral evidence, mainly from studies of disoriented preschool children, supporting the existence of two independent cognitive processes by which spatial properties of the environment are analyzed for the purposes of navigation. One process performs a geometric analysis of the environment's extended 3D surfaces, and it uses the distances and directions of surfaces to specify the navigator's position. The other process performs geometric and featural analyses of objects and 2D patterns, and it uses their distinctive properties to indicate specific goal locations. These two processes normally work together, but they can be distinguished in four ways: they operate on different kinds of input, they perform different kinds of computations, they yield different kinds of information about the navigator and the environment, and they are associated with activity in different brain systems. We consider first the evidence for these two processes in adult non-human animals and humans. Then, we turn to the evidence from studies of young animals and human children.

Mature systems of navigation

Cheng and Gallistel (Cheng and Gallistel 1984; Cheng 1986) were the first to discover that untrained rats rely primarily on the shape of the navigable space to specify a goal location. When rats were disoriented after observing the burying of food in a rectangular chamber with a variety of detectable landmarks such as odors, 2D contrast patterns, and walls of different brightness, they then dug for the food

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in two locations: its actual position and a geometrically congruent position on the opposite side of the chamber (see Fig. 1). Because the room's landmarks served to distinguish these positions, rats' search patterns suggested that they were guided only by the shape of the room. With training, rats came to use objects positioned directly at the food's location, through a curious behavioral pattern. Immediately after disorientation, trained rats headed either for the correct corner or for the geometrically equivalent opposite corner, as did their untrained counterparts. Before digging, however, the trained rats checked for patterns near the goal position, and they reversed direction if the correct pattern failed to appear.

Based on these observations, Cheng and Gallistel proposed that two distinct processes guided disoriented rats' navigation: a computation of layout geometry operating automatically and without training, and a beacon-guidance process sensitive to objects or patterns near the goal location and subject to attention and learning. Gallistel (1990) argued for the adaptiveness of a geometric process applied only to a representation of 3D surface layouts. Objects in nature such as trees and rocks are poor guides to reorientation because they have many featural look-alikes that can only be distinguished through fine-grained, computationally inefficient comparisons. Moreover, such objects tend to be movable or to have features, such as leaves, that change over time. From an ecological standpoint, therefore, extended 3D surface landscapes are the most stable, reliable, distinctive cues in the natural environment that remain distinguishable even with a relatively coarse-grained representation.

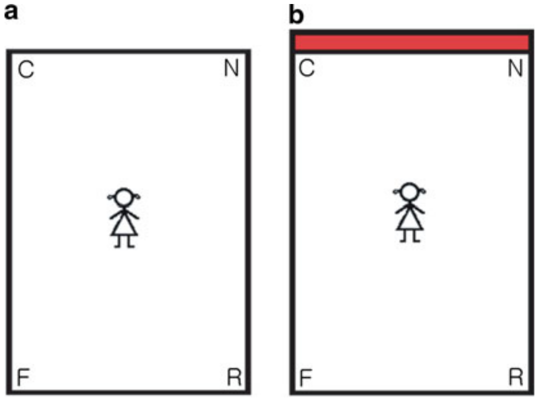

Fig. 1 Schematic, overhead depiction of two testing environments with and without a featural cue (a distinctively colored wall). After an object is hidden at *C* and participants are disoriented in (**a**), humans and non-humans animals alike use the geometric shape of the rectangular room to search the correct (*C*) and rotationally symmetric (*R*) corners more often than the near (*N*) and far (*F*) geometrically incorrect corners. Under some conditions, moreover, children and non-human animals fail to use the potential landmark in (**b**) to break the room's symmetry, and therefore search at *R* as often as at *C*

In recent years, Gallistel's argument has been supported by research in robotics. Early attempts to design autonomously navigating robots relied on raw images, either from artificial vision systems or from range-finding systems, that failed to segregate information about enduring, extended surfaces from information about objects. One difficulty faced by such systems, however, was the error caused by misrecognition of a location when the robot encountered similar or displaced objects in different parts of the environment (Thrun 2003). A second difficulty was the combinatorial explosion that accrued as the robot moved into new territory and recorded all the spatial details in the cluttered environment. By eliminating objects and representing only extended surfaces, a navigating robot can form representations that are more economical, because surfaces tend to be smooth and therefore can be presented with just a few points each (Egerton et al. 2000; Gee et al. 2008; Silveira et al. 2008). Both ecological and computational considerations therefore favor a distinct process of navigation by surface layout geometry.

