COMPARATIVE
COGNITION & BEHAVIOR
REVIEWS
2013 Volume 8, pp 78 - 97

Two Fields Are Better Than One: Developmental and Comparative Perspectives On Understanding Spatial Reorientation

Alexandra D. Twyman
University of Western Ontario

Daniele Nardi
Sapienza University

Nora S. Newcombe
Temple University

Occasionally, we lose track of our position in the world, and must re-establish where we are located in order to function. This process has been termed the ability to reorient and was first studied by Ken Cheng in 1986. Reorientation research has revealed some powerful cross-species commonalities. It has also engaged the question of human uniqueness because it has been claimed that human adults reorient differently from other species, or from young human children, in a fashion grounded in the distinctive combinatorial power of human language. In this chapter, we consider the phenomenon of reorientation in comparative perspective, both to evaluate specific claims regarding commonalities and differences in spatial navigation, and also to illustrate, more generally, how comparative cognition research and research in human cognitive development have deep mutual relevance.

Keywords: spatial reorientation, geometric module, adaptive combination, individual differences, sex differences, slope

One of the many unique characteristics of the human species is, arguably, the urge to reflect on what characteristics make us unique. There are many distinctive characteristics to consider, such as large brains, bipedal gait, lengthy childhoods, tool invention and use, symbolic representation and grammatically-structured language. But at least as interesting a question as what makes our species distinctive is the question of what we share with other species. In fact, systematic understanding of similarities as well as differences is arguably helpful to answering questions about species-uniqueness.

When we pursue a serious comparative cognition research strategy of this kind, the ability to navigate successfully is a central domain in which to work. Navigation is a crucial skill for all mobile organisms. Do all species use the same techniques to navigate successfully? Common mechanisms could arise either because the essential problem was solved long ago by a common ancestor, or because the structure of the problem itself places constraints on the possible ways it can be solved. Or do various species invent different solutions to the navigation problem, depending on their sensory and motor abilities, the kind of food they seek, the characteristics of their predators, and so forth?

At first glance, it seems likely that various species differ considerably in how they navigate (for a general overview of navigation in a comparative perspective, see Wiener et al., 2011). For example, some species have magnetic compasses or sonar capabilities, while others do not; some species migrate long distances, while others live out their lives in ancestrally-defined territories. However, despite these obvious differences between species, there may also be deeper commonalities. One such cross-species commonality in spatial navigation has been proposed to be the use of geometric information in the surrounding environment to reorient. Oc-

Contact information: Alexandra Twyman, University of Western Ontario, London, Ontario, Canada, N6A 3K7
Email: atwyman3@uwo.ca
All previously published figures are used with permission.

ISSN: 1911-4745 doi: 10.3819/ccbr.2013.80005

casionally, we lose track of our position in the world, and must re-establish where we are located in order to function. Several kinds of information could guide this process, called *reorientation*.

One parsing of the information sources for reorientation proposes two classes of cues (Gallistel, 1990). *Geometric* cues involve the relation between at least two points or two surfaces; in the lab, this has been operationalized mainly by investigating the use of relative lengths or corner angles of enclosed surfaces. Any other cue to orientation has been termed, by default, *non-geometric*, or sometimes *featural*, and operationalizations have included the study of colored walls, beacons, and odors. More recently, a third type of cue – the *slope* of the floor of an enclosed search space – has been examined, and slope appears to be a powerful reorientation cue as well.

Reorientation research has revealed some powerful cross-species commonalities. It has also engaged the question of human uniqueness because it has been claimed that human adults reorient differently from other species, or from young human children, in a fashion grounded in the distinctive combinatorial power of human language. In this chapter, we consider the phenomenon of reorientation in comparative perspective, both to evaluate specific claims regarding commonalities and differences in spatial navigation, and also to illustrate, more generally, how comparative cognition research and research in human cognitive development have deep mutual relevance. We begin with the debate over the *geometric module*, as this issue has initiated and fueled research in the field. Following an exposition of the modular approach, we first discuss claims that human language confers a unique mode of operation on human adults and older children, and then proceed to other aspects of the modularity debate, and evidence for a non-modular position, i.e., adaptive combination theory. We then transition to two sections that are aimed at broadening the focus of the debate. The first of these sections focuses on a discussion of slope as a potential reorientation cue, how it might be differentially used across species, and if slope could be considered a particular type of either geometric or feature information, or is instead an entirely new cue class. The second case for a wider perspective comes from the fact that the reorientation literature has so far focused on the behavior of groups of individuals, for example, pigeons or mice or children of various ages, considered collectively. There is a growing trend to look for individual differences within species or age groups that might be predictors of behavior. Many spatial abilities have been studied in relation to individual and sex differences in performance, and we close with a discussion of recently reported sex-related differences in reorientation.

The Original Proposal: A Geometric Module

Ken Cheng (1986) was the first researcher to observe a difference between the search behavior of oriented and disoriented rats. His rats were allowed to search for food as they wandered around in a rectangular enclosure. Each of the corners was marked with distinctive feature cues of various kinds, e.g., the number of lights, the odor (see Figure 1). Once a rat found the correct corner, it was allowed to start eating, but partway through its meal, it was removed, disoriented, and then placed in an identical enclosure. It would seem quite logical for the rat to return to the corner at which there had been food, but this only happened 50% of the time. In this situation, rats favored the corners that were geometrically correct, but did not use other cues to disambiguate the two corners. For example, even when the correct corner smelled of peppermint, rats would sometimes return to the peppermint-scented corner, but equally often go to the rotationally equivalent corner that smelled of licorice. This behavioral pattern is found only for working memory versions of the task where the correct corner changes from trial to trial. In reference memory versions of the task, where the correct location remains stable over the course of the experiment, then over time rats are able to learn to use the non-geometric properties of the space.

To explain this suboptimal behavior on the working memory task, Cheng proposed the idea of a geometric module for reorientation. He argued that when rats return to the enclosed space, the geometry of the enclosure is the overriding cue that is used to re-set their spatial position so that the two corners with identical geometric properties are indistinguishable. Importantly, the geometric information was proposed to be modular, in the sense of being encapsulated and impenetrable. This description captured the fact that rats discarded the useful feature information, even though it could have been used for better performance.

Gallistel (1990) proposed that the apparently suboptimal behavior observed in the lab might be quite advantageous in the natural world. He argued that the features of the environment change, sometimes over the course of the day as the sunlight shifts or weather patterns change, and also over the seasons, as when the leaves change color and when snow falls. Because the geometric properties of the environment are less changeable than other cues, such as odors, Gallistel proposed that there might have been selective pressure for a geometric module to evolve that excluded the variable feature properties and depended only on the stable geometric properties of the environment.

The Geometric Module-Plus-Language Hypothesis

Cheng's findings and Gallistel's analysis suggested that the geometric module might characterize the behavior of

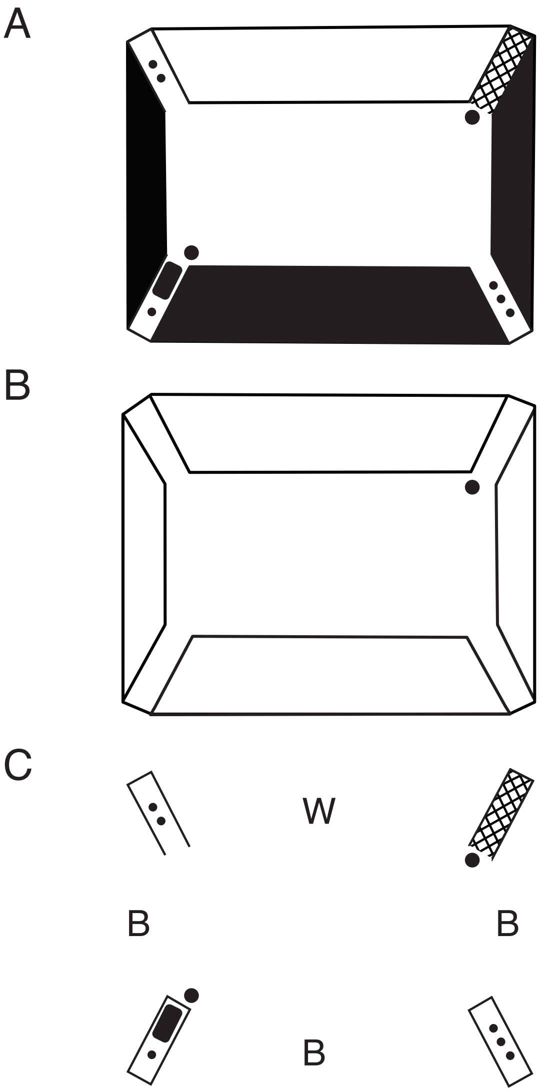

Figure 1. The paradigm used by Cheng (1986). Panel A shows the full enclosure, while Panel B abstracts the geometric information and Panel C abstracts the featural information, which in this case include both wall color and corner beacons.

many species, including humans. Indeed, children between the ages of 18 months to six years of age seemed to perform the same as Cheng's rats (Hermer & Spelke, 1994, 1996). That is, they ignored a saliently-colored feature wall in a rectangular room, and instead searched for a hidden object in the two geometrically equivalent corners (see Figure 2). Since children and rats performed similarly, it appeared that the reorientation module was evolutionarily ancient and conserved across species. However, human adults, in contrast to rats and toddlers, were able to flexibly combine feature and geometric information and searched almost exclusively for the hidden object at the correct corner. The fundamental difference between the reorientation behavior of rats and children on the one hand and adults on the other hand was proposed to be due to the production of spatial language that enabled flexible adult performance.

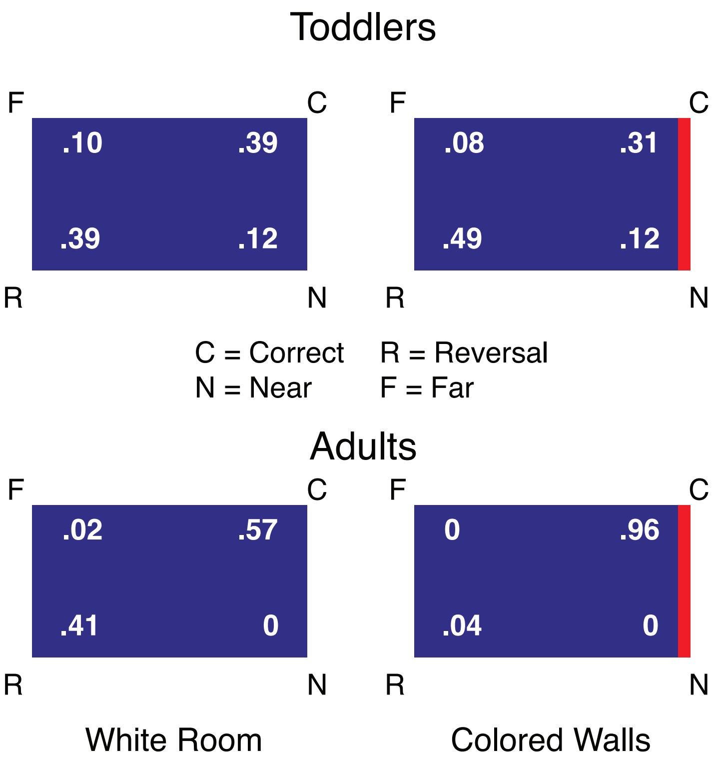

Figure 2. Top panel shows toddlers' performance, with all-white rectangular room on the left and room with colored wall on the right. Bottom panel shows adult performance.