In the years since Cheng and Gallistel's original studies with rats, research on reorientation was conducted with many species of animals, including pigeons, chicks, fish, monkeys, humans, and ants (for review, see Cheng and Newcombe 2005). The experiments on ants are of special interest, because they reveal a pattern of behavior very close to that originally reported by Cheng (1986). In these experiments (Wystrach and Beugnon 2009), oriented ants navigated from their nest to a testing space where they encountered food to be transported back to the nest, at the center of a rectangular arena. Before setting off for the nest, ants were disoriented within this arena. In the first experiments, the arena had holes in each of its four corners by which ants could return to the nest, and the surface layout beyond the arena was clearly visible, with geometric structure that uniquely specified the ant's orientation. Ants quickly learned to locate a corner exit from the arena; thereafter, they moved directly to this single corner immediately after disorientation when the larger array was visible, and they moved with equal frequency to this single corner and to the geometrically equivalent opposite corner when the larger array was hidden. The latter performance indicated that the ants were indeed disoriented and that they used the shape of the visible surface layout to reorient themselves.

In later experiments, ants were trained with distinctive patterns at each corner of the arena. Although the patterns were both visible and discriminable from the ant's starting location at the arena's center, the ants ignored them and reoriented only by the shape of the arena. The authors noted, however, that the minimal training did not strongly encourage beacon guidance, so they performed a further experiment with more extensive training, in which only one corner of the rectangular array led to the nest, with its position indicated by a unique pattern. Ants' behavior was striking. Like Cheng's rats, they learned to exit only through the corner marked by the unique pattern, but they found this corner through a circuitous route: They approached the correct corner *and* the rotationally opposite corner with high frequency and then reversed direction if they found themselves in the corner with the wrong patterning. Like rats, disoriented ants' search appeared to be guided by two distinct processes: a reorientation process sensitive to layout geometry and a beacon-guidance process sensitive to a learned, visual pattern.

Although the hypothesis of separate systems for navigating by layout geometry versus distinctive patterns or objects originally was suggested by studies of reorientation, the evolutionary and computational considerations described elsewhere suggest that separate systems would be computationally efficient for oriented animals as well. Consistent with this suggestion, there is evidence for independent representation of landmark objects versus surface layout geometry in oriented animals. For example, rats in a water maze learn the location of a hidden platform faster with respect to geometric than featural information (Benhamou and Poucet 1998). In many studies, moreover, animals encode layout geometry automatically but learn to use objects as landmarks only with heightened attention or training (Cheng and Newcombe 2005; though cf. Cheng 2008).

Consistent with these behavioral data, there is evidence that multiple systems of specialized neural structures underlie spatial behavior (Packard and McGaugh 1996, White and McDonald 2002). Research on the hippocampus and surrounding regions has resulted in the identification of regions that process surface layout geometry but not landmark objects or surface colors and patterns. Single-cell recording studies of rats' hippocampal place cells, which fire when an untrained, freely moving animal moves to a particular location in the environment, have shown that extended cues, particularly walls of the testing space, are crucial to the representation of location (O'Keefe and Burgess 1996; O'Keefe and Nadel 1978). Changes in surface boundaries affect place cell activity, but changes in surface texture and material often have no effect, unless these features change so radically that the animals represent the environment as completely novel (Lever et al. 2002). Moreover, the firing fields of place cells and nearby head-direction cells (which fire when a rat is oriented a particular way with respect to the environment) are controlled by objects placed near the walls of the testing space, but not by objects placed well within the environment (Cressant et al. 1997; Zugaro et al. 2001). All these studies suggest that freely moving rodents spontaneously encode their location with respect to the distance and direction of extended surfaces in the environment, but not with respect to the colors or textures of surfaces or to the positions of freestanding objects.

The hippocampus has also been shown to encode view-independent representations of space, capturing the relative positions of multiple elements in the environment, rather than view-specific associations to individual landmarks (Burgess et al. 2002). Hippocampal lesions produce selective impairments in spatial tasks that require the encoding of room shape or relationships between multiple environmental features but not in tasks that require the use of an object for beacon guidance (e.g., Morris et al. 1982; McGregor et al. 2004). However, the hippocampus is not the only brain region that informs spatial navigation using the 3D environmental surface layout. Representation of geometric borders has recently been found in the entorhinal cortex of rats; these cells are hypothesized to define the perimeter of the environment and serve as reference frames for encoding locations within that environment (Solstad et al. 2008).

Spatial functional specialization has also been found in the avian brain. Studies manipulating brain regions in pigeons and chicks have revealed dissociable neural architecture for geometric analysis of room shape and the use of feature cues (Nardi and Bingman 2007; Tommasi et al. 2003); for instance, left-eyed split-brained chicks reorient by both featural cues and room shape, whereas right-eyed chicks only reorient by featural cues (Vallortigara et al. 2004).

In humans, functional neuroimaging studies have shown preferential activation of the right posterior hippocampus for processing locations with respect to environmental boundaries and activation of the right dorsal striatum for landmark-related locations (Doeller et al. 2008). These researchers provided behavioral evidence, using the same visual displays and spatial memory task, that while object-related learning obeys associative reinforcement principles, boundary-related learning is incidental, consistent with the aforementioned findings from behavioral studies of animals (Doeller and Burgess 2008). Neuroimaging studies have also identified a parahippocampal region (Epstein and Kanwisher 1998; Epstein et al. 1999), as well as the transverse occipital sulcus (TOS; Epstein et al. 2005; Grill-Spector 2003), as areas that specifically respond to visual scenes but not objects. Damage to the parahippocampal place area (PPA) impairs recognition of spatial scenes while preserving object recognition (Epstein et al. 2001; Mendez and Cherrier 2003; Pitcher et al. 2009). And abnormalities in the TOS, observed in adults with Williams syndrome, are associated with impaired reorientation by geometry but preserved use of a color feature as a beacon (Lakusta et al. 2010).

Many branches of neuroscience are dedicated to the study of neural systems underlying spatial cognition and navigation, and our brief review does not do them justice. There is considerable debate concerning the functions of the various neural systems activated during navigation (e.g., Burgess 2006; Cheng 2008), the frames of reference by which navigating animals represent both the positions of objects and the distances and directions of extended surfaces (e.g., Wang and Spelke 2002; Burgess 2006; Nardini et al. 2009), and the respective roles of local versus global processing in navigation (e.g., Sutton 2009). Nevertheless, there is growing evidence for separate brain systems dedicated to the processing of geometric surface layouts on one hand and objects, colors, and surface markings on the other.

Alternative accounts

Two main alternative theories to the present two-process view have been proposed to explain reorientation behavior. One theory claims that reorientation depends on a single, coarse-grained view-matching system based on 2D retinal snapshot representations (Cheng 2008; Sheynikhovich et al. 2009) similar to those found in insects (Cartwright and Collett 1982; Collett and Collett 2002). According to this view, an animal moves to reduce the discrepancy between a stored snapshot representation of the scene and the scene it currently perceives. Consequently, the snapshot account predicts that retinal salience is the determining factor for what does and does not affect an animal's reorientation. Computer simulation studies have demonstrated that "geometric search" using long and short wall-like surfaces can result from such a model of navigation (Cheng 2008; Stürzl et al. 2008). In contrast to the two-process view, this theory makes no distinction between 2D surface features, object arrays, or surface layouts, and it gives no privileged role to 3D surface layouts apart from their retinal salience.

Retinal image–matching processes can capture a rich array of behavioral and neurophysiological findings on navigating animals, especially if they are combined with other navigation processes. For example, one problem for image-matching theories is that animals who have viewed an environment can continue to navigate effectively in the dark, while exhibiting very few neurophysiological differences between navigating in light and in darkness (Goodridge et al. 1998; Lever et al. 2009; Quirk et al. 1990). A recent computational theory accounts for this phenomenon and others through a combination of path integration and image-matching processes (Sheynikhovich et al. 2009). By itself, moreover, a single image-matching process cannot readily explain why rats and ants engage separate processes for navigating by the shape of the layout and by landmark patterns. Wystrach and Beugnon (2009) suggest, however, that two distinct image-matching processes, operating at different spatial scales, could explain this behavior pattern. Thus, image-matching views present a serious challenge to Cheng and Gallistel's thesis of a system for reorienting by layout geometry.