Support for the geometric module-plus-language account came from two primary lines of research. First, it was found that, for children between the ages of 5 and 6 years, there was a correlation between production of the words "left" and "right" and successful performance on the reorientation task (Hermer-Vazquez, Moffett, & Munkholm, 2001). The second empirical approach was to try to eliminate adults' use of language during the reorientation task (Hermer-Vazquez, Spelke, & Katsnelson, 1999). When adults were asked to perform a verbal shadowing task at the same time as the reorientation task, their reorientation behavior fell back to exclusive geometric choices similar to those of the rats and young children. These two lines of evidence were taken as support that children were limited to using geometric information for reorientation until they acquired spatial language production capabilities that enabled them to flexibly integrate feature and geometric cues.

Initial Comparative Work

Troubling evidence for the geometric module-plus-language position seemed to come from comparative data gathered since Cheng's original work. Features turned out to actually be often used for reorientation across a wide range of non-human animals, including chickens (Vallortigara, Zanforlin, & Pasti, 1990), pigeons (Kelly, Spetch, & Heth, 1998), monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001; see Figure 3 below), fish (Sovrano, Bisazza, & Vallortigara, 2003), mice (Twyman, Newcombe, & Gould, 2009), and ants (Wystrach & Beugnon, 2009). It is obviously unlikely that feature use in these non-human species could be explained through language.

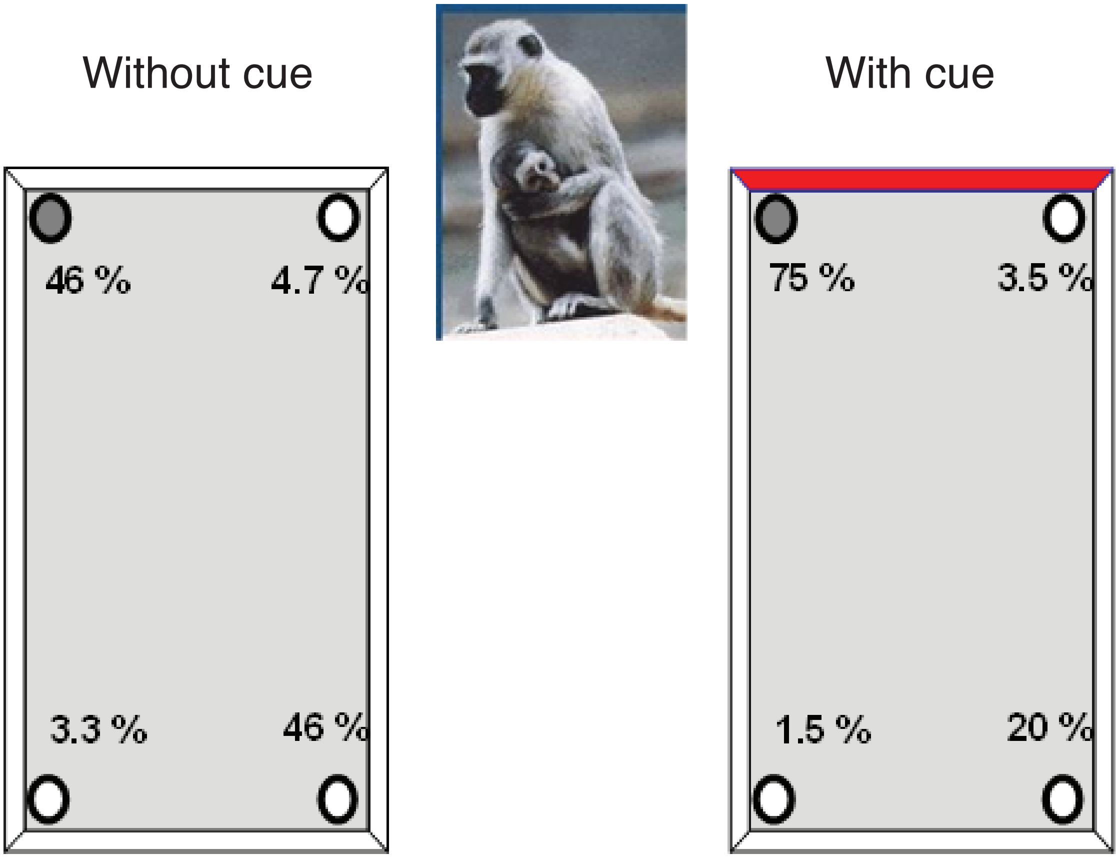

Figure 3. *Data from Gouteux et al. (2001) showing monkeys' performance in all-white rectangular room on the left and with a colored wall on the right.*

There are problems, however, with regarding these data as invalidating either the modularity hypothesis or the unique role of human language. First, many of the studies used a reference memory paradigm, in which correct search remains constant across trials. Cheng (1986) had only found modularity effects in working memory, where the correct location changes from trial to trial. Second, Hermer-Vazquez et al. (2001) objected that studies with non-human animals involve extensive training. They suggested that the distinctive power of human language comes from its ability to allow for flexible use of features without training.

Is Language Necessary for Feature Use in Reorientation?

Because work with non-human animals involves training regimens by necessity, the hypothesis that human language has a unique role can really only be examined in the human species. Focusing only on the human evidence, there is reason to doubt that language is necessary for the puncturing of a geometric module by feature cues. First, each of the two lines of supportive research presented earlier can be questioned. There are puzzling aspects to the Hermer-Vazquez et al. (2001) data, such as why it is the production of spatial terms that is associated with better performance, rather than comprehension. Additionally, as suggestive as the data are, it is possible that a third variable could account for the relationship between language production and flexible reorientation. There are also problems with the verbal shadowing experiments. While they seem to give stronger evidence than the correlational data, subsequent research has failed to replicate the dramatic fall to chance for adults concurrently performing the reorientation and verbal shadowing task. Furthermore, and crucially, while reorientation performance does diminish to some extent with verbal shadowing, the effect is not particular to a linguistic task but also occurs with spatial shadowing tasks (Hupbach, Hardt, Nadel, & Bohbot, 2007; Ratliff & Newcombe, 2008a). These data seem to suggest that, while language is a useful tool for adults, it is not a necessity.

Second, if language were crucial, it would seem that individuals with language problems should perform like young children on the reorientation task. There are two tests of this idea. In one experiment, individuals with global aphasia performed no differently from control participants (Bek, Blades, Siegal, & Varley, 2010), suggesting that the flexible behavior observed with human adults does not depend exclusively on the availability of language (although perhaps having been able to speak for many years could be argued to have crucially affected spatial reorientation). In the second experiment, deaf individuals in Nicaragua who had grown up in an environment without input from a structured sign language performed less well than deaf individuals in a second, later-born cohort who did have such input (Pyers, Shusterman, Senghas, Spelke, & Emmorey, 2010). However, the first cohort still searched at the correct corner far more than would be expected by chance (67.5% as opposed to 25% chance). Further, other aspects of the data set indicated that the first cohort had been deprived in ways that led to spatial deficits more global than deficits in feature use for reorientation. They also performed less well than the second cohort in a rotated box condition that did not involve reorientation, and they showed an odd pattern of errors in the reorientation study, in which rotational errors did not predominate, as is almost universal in reorientation studies.

Third, and most decisively, it has turned out that toddlers can in fact use features to reorient. Although far too young to be able to use or comprehend the terms left and right, and often with little spatial language at all, children as young as 18 months can succeed in using a colored wall to find the correct corner in a rectangular room, as long as the room is somewhat larger than the very small room used in the initial Hermer and Spelke studies (Learmonth, Newcombe, & Huttenlocher, 2001). We will review the room *size effect* in more detail below.

In sum, there is reason to doubt the position that language is the mechanism that facilitates a more flexible reorientation strategy in adults compared to children and non-human animals. However, this is not to say that language is not helpful. There is evidence that even just hearing relevant spatial language (*at the red wall*) or task relevant non-spatial language (*red can help you*) can be a powerful tool to help children succeed at reorientation tasks before they are normally able to reorient with a feature cue (Shusterman, Lee, & Spelke, 2011).

Are Features Really Used by Children to Reorient?

Lee, Shusterman, and Spelke (2006) and Lee and Spelke (2010) have proposed an alternative account for the apparent use of features by children and non-human animals. They argue that true reorientation can only be accomplished with geometric cues; in a separate process, features can be used to guide search to the target location, but features are not used to update position in the environment. To test this hypothesis, Lee et al. (2006) asked children to reorient in an enclosed circular space, which does not provide any useful geometric information. Three objects forming an equilateral triangle were placed in the middle of the enclosure. One of these objects was unique (a red cylinder) and two of the objects were identical (blue boxes). Lee et al. argued that the unique red cylinder could act both as a beacon (a feature that directly marks a hiding location) and also as a landmark (a feature that indirectly marks a hiding location) that could in theory differentiate search between the two identical blue box locations. For example, children might orient themselves to the red cylinder and then remember that the hiding location was the blue box on the left. This kind of performance was not found. Children searched almost perfectly at the unique container (a beacon) but divided search evenly (i.e., randomly) between the two blue containers. The authors reasoned that if features were truly capable of being used for reorientation, then children should succeed at the task when the target is hidden in any of the three containers. Therefore, it was argued that children remained disoriented in the absence of a geometric cue, but were nonetheless able to use a beacon to retrieve a hidden object.

As reorientation experiments are often conducted in rectangular enclosures, the two-step account could potentially explain the use of features by non-human animals and young children in the majority of studies to date. In the first step, the only true reorientation step, the participant or subject is able to reorient by the geometry of the space which narrows the possible search locations to two geometrically correct places. In the second step, the participant or subject chooses either the white-white geometrically correct or white-colored geometrically correct corner by beaconing to the correct target location. Thus, the Lee et al. (2006) experiment suggested that a two-step account for reorientation, with true reorientation based on geometry and beacon piloting accounting for feature use, might explain use of features by young children and non-human animals.

This study is not, however, decisive. Some of the parameters of the Lee et al. (2006) study may have made features less likely to be used for reorientation. First, although the area of the circular enclosure was quite large, the actual area of the array of objects was small. It has been demonstrated that features are less likely to be used in small spaces (Learmonth, Newcombe, & Huttenlocher, 2001; Learmonth, Nadel, & Newcombe, 2002). Features are more likely to be used for orientation when they are further away (called distal cues) because they are more accurate for indicating direction than when they are close to the hiding location (proximal cues) where left-right relations can change as one moves around the target location (Nadel & Hupbach, 2006). Second, the feature was itself a hiding container, and thus it is not surprising that it was used as a beacon. Third, the feature appeared small and portable, and in fact the children watched the experimenter move the hiding locations. Mobile parts of the environment are not reliable cues for determining a heading. Fourth, different brain regions appear to be activated when the feature is located inside a space, as opposed to against or on the periphery of an enclosure. From the animal literature, features along the periphery of the enclosure control hippocampal place cell firing, while the same landmark inside the enclosure does not (Cressant, Muller, & Poucet, 1997, 1999; Zugaro, Berthoz, & Wiener, 2001). All of these factors make it more likely that the unique container would be coded by children as a beacon, rather than as a landmark for reorientation.

In fact, there is some evidence that features can be used as a heading cue for reorientation. In square rooms, there are no useful geometric cues to aid reorientation. Success in this task would therefore depend on the use of feature cues. In square environments, toddlers are able to reorient using relative feature cues such as large versus small polka-dot patterns (Huttenlocher & Lourenco, 2007; see Figure 4) and distinct colors (Nardini, Atkinson, & Burgess, 2008). This effect was also found for mice (Twyman, Newcombe, & Gould, 2009). However, a possible rebuttal from modularity theorists would be that performance in this paradigm is based on the use of complex beacons. The corners of the enclosure can be distinguished from adjacent corners (although not from the diagonally opposite corners) based on the left-right positions of each feature (i.e. the corners might be blue/red, or red/blue). It is therefore possible that the combination of features, including relative position information, could be used as a beacon, leaving open the possibility that feature use in these experiments might be accounted for by an associative model.

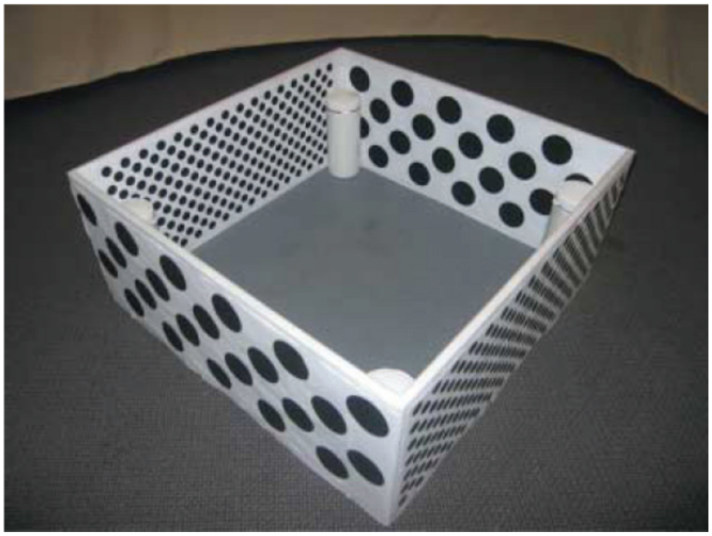

Figure 4. *The enclosure used by Huttenlocher and Lourenco (2007).*

More directly, Newcombe, Ratliff, Shallcross, and Twyman (2010) designed an experiment to directly test the Lee et al. (2006) claims. In the first experiment, children were asked to reorient in an octagon with alternating short and long walls. In this type of enclosure, the eight possible hiding locations can be reduced to the four geometrically equivalent corners that share the same wall length and sense relations to the target location (see Figure 5). For example, a participant could use the geometry of the octagon to remember that the correct location is in one of the corners with a long wall to the left and a short wall to the right. Different groups of children were asked to reorient in the octagonal space either with or without one of the walls of the octagon serving as a red feature wall. This cue could be used, for example, to remember that the target is on the left side of the red wall.

The first finding was that, in an all-white (geometry-only) condition, 2- and 3-year-old children were able to use the complex geometry of the octagon for orientation. The fact that toddlers were able to use the geometry of the octagon was quite remarkable given the complexity of the shape, the subtle obtuse corner angles, and the lack of a single principal axis of space that might have helped reorientation. The second finding was that, when a feature wall was added, 3- and 5-year-old children were able to choose among the three all-white corners that share the same geometric and feature properties; these corners can only be distinguished on the basis of indirect feature use of the red wall. (Two-year-old children were not tested.) The octagon experiments demonstrate that children are able to use the feature for true reorientation, at least in the presence of geometric information.

To determine what happens in the absence of geometric information, a second experiment was conducted in a circle with a design similar to that of the Lee et al. (2006) study. Four year old children were asked to reorient in a circular enclosure and were asked to find a hidden object in small hiding boxes (see Figure 6). The most important difference between the Lee et al. and Newcombe et al. experiments is that in the former, the feature is actually one of the hiding locations and is centrally placed within the enclosure while in the latter the feature is a stable part of the enclosure boundary. When the feature is stable and integrated into the space, children are able to reorient with the feature cue. They are able to correctly search at a hiding location within an array of either two or three boxes placed in the middle of the enclosure. Together, studies with children that use a more stable feature cue suggest that features are truly used for reorientation, and not just as beacons marking the target. There are at least two lines of research that could extend these findings. For the first, although children searched above chance in the

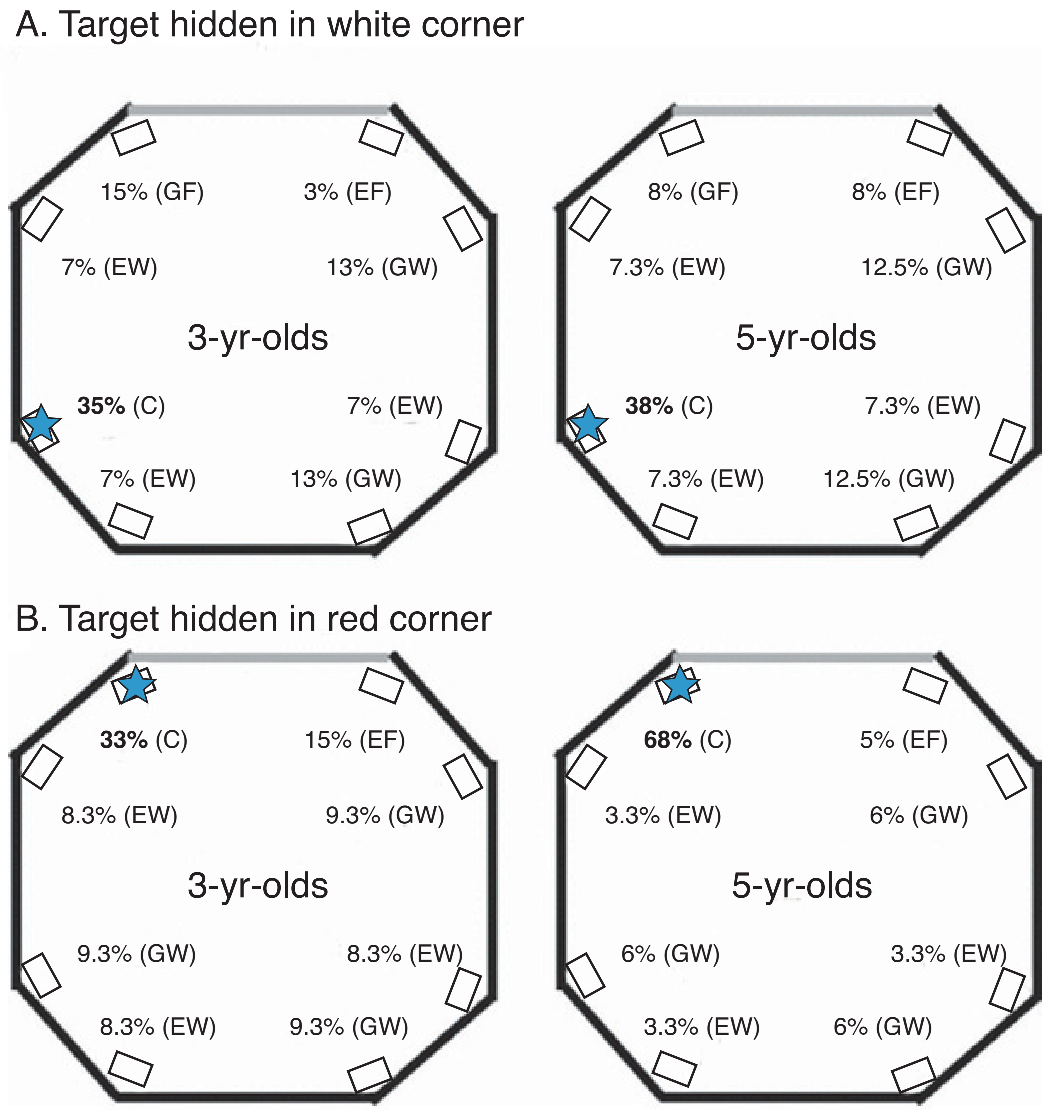

Figure 5. *Data from Newcombe et al. (2010). Searches at the correct corners that were significantly above chance are indicated by numerals in bold typeface.*

octagon and circle experiments, adults were quite a bit more accurate. Therefore it appears that both the use of geometric and feature cues develops beyond the first five years of life. These paradigms could be used to chart the developmental trajectories of both cue classes. In a complementary fashion, it would be interesting to extend these paradigms with non-human animals to determine if they too are able to truly use feature cues for reorientation.

An Alternative Proposal: Adaptive Combination Theory

Spatial memory and judgments are typically based on a variety of cues, and there is evidence that these cues are combined in a Bayesian fashion (Cheng, Shettleworth, Huttenlocher & Rieser, 2007; Huttenlocher, Hedges & Duncan, 1991; Waismeyer & Jacobs, 2012). This idea can be applied to the data on use of geometric and featural cues. In contrast to modularity theory, adaptive combination theory proposes that geometric and featural cues can both be used for reorientation in a fashion that depends on a combination of cue weights, with the weights determined by factors such as the perceptual salience of the cues (which affects their initial encoding), the reliability of the memory traces (i.e., subjective uncertainty, which is related to the variability of estimates), and the success with of that kind of cue given prior experience (Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). Information that is more salient, more reliable as a predictor of the goal, more familiar, or low in variability, should be taken into account more than other competing sources of information. The flexibility of adaptive combination theory suggests that, when features and geometry have similar weights on these dimensions, they should be integrated, but when the combination of weights on these dimensions strongly favors one kind of cue over the other, that cue should dominate.

We should pause for a moment to discuss cue salience.

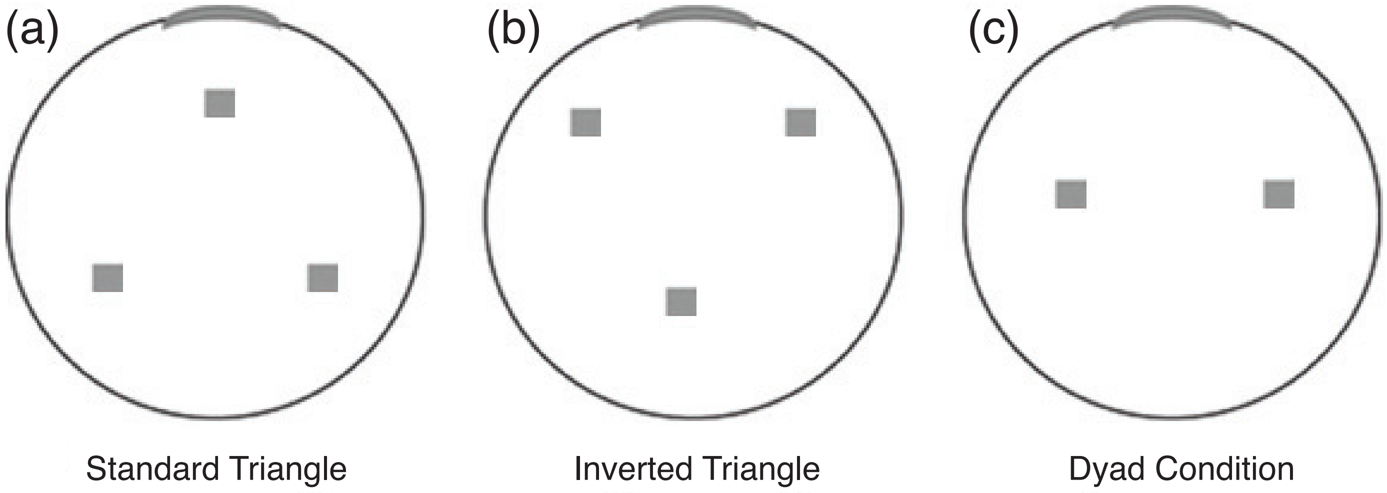

Figure 6. *The search arrays from Newcombe et al. (2010).*

Geometry and features have been the main cue classes that have been examined in the reorientation literature. It might be argued that it is difficult to compare how much each contributes to behavior because the saliencies of the cue type are impossible to equate, and may well differ across periods of development or between species. While it is true that the absolute salience of each cue cannot be know for each participant or subject, what is important for adaptive combination theory is that the salience can be varied. For any given situation, when the salience of the cue is increased, then the adaptive combination theory predicts that it will be more heavily used. This kind of finding has been demonstrated. For example, we see a reduced reliance on geometric information in increasingly large rooms (the room size effect discussed below) where the feature cue becomes more salient because it is more distal. As another example, when subjects have spent the early part of their lives in either geometrically or featurally rich environments, we see rearing effects, also to be discussed further below.