The second theory is the *adaptive combination theory*, which holds that both landmarks and geometry are processed by the same underlying mechanism, weighted according to their experienced validity and salience (Newcombe and Ratliff 2007). On this view, individuals learn through experience that small, movable objects are unreliable as cues to reorientation. Large objects in a large room, on the other hand, are distal, stable, and salient; children learn that such potential landmarks are reliable cues for navigation and assign high weights for their use in the task of reorienting (Learmonth et al. 2001). Like the snapshot view, the adaptive combination view grants no special advantage for 3D surface layouts other than the higher influence they have on behavior due to their salience, size, stability, and learned reliability.

In contrast to these two theories, we propose, following Cheng and Gallistel's original theory, that humans and animals navigate by (a) an automatic process for analyzing the shape of the extended surface layout and (b) an attention-dependent process for locating objects relative to perceptible, nearby beacons. This view makes three specific predictions that distinguish it from the image-matching or adaptive combination theories. First, animals will navigate by the geometry of the extended surface layout even if they are raised under conditions that give them no experience of the reliability of this information. Second, even subtle perturbations to the 3D surface layout will guide navigation automatically, whereas large and salient 2D image features will not. Third, objects, 2D patterns, and surface colors will be used by navigating animals through a separate, beacon-guidance process. We now review behavioral studies of young animals and children that test these predictions.

Controlled-rearing studies

Studies of controlled-reared animals, conducted by two independent groups of researchers, provide evidence that the capacity to navigate by surface layout geometry develops in the absence of experience navigating in environments with informative shapes. Brown et al. (2007) reared separate groups of fish in environments with no informative geometrical structure (a circular tank) or environments with walls of distinctive lengths and directions (a rectangular tank). When both groups of fish subsequently were disoriented in a rectangular environment, those with prior experience in the rectangular environment performed no better than those with no such experience. In contrast, use of surface features (wall color) was influenced by these rearing conditions. When fish were trained to use a blue wall to reorient, those who were reared in a circular tank learned to use the feature faster and relied on it more heavily when geometric and featural cues were placed in conflict. These findings suggest that processing of featural cues depends in part on past experience, whereas processing of layout geometry does not.

In similar experiments, Chiandetti and Vallortigara (2008) reared chicks in circular, rectangular, or C-shaped environments and then tested their reorientation in a rectangular space. Chicks in all three rearing groups were equally good at reorienting by surface layout geometry, consistent with the findings with fish. Interestingly, chicks reared in the circular and rectangular environments also were equally good at learning to use the features of corner panels as beacons to the correct corner of the rectangular testing space, and all continued to rely on surface layout when the corner features were removed. While the feature conflict tested by Brown et al. (2007) may not be directly comparable to the feature removal tested by Chiandetti and Vallortigara (2008), both studies clearly show that reorientation by the 3D layout geometry occurs independently of past experience with those geometric properties, in contrast with the predictions of the adaptive combination view.

Developmental studies of reorientation

Young human children show navigational abilities and limits that are similar to those of non-human animals. In the first studies, children aged 18–24 months saw a toy hidden in one corner of a rectangular testing arena with one blue and three white walls and then were disoriented by slow turning at the center of the room with eyes covered. When the children were released and encouraged to locate the toy, they tended to search at both the correct corner and the geometrically equivalent opposite corner (see Fig. 1; Hermer and Spelke 1994, 1996). Children's search at these two corners provided evidence that they, like rats, navigated in accord with the shape of the surrounding surface layout. Children's failure to search the correct corner more often than the opposite corner suggested that children, like rats, encode surface layout geometry more automatically than non-geometric features like wall color (Cheng and Newcombe 2005).

Further experiments extended these findings and revealed that disoriented children also use objects and 2D patterns as direct beacons to guide their search. When children were tested in a circular room with a rectangular or triangular array of identical freestanding objects, they searched only at the objects in the room, showing that they encoded the spatial relationship of the hidden toy to its container and remembered this relationship at test (Gouteux and Spelke 2001). Interestingly, however, children searched the containers at random, suggesting that children failed to encode or use their geometric configuration.

Subsequent research revealed that toddlers do respond to the configural properties of a rectangular array of objects when the objects are placed at the periphery of a circular enclosure (Garrad-Cole et al. 2001; Lew et al. 2010). Further experiments suggest that children respond to objects at the walls of the room as part of surface layout geometry. Although children failed to use a freestanding object on one side of a room to distinguish between geometrically identical corners (Hermer and Spelke 1996), they succeeded when the object was replaced by a 3D bulge on one of the walls of the room (Wang et al. 1999). Moreover, children failed to reorient by an arrangement of two objects offset from the walls of a circular room, but they successfully reoriented by the same two objects when they were placed flush against those walls (Lee and Spelke 2010c). Like rats, children navigate primarily in relation to the positions of the borders of the array (O'Keefe and Burgess 1996; Solstad et al. 2008).

These findings suggest that children are especially sensitive to 3D surface layouts, contrary to both the image-matching and adaptive combination theories and in accord with the prediction that the geometry of extended 3D surfaces, both subtle and small, guides navigation. We tested this prediction further by comparing children's reorientation in rectangular environments varying in height, connectedness, and dimensionality (Lee and Spelke 2008). Children reoriented by the geometric shape of an arena made of short walls that blocked neither their vision nor locomotion, but they failed to reorient by a rectangular array of large freestanding columns. Children also failed to reorient either by a 2D rectangular figure on the floor (Lee and Spelke 2008) or by a pair of large, 2D rectangular patches on the walls (Lee and Spelke 2010c; cf. Newcombe et al. 2009). Importantly, children confined their search to one of the columns, 2D corners, or 2D patches in these environments, showing that they encoded and remembered the hiding places. Nevertheless, they searched randomly at the various columns, corners, or patches. These findings suggest that children's reorientation is guided neither by the immediate functional relevance of walls nor by their size or connectedness, but rather by a specific sensitivity to the shape of the 3D surface layout.

More recent work has shown even more striking differences in children's use of featural cues and surface layout geometry (Lee and Spelke 2010b). Children aged 3–4 years, tested in a white circular room, oriented themselves in accord with a tiny (2-cm-thick, 2-cm-high) light-colored frame placed on the floor and also in accord with two smooth bumps on the floor, showing sensitivity to highly subtle perturbations in the 3D surface layout. In contrast, children failed to orient by the shape of a salient, dark, 2D rectangle or by an array of cylinders connected by a string that delimited the rectangular space as effectively as did the bumps and frame. These findings provide evidence that children's reorientation depends not on the visual salience of layout features but on 3D surface layout geometry.

Children's failure to navigate with respect to the relative distances and sense relations between large, salient objects and 2D forms, in contrast to their successful reorientation by subtle 3D surface layouts, provides compelling evidence that the cognitive processes involved in reorientation do not apply to an array of objects as they do to an array of extended 3D surfaces. Yet, in all experiments, children correctly remembered the relevant hiding locations according to the features, confirming the third contrasting prediction of the theories of reorientation, that objects and surface features are used as beacons or direct markers to location but not as relative position cues for reorientation.

Despite the privileged status of extended 3D surface layouts for reorientation, disoriented children and non-human animals are clearly able to use featural cues to remember locations (for review, Cheng and Newcombe 2005). For instance, when the testing space is large and contains a large colored wall, both human toddlers and animals are much better at using the wall color cue to guide their search (Learmonth et al. 2001; Learmonth et al. 2002; Sovrano et al. 2006). There are two possible interpretations of these data. First, a large colored wall, like room shape, may be used as a relative position cue (i.e., "the correct location is northwest when I am oriented to the blue wall"). Alternatively, a colored wall may serve as a beacon that indicates whether the goal location is toward it or away from it.

Research with non-human animals suggests that objects and surface features are used as direct markers or beacons to location but are not used spontaneously as indirect cues to direction and orientation. Fish (Sovrano et al. 2003) and chicks (Vallortigara et al. 1990) use the features at the goal location to distinguish a corner of a rectangular space, but when the direct features are removed, they fail to find the correct corner with respect to more distant featural cues. Similarly, children's search is guided by a large colored wall when objects are hidden at the corners of a large room, but not when they are hidden near the room's center, displaced from the cue (Learmonth et al. 2008). Moreover, children search more effectively when objects are hidden at one of the two corners that are adjacent to the colored wall than when objects are hidden far from the wall (Shusterman et al. 2010). Because these studies involved the use of features within a room with informative geometric shape, however, it is possible either that the room shape cues dominated the reorientation behavior or that the children were simply drawn to the distinctively colored wall, decreasing its influence as a distal landmark.