Despite the strengths of the adaptive combination approach, its potential weakness is being overly general, and future work clearly needs to more rigorously specify the parameters in a well-defined model, and test novel predictions. Nonetheless, in this section we review the data that suggest that some model more flexible than geometric modularity is necessary.

The Room Size Effect

In an important illustration of adaptive combination theory, and a challenge to modularity theorists, the dominance of geometric information over feature use, has turned out to depend critically on the size of the enclosure. Geometry is more likely to be used in small spaces and features are more likely to be used in large spaces, for children (Learmonth et al., 2001, 2002, 2008), adults (Ratliff & Newcombe, 2008b), fish (Sovrano et al., 2007), chicks (Chiandetti et al., 2007; Sovrano & Vallortigara, 2006; Vallortigara et al., 2005), and pigeons (Kelly et al., 1998). These data cannot be explained by any interesting version of modularity theory because an adaptive module should operate across variations in scale and should especially operate in large spaces. It is true that there might be a module that applies only to very small enclosures, but it is hard to see how such a module would be central to survival and reproduction in any plausible environment of adaptation.

Why does the size of the space make a difference? One possibility is that the geometric cue is more salient in small spaces because the relative difference between wall lengths is more noticeable when the aspect ratio is greater and when the wall lengths can be compared within a single view. Therefore, as the room size increases, the weight assigned to the geometry cue is reduced. However, the attractiveness of this idea is decreased by a recent demonstration that the distance of the walls from the center of the room is the potent cue in this paradigm, rather than the lengths of the walls (Lee, Sovrano & Spelke, 2012). If distance is more important than length, then one could postulate that differences in two short distances are easier to compare than differences in two longer distances.

There are other explanations for the room size effect. As the room size increases, the weight assigned to the feature cue is increased because a landmark is more useful for determining heading when it is a distal rather than a proximal cue (Lew, 2011). In addition, the increased possibility for movement in the larger room may engage more spatial processing. In several experiments on these issues, Learmonth, Newcombe, Sheridan, and Jones (2008) found that both the distance of features from the participant and the possibilities for action in the larger space have an impact on the age at which children succeed in using features. The changing relative use of geometric and feature cues based on the scale of space is difficult for the modular position to explain, as it would predict invariant use of geometry. In contrast, the changing weights of cues as a function of their salience and reliability are at the heart of adaptive combination theory.

Short-Term Experience Effects

Experience effects are not predicted by modularity theory; modules are supposed to be inflexible and relatively impermeable. However, adaptive combination theory suggests that familiarity with a cue should be an important determinant of use of features versus geometry. There are several training experiments that provide support for the effects of recent experience. In one study, children were given practice using a feature for reorientation in an equilateral triangle (no useful geometry) with three different colored walls (Twyman, Friedman, & Spetch, 2007). In as few as four practice trials with the feature, 4- and 5-year-old children came to use the feature wall to reorient even in the small spaces used by Hermer and Spelke (1994;1996), in which same-aged children had been shown to rely exclusively on geometric cues. The short training period was effective in either the presence (a rectangle) or absence (equilateral triangle) of relevant geometric information. This experiment highlights that the relative use of geometric and feature cues can change. Along similar lines, four trials of experience in a larger enclosure lead to young children's use of features in the small enclosure (Learmonth et al., 2008).

Newcombe and Ratliff (2008b) demonstrated a similar pattern for adults. Participants were asked to perform a reorientation task in either a small or a large room and to switch room sizes halfway through the experiment. People who had started in the large room (where features are salient) relied more heavily on the feature cue than people who had spent all trials in a small room. In contrast, individuals who had started in the small room (where geometry is salient) began to use feature information when moved to the larger room; in fact, they performed no differently from individuals who had remained in the large room for all trials. Therefore, it seems likely that the successful search using the feature in the large space increased the relative dependence on the feature cue, and this change in relative cue weights was reflected when participants were asked to perform the same task in the smaller space.

Short-term experience also matters for pigeons. Kelly and Spetch (2004) trained pigeons on the reorientation task. Some of the pigeons were initially trained with geometry and others were trained with features. Then the pigeons experienced training with both cues and were tested for their relative use. The pigeons with the geometry pre-training relied both on geometric and feature cues, while the pigeons with the feature pre-training relied mainly on just the feature cues.

These experiments with children, adults, and pigeons indicate a common theme: reorientation is a flexible system that is updated, based on prior experiences. Next we turn to experiences over a longer period of time and earlier in development.

Rearing Effects

The previous sections demonstrated that changes in the salience of the cues or in the participants' short-term experiences influence reorientation behavior. A series of rearing experiments have demonstrated that there are differences that emerge over a longer period, at least for some species. Initially, the reorientation ability of wild-caught mountain chickadees (*Poecile gambeli*) was examined (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005). This group of researchers used wild-caught birds as they were likely to have experienced rich feature information in their natural habitat. This species typically lives in forested areas near streams and mountains. The environment just described contrasts greatly with the standard housing conditions in labs, which are comprised largely of uniform rectangular enclosures. The wild-caught chickadees relied more heavily on feature cues than did other standard-reared species. However, when the reorientation abilities of wild-caught and lab-reared black-capped chickadees (*Poecile atricapillus*) were examined, their behavior was much closer to the standard-reared subjects (Batty, Bloomfield, Spetch, & Sturdy, 2009). Therefore, it is unclear if there is something different about the experiences of black-capped and mountain chickadees that cause these differences, or if there is a difference across species.

An alternative approach is to tightly control the rearing environment. This approach has been used with chicks, fish, and mice. For chicks, there does not seem to be any difference between chicks reared in a circular (lacking relevant geometry) and rectangular (containing relative wall lengths) environment in their relative use of feature or geometric cues (Chiandetti & Vallortigara, 2008, 2010). However, the chicks were only housed for two days before starting training, and they are a precocial species that may not have as much of a sensitive period for rearing effects. In experiments with longer rearing periods, a different pattern has emerged. Convict fish were reared in either circular or rectangular environments. Subsequent tests showed that the fish in the circular environments relied more heavily on feature cues than did the rectangular reared fish (Brown, Spetch, & Hurd, 2007).

Similar to fish, there are differences between mice that have been raised in feature rich environment (a circle with one half white one half blue) and a geometrically rich envi-

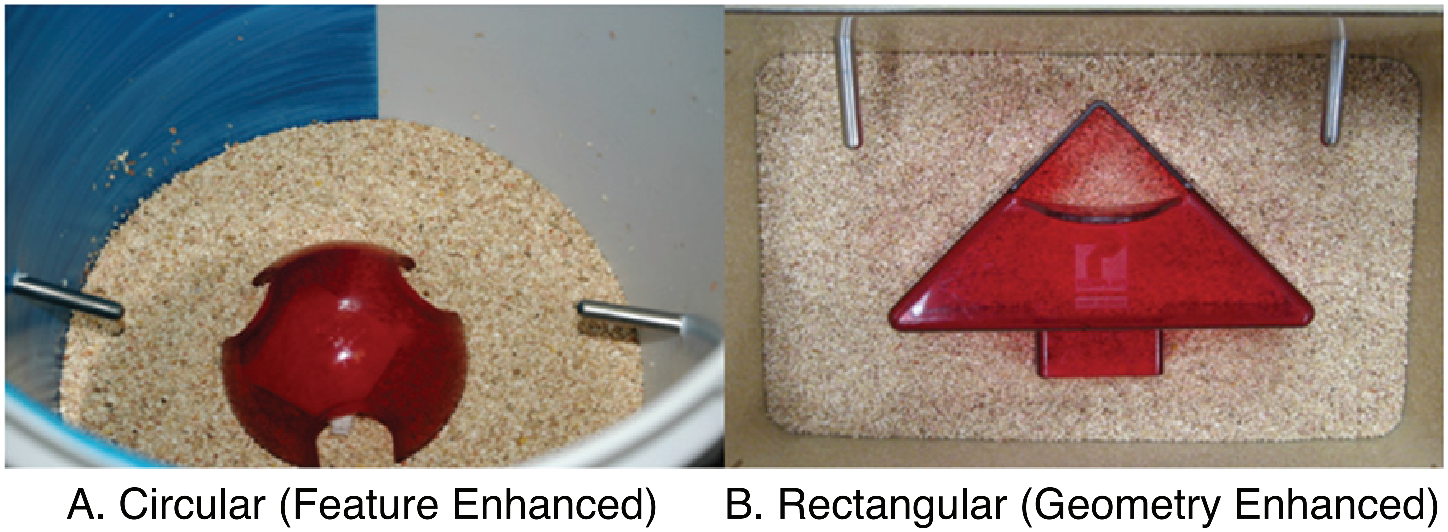

Figure 7. *The rearing environments from Twyman et al. (2012).*

ronment (rectangular enclosure with a triangular nest box; see Figure 7). Although there were no differences in the acquisition of geometric information alone, the circular-reared mice were faster to learn a feature panel task. Additionally, and crucially, on a test of incidental geometry encoding (a rectangle with a feature panel marking the correct location), the rectangular- reared mice had encoded the geometry while the circular-reared mice had not (Twyman, Newcombe, & Gould, 2012).

In summary, for chicks and black-capped chickadees, early environment does not have a large impact on reorientation behavior. However, for mountain chickadees, mice, and fish, the rearing environment alters the relative use of geometric and feature cues.

Facilitation and Interference Effects

One reason given initially to favor a modularity hypothesis was the claim that geometric and featural information are both learned in situations where one might expect overshadowing or blocking effects (Cheng & Newcombe, 2005). This pattern of independence suggested separable systems. However, subsequent research has shown a far more complex pattern of results, with the two kinds of information sometimes learned independently, sometimes showing overshadowing or blocking of one by the other, and sometimes showing facilitation of one by the other (Cheng, 2008; Miller & Shettleworth, 2008). Furthermore, it has been shown that rats can integrate these kinds of information across successive phases of an experiment to make correct spatial choices (Rhodes, Creighton, Killcross, Good & Honey, 2009).

Just considering facilitation effects, there are two recent examples, one from research with birds and other from research with humans. Kelly (2010) trained two groups of Clark's nutcrackers (*Nucifraga columbiana*) with an array of objects at the four corners of a rectangle. When the objects were identical, the birds did not learn the task after an extensive training program. When the objects were unique, the birds learned the task and, maybe surprisingly, had also encoded the rectangular shape of the array. In another example of a facilitation effect, human individuals with Williams Syndrome, a genetic defect that has important effects on spatial functioning, failed to encode the geometry of an all-white rectangular enclosure, but showed geometric encoding when a colored feature wall was added (Lakusta, Dessalegn & Landau, 2010).