Lee et al. (2006) tested whether disoriented children use landmarks to reorient or only as beacons. In a series of studies, children were tested in a circular room with three equidistant containers forming a triangle at its center. In one study, the three containers differed in color and shape: when an object was hidden in one container and then children were disoriented, they readily retrieved it. In a second study, the array consisted of two identical containers and one distinctive container. Disoriented children searched correctly when an object was hidden in the featurally distinctive container, but they searched correctly only about half of the time when it was hidden in one of the two identical containers. This finding suggested that children used the containers as beacons but not as relative reorienting cues, but it was possible that children reoriented by the goal container but ignored the other containers, resulting in successful reorientation when the critical container was distinctive and *mis*orientation on half of the trials when it was not. The authors addressed this possibility with two further experiments in which two objects were hidden in two different containers on each trial. When all three containers were featurally distinctive, disoriented children accurately retrieved both objects, showing that hiding two objects did not overly tax children's memory or goal-directed action. When presented with one distinctive and two identical containers, however, disoriented children were only able to correctly locate the object in the distinctive container and searched randomly between the two featurally identical containers. These findings provide the clearest evidence that children used the features of the containers only as direct indicators of the hidden object's location and not as guides to reorientation.

Huttenlocher and Lourenco (2007) investigated the effects of 2D surface features in a square-shaped room whose opposing pairs of walls differed in color or pattern. Contrary to the predictions of image-matching theories, children failed to reorient when adjacent walls differed in color[1] or pattern. Interestingly, however, children succeeded when tested in a room whose opposite walls displayed circles that were either large or small. Similar results were found with mice (Twyman et al. 2009), suggesting homologous systems of reorientation across distantly related species. The authors proposed that children's reorientation was driven by a relational comparison along a common dimension, but this account fails to explain why variations along the size dimension were effective when variations along the color dimension were not.

An alternative interpretation of Huttenlocher and Lourenco's findings rests on the evidence from studies of depth perception that adjacent arrays of small and large circles present children with the visual depth cue of *relative size* (e.g., Yonas et al. 1985). By presenting large circles on two walls and small circles on the others, the investigators may

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[1] In a similar test with toddlers, Nardini et al. (2008) found success with two white walls and two blue walls, both plain and patterned. Lourenco et al. (2009), on the other hand, replicated their failure of alternating features using red or blue patterns, rather than solid walls. Because of these conflicting results, children's ability to use of color cues for reorientation remains unclear.

have created an illusion of distance such that the room was perceived as slightly rectangular. But can young children reorient by only a slightly rectangular array? To address this question, we tested children's reorientation in a slightly rectangular room (Lee et al. 2010). Children confined their search to the two geometrically appropriate corners of a rectangular arena 132 cm by 122 cm (about 8:9 ratio), suggesting that children show considerable sensitivity to subtle differences in the positions and directions of walls. If the depth cue of relative size can induce a perception of differences of this magnitude, then the findings of Huttenlocher and Lourenco may be explained by a reorientation system that is highly sensitive to perceived layout geometry.

A final source of evidence for a distinctive process of navigating by layout geometry comes from a recent study comparing the navigation performance of young children to that of adults with Williams syndrome (Lakusta et al. 2010). Typically developing young children and WS adults were given the same reorientation task in the same environment: a rectangular chamber with a single distinctively colored wall. As in past studies of children, the young children's search after disorientation was guided by the shape of the room and not by the color of the wall. Adults with WS, however, showed the opposite pattern: their search benefitted from the colored wall but not from the distinctive shape of the room. This double dissociation provides the clearest evidence in humans for separate processes of navigating by layout geometry vs. surface features. Because Williams syndrome results from a specific genetic deletion, moreover, the abject failure of adults with Williams syndrome to reorient by layout geometry suggests that this reorientation system has quite a specific genetic basis.

Despite all these findings, there is robust evidence that human adults and older children can use purely non-geometric color cues to locate hidden objects. When human adults are disoriented in a rectangular room with one colored wall, they readily and consistently confine their search for a hidden object to its uniquely correct location, despite the room's symmetry (Hermer and Spelke 1994; Hermer-Vazquez et al. 1999; Ratliff and Newcombe 2008). Children begin to show this pattern at about 5–7 years of age (Hermer-Vazquez et al. 2001). This developmental change suggests the emergence of new navigation processes that may be unique to humans and dependent on capacities for language and symbolic representation (Landau and Lakusta 2009; Shusterman and Spelke 2005). Like the uniquely human system of natural number that is constructed from core systems shared with other animals (Carey 2009), a uniquely human system of spatial representation may be constructed from independent parallel systems of navigation and object recognition (e.g., Spelke et al. 2010). Such processes are beyond the scope of the present article.