This literature is now much too large to review thoroughly here, but it clearly challenges modularity theory (Twyman & Newcombe, 2010). More important, it represents a challenge to any viable comprehensive theory, which must be able to account in precise quantitative terms for the pattern of effects, and make novel predictions. An interesting direction for future research has been indicated by recent studies on rodents which suggest that cue interaction (blocking, overshadowing, and facilitation) between geometry and features might be modulated by sex because male and female rats tend to assign different weights to these cues (Rodriguez, Chamizo, & Mackintosh, 2011; Rodriguez, Torres, Mackintosh, & Chamizo, 2010); this should be explored in additional species.

Section Summary

The available evidence indicates that geometric and featural information can both be used for reorientation by a wide variety of species and (within the human species) across a broad range of ages. However, the relative use of these cues depends on their salience, the reliability of their encoding, and their familiarity across both recent and longer-term experience. Human language is one of several factors that can facilitate the use of features in situations in which it might otherwise be weak, but it is not the only way this end can be accomplished. From the general point of view of a field of comparative cognition, a striking fact is how vigorous the dialogue between the developmental and comparative communities has been, and how many species have been investigated using how many techniques. Wider development of this dialogue is likely to be very fruitful.

Slope as a Reorientation Cue

Most spatial experiments, including reorientation studies, have been conducted on flat surfaces. But, as we all know after climbing a hill or admiring an amazing view from a mountain top, the world is not flat. The slope of the terrain might clearly be an important cue for polarizing space, and hence for reorienting. One could imagine using "uphill" in a similar manner to "north" to anchor a direction in the environment. But is it in fact used this way?

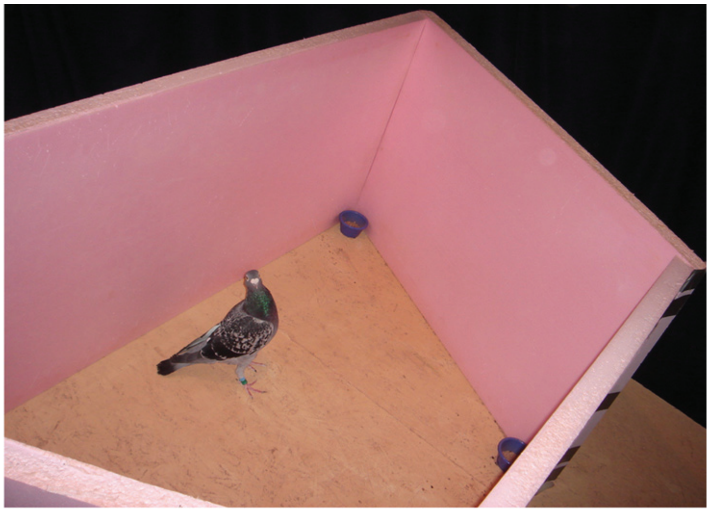

Figure 8. *A pigeon in the trapezoid search space with a 20° sloped floor.*

Nardi and Bingman (2009a) compared the reorientation performance of pigeons which were trained to a correct corner of a trapezoid on a flat surface (geometry-only) with pigeons which were trained in the same trapezoid enclosure, but now with the floor sloped at 20 degree angle (geometry + slope, see Figure 8). Both groups of pigeons learned the task, but the geometry + slope group learned about three times faster than the geometry only group. The follow up tests for the geometry + slope group revealed that the pigeons had readily encoded slope (92% correct), had encoded geometry at above chance levels although accuracy was not very high (63%), and that the pigeons overwhelmingly preferred the slope-correct (75%) over the geometry-correct corner (0%) on conflict trials. Overall, these data suggest that slope is a powerful cue for reorientation compared to the geometry of the sides of the enclosure.

As acquisition was so much faster in the combined group, Nardi and Bingman wondered if slope might facilitate geometry acquisition. In a second experiment, they trained groups of pigeons with only geometry or with combined geometry and slope cues. Over the course of training, no differences were found in geometry acquisition between groups. Thus, it appears that geometry and slope cues neither facilitate nor inhibit learning of each other, a pattern traditionally interpreted as supporting the idea that they are fundamentally different classes of cues.

Thus far, geometry has been considered a single cue. As Sutton (2009) points out, there are several possible cue types of a geometric nature. These levels of geometric cues may be nested within each other, where local cues are located near the correct location and the global cues encompass relations in the larger space. For example, the trapezoid enclosures that have been reviewed thus far include two types of geometric cues: local corner angles (acute or obtuse) and global relations between relative wall lengths (for example a long wall to the right and a shorter wall to the left). Nardi, Nitsch and Bingman (2010) conducted a series of geometry and slope learning experiments with pigeons that examined the contributions of local and global geometry as well as slope to reorientation performance. Over the course of training, pigeons first learned to go to the two acute corners within the first three days. It took about nine days for pigeons to learn the global geometry of the space. Therefore, local geometry learning is much faster than global geometry learning. As one of the follow up tests, Nardi et al. rotated the training apparatus so that pigeons could not match all of the local geometry, global geometry, and the slope. In this manipulation, pigeons matched the correct slope and local geometric cue, at the expense of the global geometric cue. In training conditions where the global geometry is made two- or three-times as predictive as slope as an indicator of the correct target location, pigeons still rely more heavily on the slope rather than the global geometric cue. Therefore, for pigeons, the multimodal slope cue, which includes visual, kinesthetic, and vestibular information, appears to be particularly salient, and more important than geometry for a reorientation task.

Humans

Pigeons encode slope, but what about other species? The fact that pigeons can fly might be taken to argue that they are less likely to encode slope than species that cannot transcend the terrestrial environment, but is that in fact true? Nardi, Shipley and Newcombe (2011) put adult humans in a uniform white square enclosure with no useful geometric or feature cues for orientation. The 5° sloped floor of the enclosure provided visual, kinesthetic, and vestibular cues that could guide search (see Figure 9). A bowl was located in each corner of the room and participants saw a $1 bill hidden under one of the bowls. The correct hiding bowl remained the same for each of the four training trials for each participant, but was counterbalanced across subjects. After seeing the correct location, participants were disoriented and then asked to find the $1 bill. Once training was complete, two post-training tests compared search with the 5° sloped floor to the same space with a flat floor. People performed at chance (25%) when the floor was flat, showing that they had been thoroughly disoriented and that there were no stray cues that could be used to reorient. When the floor was sloped at a 5° angle, people were able to retrieve the hidden object on the majority of the trials, although there was a significant difference between men (79%) and women (43%) during the training trials. (This sex difference will be discussed further later in the paper.) This study showed that people can use slope as a reorientation cue, although less clearly than the pigeons had; however, the fact that the slope was at a much reduced angle for humans may have contributed to this apparent species difference. The Institutional Review Board declined Nardi et al. (2011) to tilt the floor of the room at a steeper angle. Therefore, studying pigeons (or other animals) at gentler angles would allow for a better comparison across species.

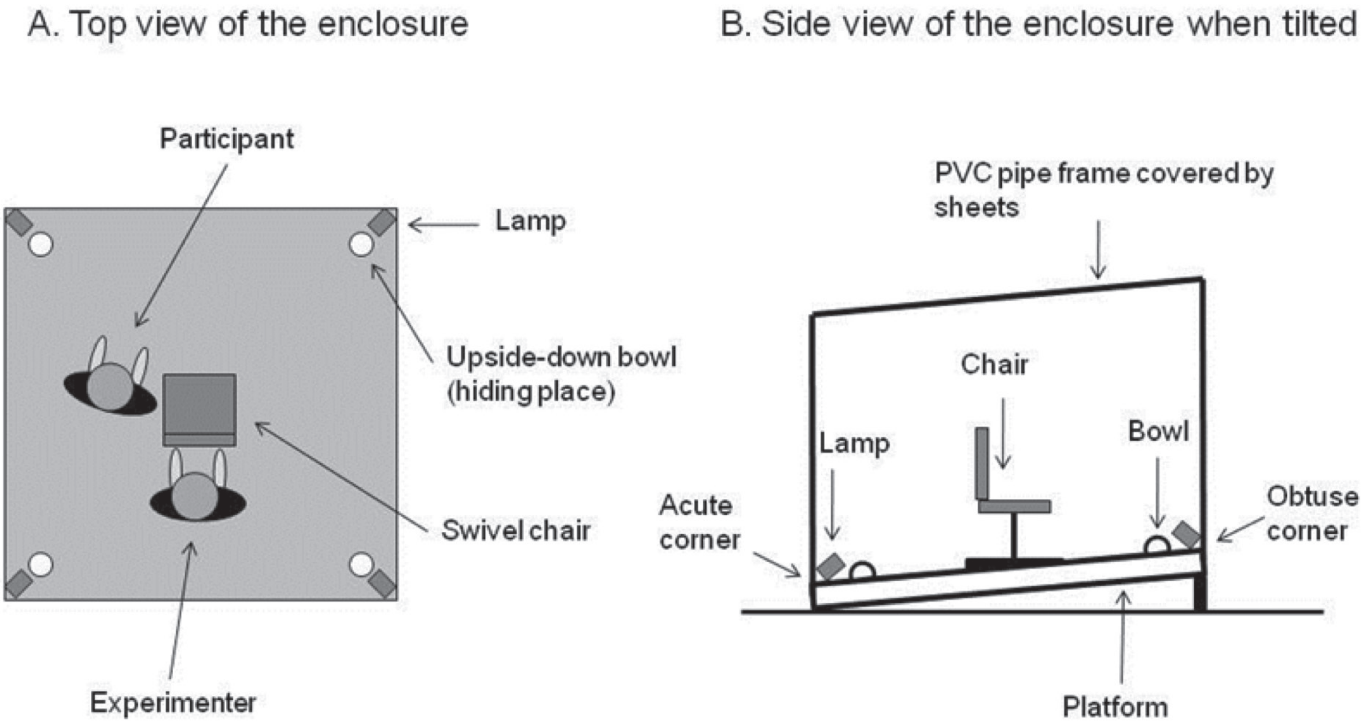

Figure 9. *The experimental set-up used in the human slope experiments.*

What Kind of Cue is Slope?

Thus far, we have seen that both an aerial species (pigeons) and a terrestrial species (people) use slope for reorientation; additionally, for pigeons, slope is a very powerful cue, which does not appear to interact with geometric cues in spatial learning. Now we turn to the question, important in the context of the reorientation literature, of whether to categorize slope as geometric information, feature information, or something else. There are arguments for slope being considered a geometric cue. The slope of the floor, say a 10 degree incline, is measured as the difference between a perfectly horizontal surface, perpendicular to gravitational force, and the angle of the floor. Therefore, the slope could be defined by comparing a surface to a surface in terms of angle, which would fall under Gallistel's (1990) definition of a geometric cue. Additionally, determining that the floor is sloped could be accomplished by comparing relative lengths of walls (assuming a horizontal ceiling, the participant could judge the distance between the floor and the ceiling and note that the "up" end of the slope has a shorter wall height than the "down" end of the slope) or by noting the angle at which the floor meets the walls (acute at the uphill end and obtuse at the downhill end).

However, slope could be considered a type of feature information if viewed as a property of non-horizontal surfaces. One could use the slope direction to determine the facing orientation and to encode a location. For example, a navigator moving on a slope might know that the top of the hill should be on the left in order to get to a desired destination. This is analogous to the role that distant landmarks – another type of feature cue – play in horizontal environments; if there were a conspicuous landmark in the horizon (e.g., a mountain), then one could use it to determine heading. Therefore, slope polarizes the environment and provides a directional frame of reference that can be used for (re)orientation, in the same way as a distant landmark. In this sense, varying the inclination of the tilt affects the salience of slope information (steeper slopes are obviously more salient than gentle ones), just like varying the size of a landmark makes it more or less salient.

Research from a neuroscience perspective with pigeons is relevant to this issue. Previously, it had been shown that bilateral lesions to the pigeon hippocampal formation, an analogous structure to the human hippocampus, disrupt the processing of geometric cues, but not feature cues (Vargas, Petruso, & Bingman, 2004). Similarly, Nardi and Bingman (2007) found that lesions to the left hippocampal formation of pigeons decreased reliance on geometry for reorientation. Pigeons that had undergone a control surgery performed identically to pigeons with a lesioned right hippocampal formation. Since the hippocampus appears to be more heavily involved in the use of geometric cues than feature cues in pigeons, Nardi and Bingman reasoned that lesions to the hippocampal formation should disrupt slope-based reorientation if slope is a type of geometric cue.

Nardi and Bingman (2009b) examined the reorientation of control and bilaterally lesioned pigeons when geometric and slope cues were available for reorientation. The training apparatus was a trapezoid shaped room with the correct corner in one of the acute corners. Additionally, the floor was sloped at a 20 degree angle. Both groups of pigeons learned the task. Supporting previous research, the pigeons with the bilaterally lesioned hippocampal formation had more difficultly using the geometric cue than the control pigeons. Interestingly, there were no differences between groups in the use of slope. All pigeons rapidly learned the task, had encoded the slope cue when it was tested in isolation, and selected the slope correct corner on conflict trials. Therefore, it not only appears (again) that slope is a powerful reorientation cue for pigeons, since all pigeons preferred to reorient with slope rather than geometry, but also that slope does not seem to recruit the same neural circuits used by geometric cues. The identical performance of control and hippocampal lesioned pigeons with a slope reorientation cue implies that slope is hippocampal independent, and therefore is more like a feature cue than a geometric cue. The authors characterize slope as a gravity-dependent feature cue. However, given the distinctive characteristics of this cue – because it provides multimodal sensory stimuli, because it is associated with effortful movement, and because it involves the vertical dimension – it may be that slope is a unique type of information.

Slope Cues Versus Feature Cues In Pigeons and People

If slope cues are similar in some ways to feature cues, how do they interact and which kind of cue is more powerful? Nardi and colleagues have asked these questions in behavioral studies with both pigeons and people. In both experiments, the experimental space was a square so that the geometric information was identical throughout the space. (Recall, however, that the floor was sloped at a 20 degree angle for pigeons and at a 5 degree angle for people.) Unique feature cards were placed in each corner of the room; therefore the correct target location could be identified based on the beacon alone.

Pigeons readily learned the reorientation task (Nardi, Mauch, Klimas, & Bingman, 2012). Post training tests indicated that the pigeons had encoded both cues. When slope (all feature cards identical) or beacon (flat floor) cues were presented in isolation, pigeons were highly accurate (96%). On the conflict test, where the trained beacon location was moved to an incorrect slope location, pigeons divided their search evenly between the beacon-correct and *slope-correct* corners. Interestingly, choices on the conflict tests depended on the location of the correct corner during training. When pigeons were required to go uphill during training, pigeons selected the slope-correct corner 76% of the time. In contrast, when pigeons went downhill to the correct training location, pigeons selected the *beacon-correct* corner 75% of the time. When pigeons go uphill, they exert more effort than when they follow the slope downhill. Nardi et al. propose that the role of effort might modulate the weighting of the slope and beacon cue for reorientation.

Using a similar paradigm, Nardi, Newcombe, and Shipley (2012) examined the interaction between slope and feature cues with people. Like pigeons, people readily learned to reorient. Unlike pigeons, who encoded both the feature and the slope, about two-thirds of the participants only encoded one or the other cue. Individuals performed similarly during the training trials with either the slope-strategy (78% accurate) or a feature-strategy (90% accurate). When people did not clearly follow a single strategy, they were not nearly as accurate, although still above 25% chance, on the training trials (50% accurate).

In sum, pigeons encode both slope and beacon cues during a reorientation task, with both information sources being given equal importance. Interestingly, this balance seems to shift based on the amount of effort required during training. When pigeons require extra effort to go to an uphill location, then slope is given more importance than a beacon cue and vice versa. People are also able to encode and use slope and feature cues for reorientation. In contrast to pigeons, people tend to use a single strategy for reorientation, either a slope-based or a feature-based approach. They show consistent individual differences in which class of cue they prefer.

Section Summary

Overall, both pigeons and people are able to use slope as a reorientation cue. It appears that slope should be considered a different cue class from geometry. When the hippocampus of pigeons is lesioned, geometry performance is impaired, particularly when the left hippocampal formation is lesioned. Slope behavior is unaffected by bilateral hippocampal formation lesions. Thus, slope and geometry appear to be processed by different areas of the pigeon brain. When pigeons are required to choose between feature, slope and geometry cue types, subjects weigh slope and feature cues about equally, and prefer to use slope over geometry. The over-reliance on slope when given also geometric information is compelling, as it occurs even if geometry is a better predictor of the goal. The balance between slope and feature cue use depends in part on the amount of effort during training. When the trained corner is located uphill, then pigeons rely more heavily on the slope cue. When the trained corner in located downhill, then pigeons rely more heavily on the feature cue. Thus, effort modulates the relative weighting of feature and slope cues in spatial memory for pigeons. When both slope and features are present during training, pigeons encode both cue types. In contrast, the majority of people tend to use one or the other cue type, in about equal proportions, to solve the reorientation task.

Sex Differences in Reorientation?

There are striking sex-related differences in some (but not all) kinds of human spatial functioning, particularly in mental rotation and in orientation to gravitationally-defined horizontal and vertical (Voyer, Voyer, & Bryden, 1995). There are also probably sex differences in navigation tasks. For example, men perform better than women in constructing a survey representation (Ishikawa & Montello, 2006), in using the geometry of a surrounding trapezoid to locate a hidden platform (Sandstrom, Kaufman, & Huettel, 1998), and in selecting the initial heading in a virtual Morris Water Maze task (Woolley, Vermaercke, Op de Beeck, Wagemans, Gantois, D'Hooge, Swinner, & Wenderoth, 2010). There are also probably sex differences in non-human species, although the differences vary across species, for example, mice show fewer such differences than rats (Jonasson, 2005).

Until recently, however, possible sex differences in reorientation have received little attention. In the animal literature, subjects are often all male, of unspecified sex, or comprise too small a sample to look for sex differences (Cheng & Newcombe, 2005). Of course, human studies of reorientation are more often able to look for sex differences, but they have mostly not found them. And when sex has been examined in studies of non-human animals, it seems to have weak and inconsistent effects (Sovrano, Bisazza, & Vallortigara, 2003 for fish; Twyman, Newcombe, & Gould, 2009, 2012 for mice). In sum, because of all-male samples, unknown sex, or too small sample sizes, it is unclear if there are differences between the sexes in reorientation, but they have not seemed impressive. However, more recently, some sex differences have emerged, concerning three areas. Arranged in ascending order by the power of the findings, they are: the use of local geometric cues, geometry in the presence of a beacon feature cue, and the use of slope for reorientation.

Local versus Global Geometry

It has been proposed that men rely more on directional cues such as cardinal position, gradients or distal landmarks, while women seem to depend on positional cues like local landmarks (Jacobs & Schenk, 2003). In a reorientation study linked to this issue, adults were asked to reorient in a space with both local and global reorientation cues (Reichert & Kelly, 2011). An array of four posts formed a mental rectangular search space that could be used as a global cue (see Figure 10). The diagonal pairs of corner posts were set at angles of either 50 or 75 degrees and served as local geometric cues.

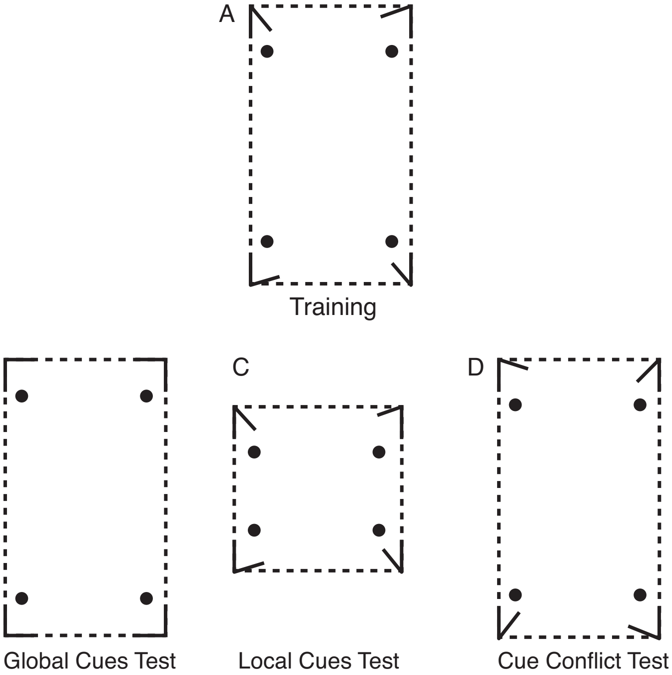

Figure 10. *The training condition and the three testing conditions used by Reichert and Kelly (2011).*

Neither sex encoded the global geometric shape of the array; men, but not women, encoded the local geometric cues (i.e., angle size). Therefore, men appeared to be better able to use local geometric cues for reorientation than were women, in contradiction of the Jacob and Schenk hypothesis. These findings are puzzling, however, not only because they seem to contradict the Jacobs and Schenk hypothesis, but also because Sutton, Twyman, Joanisse and Newcombe

(2012) found that, at least in virtual reality, adults could infer the global geometric shape from and array of four columns. Additionally, Lubyk, Dupuis, Gutiérrez, and Spetch (2012) found that adults were able to reorient with local acute and obtuse angles in a virtual reality search task, and importantly, no sex differences were found.

Beacon Cues and Geometric Cues

The bulk of the previous research with humans has used a rectangular enclosed space as the geometric cue, and one of the walls of the rectangle was a unique color to provide the feature cue. In this type of task, gender differences have not been found with adults or with children (Hermer & Spelke 1994; 1996; Learmonth, Nadel, & Newcombe, 2002; Twyman, Friedman, & Spetch, 2007). However, two studies have used a distinctive object directly at or near the correct hiding location within a rectangular search space, i.e., a beacon. Kelly and Bischof (2005) created a 3D virtual environment of a rectangular search space. In each corner of the room was a distinctive object. Both men and women readily learned the task, which could have been accomplished by either encoding both the geometric cue and the beacon, or just paying attention to the beacon. When the beacons were removed, it was found that the men, but not the women, had encoded the geometry of the space. Importantly, in a similar experiment, when a feature wall was used, the sex difference went away and both men and women encoded the geometry of the space (Kelly & Bischof, 2008). Lourenco, Addy, Huttenlocher and Fabian (2011) found similar results with toddlers. In a real-world version of the task with an enclosed rectangular search space and either a unique hiding container or a distinctive flag placed on top of the target container, toddlers learned to reorient. On the geometry-only test in which all of the containers were identical, only the boys turned out to have encoded the geometry of the enclosure.