Summary

The findings reviewed earlier support three key predictions of Cheng and Gallistel's original two-process account of reorientation against the predictions of both visual snapshot theories and adaptive combination theories. First, animals raised in environments that provide them with no experience with informative geometric shape nevertheless reorient by environmental shape just as well as those raised in geometrically informative environments. Second, children use even small and subtle properties of the 3D surface layout for reorientation, but they fail to use large and salient properties of objects or surface features such as color or 2D patterns. Thus, disoriented children's selective use of 3D surface layouts fails to be explained by effects of cue salience, size, stability, distance, rectilinearity, or brightness contrast. Finally, children and animals use objects and 2D surface features as direct cues to a hidden object's location, even as they fail to reorient by them, providing evidence for distinct processes of reorientation and beacon guidance.

It is important to note that evidence for the presence of a geometric computation of 3D surface layouts and a separate mechanism of beacon-use does not rule out the existence of visual snapshots or adaptive learning. Image matching and adaptive learning are navigational strategies that are available to non-human animals (Cartwright and Collett 1982) and to humans (Wang and Spelke 2002). The evidence suggests, however, that these mechanisms cannot explain children's reorientation by the shape of the 3D surface layout.

Conclusion

Characterizing core knowledge systems is important in understanding the organization of the mind, because they form the basis for later learning and conceptual change. The study of early developing navigation abilities and of the cognitive capacities, which allow humans to combine the outputs of specialized mental computations, together promises to shed light on the process through which human children and adults come to build new, more powerful human knowledge systems, including systems of formal geometry (Spelke et al. 2010).

Research using behavioral, neuroimaging, and neurophysiological measures, conducted on animals from ants to educated adult humans, provides evidence for at least one core system at the foundations of knowledge of geometry: a system for recording one's position relative to the distances and directions of the extended surface borders in the layout. This evidence, however, leaves many questions unanswered. First, what are the geometric relationships that this system captures? In all of the aforementioned studies involving rectangular arrays, children and animals navigated in accord with the distances and directions of surface borders. In Euclidean geometry, however, shape is characterized by *angle* as well as *distance* and *direction.* Behavioral and neurophysiological studies raise questions concerning both rats' and children's abilities to navigate by angle information (Lever et al. 2002; Hupbach and Nadel 2005; Lee and Spelke 2010a; Lourenco and Huttenlocher 2006). It is possible, therefore, that the system for navigating by the extended surface layout captures only part of the information at the heart of formal Euclidean geometry.

A second question concerns the accessibility of the geometric information by which children reorient: Can information about the shape of the surrounding surface layout be harnessed by other cognitive systems to permit uniquely human forms of navigation such as map use or abstract geometrical reasoning? When children first begin to navigate by purely geometric maps, their navigation appears to be guided by distance relations, but not by angular relations, suggesting a connection between maps and representations of the extended surface layout (Shusterman et al. 2008). Moreover, when children's intuitions about points and lines first are probed in purely abstract contexts, they reason about distance but not angle relations among paths through space (Izard et al. 2010). Both these findings suggest that children's developing capacities for geometrical reasoning build, in part, on their sensitivity to geometry for navigation. Nevertheless, much more research needs to be conducted linking children's navigation to their geometrical reasoning.

A final question concerns the development of abstract geometry. For adults, geometrical forms and relations apply not only to navigable environments but to everything of which we can conceive, including lines and planes extend infinitely in space. Moreover, humans use space to represent relations among colors (the color *space*), sounds (a *high* note), social partners (a *close* relationship), and time (a *short* trip). We use space to characterize entities that cannot be perceived either in practice (bacteria are *larger* than viruses) or in principle (justice is a *distant* goal). Core systems of navigation, in contrast, are highly limited in their application. If abstract geometry is founded upon them, then its development must pose a significant challenge for children, and understanding of that development poses a central challenge for the students of developmental cognitive neuroscience. Studies of children's navigation may help to meet this challenge.

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