On the basis of these two studies, it is possible that gender differences in reorientation are specific to the case in which there are salient beacons, which somehow have an especially strong pull on females. It would be nice to know the pattern with non-human animals, but researchers will need to use female as well as male animals to answer this question. However, some geometric information may exist even when geometry-only tests are failed. Lourenco et al. (2011) included conflict trials designed to assess the relative use of geometric and feature cues. All toddlers preferred the beacon cue to geometry, and all toddlers, both boys and girls, were slower to respond on the conflict trials than they had been during training. If the girls truly had not encoded the geometry during training, then their search times should have remained fast. Thus, the girls probably had noticed something about the shape of the environment even though not at a level sufficient to support active search with the geometric cue.

Sex Differences in Slope Cues

As we reviewed earlier, people are able to reorient with slope as the sole orientation cue (Nardi et al., 2011). Participants were disoriented in a uniform square room and then were asked to find a target location using the floor that was slanted at a 5° angle. Overall, people were able to use the sloped floor to guide search. However, men and women performed quite differently on this task. When participants were not given any extra instructions, men were about 35% more accurate (1.4 standard deviation difference). Additionally, each sex adopted different strategies. The vast majority of the men reported using slope, while only about half of women attempted to use the slope. The other half attempted to use other ineffective strategies: about a third of the women attempted to use a path integration strategy (trying to keep track of the number of rotations), and the remaining tried to use small features in the environment like a wrinkle in the fabric or a filament thread in the light bulb. Therefore, it is possible that the lower accuracy of women on this task could be because of strategy choice rather than a difference in ability.

In an effort to make the sloped floor more salient, Nardi et al. showed a ball rolling down the floor and told participants that the slanted floor could help them succeed at the task. All participants reported using a slope-based strategy. And people did improve, but men were still more accurate than women. To further investigate this sex difference, the authors wondered if women might have a difficult time perceiving the slanted floor. To test this hypothesis, participants were required to stand in the middle of the room and they were asked to point in the up direction of the slope as quickly and accurately as possible. Both sexes were able to correctly identify the direction of the slope in just over 3 seconds, but men were over 1 second faster than women.

Might women have more difficulty using slope since they are often wearing heeled footwear that might make slope difficult to perceive and use? Probably not. In Nardi et al. (2011), when the footwear was uncontrolled (i.e. women performed the task in the shoes they showed up with on the given day) and when women were required to wear flat slippers provided by the experimenters, they performed identically in the slope task. Further, when Nardi, Newcombe, and Shipley (2012) asked women to complete a survey about the height of footwear they wear for everyday use, there was no correlation between slope use and typical heel height. On a different note, an interesting aspect of this study was the finding that men were generally more confident in solving the reorientation task on a slope, suggesting that sex differences in spatial confidence might play a role in the performance advantage with slope.

In summary, there appear to be large sex difference in the use of slope-based strategies for reorientation. Men are more accurate than women by about 1.4 standard deviations, a difference that is larger than the sex difference for the mental rotation test. Men are twice as likely to adopt a slope based strategy when this is the only effective cue available. If the slope is made more salient, then almost everyone attempts to use slope, but men are still more accurate. Women are also slower to correctly identify the direction of a slope.

Section Summary

In the vast majority of studies with animals and humans, sex differences have not been found for reorientation behavior, particularly when experiments are conducted in enclosed rectangles with a feature wall. More recently, there have been a few findings that suggest sex differences when reorientation is tested with embedded local and geometric cues or with a beacon as a feature cue. From this small set of findings, it appears that men might be better at using geometric cues compared to women. This would parallel the sex differences that have been found for rats in water-maze search tasks, where both sexes can use geometric or proximal feature cues to locate a hidden platform, but male rats rely more heavily on geometric cues and female rats prefer to use a proximal feature cue (Rodriguez, Chamizo, & Mackintosh, 2011; Rodriguez, Torres, Mackintosh & Chamizo, 2010). However, these studies were not about orientation, and therefore any claims about sex differences in reorientation ability are currently far from definitive. Further experiments with non-human animals would be more likely to shed light on sex differences than work with humans because various social and cultural differences could be excluded. Nevertheless, the most striking sex difference we have reviewed concerns the use of slope cues. Comparative work and work investigating the neural bases of these effects might shed more light on these differences.

Conclusion

Research on spatial cognition has been generally more open to a comparative approach than research in many other domains, and research on the geometric module theory has been an especially vigorous example of the kind of interchange that would be desirable for a comprehensive account of cognitive biology. In this article, we have seen that each field and sub-field often contributes distinctive methods and concepts to the collective enterprise. As a result, we know a great deal more about reorientation than we did in 1986. It has become clear that the twin hypotheses of a geometric module and a unique and necessary role for human language in reorientation cannot stand. It has also become clear that there is a need for expansion of the taxonomy of cues that can be used for reorientation, with slope a good example. There is also a need for definitional clarification and possibly for a change in nomenclature, because it is difficult to postulate a geometry that includes distance and direction, but not angle and length as suggested by Lee et al. (2012). It may be that a renewed focus on contact with the overall literature on spatial navigation will lead to a more comprehensive view (Lew, 2011). The challenge for the future will be in formulating a precise, quantitatively-specified model that can account for the hundreds of effects found to date, with more data being reported each month.

References

Batty, E. R., Bloomfield, L. L., Spetch, M. L. & Sturdy, C. B. (2009). Comparing black-capped (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*): use of geometric and featural information in a spatial orientation task. *Animal Cognition, 12,* 633-641. doi.org/10.1007/s10071-009-0222-3 PMid:19381699

Bek, J., Blades, M., Siegal, M., & Varley, R. (2010). Language and spatial reorientation: Evidence from severe aphasia. J*ournal of Experimental Psychology: Learning, Memory, and Cognition, 36*, 646 – 658. doi.org/10.1037/a0018281 PMid:20438263

Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles: Rearing environment alters spatial navigation in fish. *Psychological Science, 18*, 569-573. doi.org/10.1111/j.1467-9280.2007.01941.x PMid:17614863

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149-178. doi.org/10.1016/0010-0277(86)90041-7

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences, 12*, 355-361. doi.org/10.1016/j.tics.2008.06.004 PMid:18684662

Cheng, K. & Newcombe, N.S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin and Review, 12*, 1-23. doi.org/10.3758/BF03196346 PMid:15945200

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin, 133*, 625-637. doi.org/10.1037/0033-2909.133.4.625 PMid:17592958

Chiandetti, C., & Vallortigara, G. (2008). Is there an innate geometric module? Effects of experience with angular geometric cues on spatial reorientation based on the shape of the environment. *Animal Cognition, 11*, 139-146. doi.org/10.1007/s10071-007-0099-y PMid:17629754

Chiandetti, C., & Vallortigara, G. (2010). Experience and geometry: Controlled-rearing studies with chicks. *Animal Cognition, 13*, 463-470. doi.org/10.1007/s10071-009-0297-x PMid:19960217

Chiandetti, C., Regolin, L., Sovrano, V. A., & Vallortigara,

G. (2007). Spatial reorientation: The effects of space size on the encoding of landmark and geometry information. *Animal Cognition, 10*, 159-168. doi.org/10.1007/s10071-006-0054-3 PMid:17136416

Cressant, A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. *Journal of Neuroscience, 17*, 2531-2542. PMid:9065513

Cressant, A., Muller, R. U., & Poucet, B. (1999). Further study of the control of place cell firing by intro-apparatus objects. *Hippocampus, 9*, 423–431. doi.org/10.1002/(SICI)10981063(1999)9:4<423::AID-HIPO8>3.0.CO;2-U

Gallistel, C. R. (1990). *The organization of learning*. Cambridge: MIT Press.

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General, 130*, 505-519. doi.org/10.1037/0096-3445.130.3.505 PMid:11561924

Gray, E. R., Bloomfield, L. L., Ferrey A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters, 1*, 314-317. doi.org/10.1098/rsbl.2005.0347 PMid:17148196 PMCid:1617142

Hermer, L., & Spelke, E. (1994). A geometric process for spatial representation in young children. *Nature, 370*, 57-59. doi.org/10.1038/370057a0 PMid:8015605

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61*, 195-232. doi.org/10.1016/S0010-0277(96)00714-7

Hermer-Vasquez, L., Moffet, A., & Munkholm, P. (2001). Language, space, and the development of cognitive flexibility in humans: The case of two spatial memory tasks. *Cognition, 79*, 263-299. doi.org/10.1016/S0010-0277(00)00120-7

Hermer-Vazquez, L., Spelke, E., & Katsnelson, A. (1999). Sources of flexibility in human cognition: Dual task studies of space and language. *Cognitive Psychology, 39*, 3-36. doi.org/10.1006/cogp.1998.0713 PMid:10433786

Hupbach, A., Hardt, O., Nadel, L., & Bohbot, V. D. (2007). Spatial reorientation: Effects of verbal and spatial shadowing. *Spatial Cognition and Computation, 7*, 213-226. doi.org/10.1080/13875860701418206

Hupbach, A., & Nadel, L. (2005). Reorientation in a rhombic environment: No evidence for an encapsulated geometric module. *Cognitive Development, 20*, 279-302. doi.org/10.1016/j.cogdev.2005.04.003

Huttenlocher, J., & Lourenco, S. F. (2007). Coding location in enclosed spaces: Is geometry the principle? *Developmental Science, 10*, 741-746. doi.org/10.1111/j.1467-7687.2007.00609.x PMid:17973790

Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review, 98*, 352-376. doi.org/10.1037/0033-295X.98.3.352 PMid:1891523

Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology, 52*, 93-129. doi.org/10.1016/j.cogpsych.2005.08.003 PMid:16375882

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review, 110*, 285-315. doi.org/10.1037/0033-295X.110.2.285 PMid:12747525

Jonasson, Z. (2005). Meta-analysis of sex differences in rodent models of learning and memory: A review of behavioral and biological data. *Neuroscience and Biobehavioral Reviews, 28*, 811-825. doi.org/10.1016/j.neubiorev.2004.10.006 PMid:15642623

Kelly, D. M. (2010). Features enhance the encoding of geometry. *Animal Cognition, 13*, 453-462. doi.org/10.1007/s10071-009-0296-y PMid:20012120

Kelly, D. M., & Bischof, W. F. (2005). Reorienting in images of a three-dimensional environment. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 1391-1403. doi.org/10.1037/0096-1523.31.6.1391 PMid:16366797

Kelly, D. M., & Bischof, W. F. (2008). Orienting in virtual environments: How are surface features and environmental geometry weighted in an orientation task? *Cognition, 109*, 89-104. doi.org/10.1016/j.cognition.2008.07.012 PMid:18834974

Kelly, D. M., & Spetch, M. L. (2004). Reorientation in a two-dimensional environment: II. Do pigeons (*Columba livia*) encode the featural and geometric properties of a two-dimensional schematic of a room? J*ournal of Comparative Psychology, 118*, 384-395. doi.org/10.1037/0735-7036.118.4.384 PMid:15584775

Kelly, D. M., Spetch, M.L., & Heth, C. D. (1998). Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology, 112*, 259-269. doi.org/10.1037/0735-7036.112.3.259

Lakusta, L., Dessalegn, B., & Landau, B. (2010). Impaired geometric reorientation caused by genetic defect. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 107*, 2813-2817. doi.org/10.1073/pnas.0909155107 PMid:20133673 PMCid:2840366

Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddler's use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology, 80*, 225-244. doi.org/10.1006/jecp.2001.2635 PMid:11583524

Learmonth, A.E., Nadel, L. & Newcombe, N.S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science, 13*, 337-341. doi.org/10.1111/j.0956-7976.2002.00461.x PMid:12137136

Learmonth, A.E., Newcombe, N.S., Sheridan, N. & Jones, M. (2008). Why size counts: Children's spatial reorientation in large and small enclosures. *Developmental Science, 11*, 414-426. doi.org/10.1111/j.1467-7687.2008.00686.x PMid:18466375

Lee, S. A., Shusterman, A., & Spelke, E. S. (2006). Reorientation and landmark-guided search by young children: Evidence for two systems. *Psychological Science, 17,* 577-582. doi.org/10.1111/j.1467-9280.2006.01747.x PMid:16866742

Lee, S. A., Sovrano, V. A., & Spelke, E. S. (2012). Navigation as a source of geometric knowledge: Young children's use of length, angle, distance, and direction in a reorientation task. *Cognition, 123*, 144-161. doi.org/10.1016/j.cognition.2011.12.015 PMid:22257573

Lee, S. A., & Spelke, E. S. (2010). A modular geometric mechanism for reorientation in children. *Cognitive Psychology, 61*, 152-176. doi.org/10.1016/j.cogpsych.2010.04.002 PMid:20570252 PMCid:2930047

Lew, A. R. (2011). Looking beyond the boundaries: Time to put landmarks back on the cognitive map? *Psychological Bulletin, 137*, 484-507. doi.org/10.1037/a0022315 PMid:21299273

Lourenco, S. F., Addy, D., Huttenlocher, J., & Fabian, L. (2011). Early sex differences in weighting geometric cues. *Developmental Science, 14*, 1365-1378. doi.org/10.1111/j.1467-7687.2011.01086.x PMid:22010896

Lubyk, D. M., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review, 19*, 436 – 442. doi.org/10.3758/s13423-012-0232-z PMid:22382695

Miller, N. Y., & Shettleworth, S. J. (2008). An associative model of geometry learning: A modified choice rule. J*ournal of Experimental Psychology: Animal Behavior Processes, 34*, 419-422. doi.org/10.1037/0097-7403.34.3.419 PMid:18665724

Nadel, L., & Hupbach, A. (2006). Species comparisons in development: the case of the spatial "module". In M. Johnson and Y. Munakata (eds), *Processes of change in brain and cognitive development*. *Attention and Performance*, vol. XXI. Oxford, UK: Oxford University Press.

Nardi, D., & Bingman, V. P. (2007). Asymmetrical participation of the left and right hippocampus for representing environmental geometry in homing pigeons. *Behavioural Brain Research, 178*, 160-171. doi.org/10.1016/j.bbr.2006.12.010 PMid:17215051

Nardi, D., & Bingman, V. P. (2009b). Slope-based encoding of goal location is unaffected by hippocampal lesions in homing pigeons (*Columba livia*). *Behavioural Brain Research, 205*, 322-326. doi.org/10.1016/j.bbr.2009.08.018 PMid:19703498

Nardi, D., Mauch, R. J., Klimas, D. B., & Bingman, V. P. (2012). Use of slope and feature cues in pigeon (*Columba livia*) goal-searching behavior. *Journal of Comparative Psychology*. Advance online publication. doi:10.1037/a0026900

Nardi, D., Newcombe, N.S. & Shipley, T.F. (2011). The world is not flat: Can people reorient using slope? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 37*, 354-367. doi.org/10.1037/a0021614 PMid:21171808

Nardi, D., Newcombe, N.S. & Shipley, T. F. (2012). Reorienting with terrain slope and landmarks. *Memory & Cognition,* advance online publication. doi: 1. 3758/s13421-012-0254-9

Nardi, D., Nitsch, K. P., & Bingman, V. P. (2010). Slope-driven goal location behavior in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 36*, 430-442. doi.org/10.1037/a0019234 PMid:20718551

Nardini, M., Atkinson, J., & Burgess, N. (2008). Children reorient using the left/right sense of coloured landmarks at 18-24 months. *Cognition, 106*, 519-527. doi.org/10.1016/j.cognition.2007.02.007 PMid:17379204

Newcombe, N. S., & Huttenlocher, J. (2006). Development of spatial cognition. In W. Damon & R. Lerner (Series Eds.) and D. Kuhn & R. Seigler (Vol. Eds.), *Handbook of child psychology: Vol. 2. Cognition, perception and language* (6th ed., pp. 734-776). Hoboken, NJ: John Wiley & Sons.

Newcombe, N. S., & Ratliff, K. R. (2007). Explaining the development of spatial reorientation: Modularity-plus-language versus the emergence of adaptive combination. In J. Plumer & J. Spencer (Eds.), The emerging spatial mind (pp. 53-76). New York, NY: Oxford University Press. doi.org/10.1093/acprof:oso/9780195189223.003.0003

Newcombe, N. S., Ratliff, K. R., Shallcross, W. L., & Twyman, A. D. (2010). Young children's use of features to reorient is more than just associative: Further evidence against a modular view of spatial processing. *Developmental Science, 13*, 213-220 doi.org/10.1111/j.1467-7687.2009.00877.x PMid:20121877

Pyers, J. E., Shusterman, A., Senghas, A., Spelke, E. S., & Emmorey, K. (2010). Evidence from an emerging sign language reveals that language supports spatial cognition. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 107*, 12116-12120 doi.org/10.1073/pnas.0914044107 PMid:20616088 PMCid:2901441.

Ratliff, K. R., & Newcombe, N. S. (2008a) Is language necessary for human spatial reorientation? Reconsidering evidence from dual task paradigms. *Cognitive Psychology, 56*, 142-163. doi.org/10.1016/j.cogpsych.2007.06.002 PMid:17663986

Ratliff, K. R., & Newcombe, N. S. (2008b). Reorienting when cues conflict: Using geometry and features following landmark displacement. *Psychological Science, 19*, 1301- 1307. doi.org/10.1111/j.1467-9280.2008.02239.x PMid:19121141

Reichert, J. F., & Kelly, D. M. (2011). Use of local and global geometry from object arrays by adult humans. *Behavioural Processes, 86*, 196-205. doi.org/10.1016/j.beproc.2010.11.008 PMid:21144887

Rhodes, S. E. V., Creighton, G., Killcross, A. S., Good, M., & Honey, R. C. (2009). Integration of geometric with luminance information in the rat: Evidence from within-compound associations. *Journal of Experimental Psychology: Animal Behavior Processes, 35*, 92-98. doi.org/10.1037/0097-7403.35.1.92 PMid:19159164

Rodriguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2011). Overshadowing and blocking between landmark learning and shape learning: the importance of sex differences. *Learning & Behavior, 39*, 324-35. doi.org/10.3758/s13420-011-0027-5 PMid:21472414

Rodriguez, C. A., Torres, A. A., Mackintosh, N. J., & Chamizo, V. D. (2010). Sex differences in preferential strategies to solve a navigation task. *Journal of Experiemental Psychology: Animal Behavior Processes, 36*, 395-401. doi.org/10.1037/a0017297 PMid:20658870

Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research, 6*, 351–360. doi.org/10.1016/S0926-6410(98)00002-0

Shusterman, A., Ah Lee, S., & Spelke, E. S. (2011). Cognitive effects of language on human navigation. *Cognition, 120*, 186-201. doi.org/10.1016/j.cognition.2011.04.004 PMid:21665199

Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module: A sense linkage for metric and landmark information in animals' spatial reorientation. *Psychological Science, 17*, 616-621. doi.org/10.1111/j.1467-9280.2006.01753.x PMid:16866748

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish (*Xenotoca eiseni*) views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 199-210. doi.org/10.1037/0097-7403.29.3.199 PMid:12884679

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition, 10*, 47-54. doi.org/10.1007/s10071-006-0029-4 PMid:16794851

Sutton, J. E. (2009). What is geometric information and how do animals use it? *Behavioural Processes, 80*, 339-343. doi.org/10.1016/j.beproc.2008.11.007 PMid:19084055

Sutton, J. E., Twyman, A. D., Joanisse, M. F. & Newcombe, N. S. (2012). Geometry three ways: An fMRI investigation of geometric processing during reorientation. J*ournal of Experimental Psychology: Learning, Memory and Cognition, 38*, 1530 – 1541. doi.org/10.1037/a0028456 PMid:22582967

Twyman, A. D., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology, 43*, 1523-1530. doi.org/10.1037/0012-1649.43.6.1523 PMid:18020829

Twyman, A. D., & Newcombe, N. S. (2010). Five reasons to doubt the existence of a geometric module. *Cognitive Science, 34*, 1315-1356. doi.org/10.1111/j.1551-6709.2009.01081.x PMid:21564249

Twyman, A. D., Newcombe, N. S., & Gould, T. J. (2009). Of mice (*Mus musculus*) and toddlers (*Homo sapiens*): Evidence for species-general spatial reorientation. *Journal of Comparative Psychology, 123*, 342-345. doi.org/10.1037/a0015400 PMid:19685977

Twyman, A. D., Newcombe, N.S. & Gould, T.G. (2012). Malleability in the development of spatial reorientation. Developmental Psychobiology, advanced online publication. doi.org/10.1002/dev.21017

Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different size. *Developmental Science, 8*, 393-401. doi.org/10.1111/j.1467-7687.2005.00427.x PMid:16048511

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representations: A test with chicks (*Gallus gallus domesticus*). *Journal of Comparative Psychology, 104*, 248-254. doi.org/10.1037/0735-7036.104.3.248 PMid:2225762

Vargas, J. P., Petruso, E. J., & Bingman, V. P. (2004). Hippocampal formation is required for geometric navigation in pigeons. *European Journal of Neuroscience, 20*, 1937–44. doi.org/10.1111/j.1460-9568.2004.03654.x PMid:15380016

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin, 117*, 250-270. doi.org/10.1037/0033-2909.117.2.250 PMid:7724690

Waismeyer, A. S., & Jacobs, L. F. (2012). The emergence of flexible spatial strategies in young children. *Developmental Psychology*. Advance online publication.

doi.org/10.1037/a0028334

Wiener, J., Shettleworth, S., Bingman, V.P., Cheng, K., Healy, S., Jacobs, L.F., Jeffery, K.J., Mallot, H.A., Menzel, R. & Newcombe, N.S. (2011). Animal navigation: A synthesis. In R. Menzel & J. Fischer (Eds.), *Animal thinking: Contemporary issues in comparative cognition* (pp. 51-76). Strüngmann Forum Report, Vol. 8, J. Lupp, series ed. Cambridge, MA: MIT Press.

Woolley, D. G., Vermaercke, B., de Beeck, H. O., Wagemans, J., Gantois, I., D'Hooge, R., . . . Wenderoth, N. (2010). Sex differences in human virtual water maze performance: Novel measures reveal the relative contribution of directional responding and spatial knowledge. *Behavioural Brain Research, 208*, 408-414. doi.org/10.1016/j.bbr.2009.12.019 PMid:20035800

Wystrach, A., & Beugnon, G. (2009). Ants learn geometry and features. *Current Biology, 19*, 61-66. doi.org/10.1016/j.cub.2008.11.054 PMid:19119010

Zugaro, M. B., Berthoz, A., & Wiener, S. I. (2001). Background, but not foreground, spatial cues are taken as references for head direction responses by rat anterodorsal thalamus neurons. *Journal of Neuroscience, 21*, 1-5.