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Standing on shoulders of a giant: Marcia Spetch's contributions to the study of spatial reorientation

Alexandra D. Twyman[a,b,c,*]

[a] *Athabasca University, Canada*
[b] *Mount Royal University, Canada*
[c] *University of Calgary, Canada*

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ABSTRACT

Navigation is an important skill for mobile creatures. One important aspect of navigation is the ability to regain your position (reorient) if you become lost. Over the last 20 years, Marcia Spetch has added substantially to our understanding of reorientation and has advanced the fields of both comparative cognition and spatial cognition. The aim of the paper is to review her contributions, and in particular focus on a) the complexity of geometric cues that can guide reorientation; b) how short- and long-term experiences influence the relative use of geometric and feature cues; c) comparisons of reorientation behavior across species; d) discuss her contributions to theories of reorientation.

1. The reorientation puzzle: an important component of navigation

Marcia Spetch began her Master Lecture with the words, "I like puzzles" (International Society for Comparative Cognition's Annual Meeting, C03, April 6th, 2018). One puzzle that has captured the attention of many psychologists for the last 30 years is the study of spatial reorientation. In our everyday lives, there are many ways for us to lose track of our position. For example, this can happen if we take the subway, wake up in a new hotel room, get immersed in conversation during travels, or perhaps tumble down a hill. And the question that has us all fascinated is: how do we regain our sense of position? How are we able to rediscover where we are? Before we can start a successful journey, we must discover our current spatial position. This phenomenon has been called the ability to reorient, and has been extensively studied in the lab across a wide range of fields, including comparative cognition, human cognition, developmental psychology, and neuroscience. Marcia Spetch has been researching reorientation for over half her career, and for over two-thirds of the lifespan of this research area. Her contributions to this reorientation puzzle, and to all these mentioned areas of psychology, have been substantial. This paper will begin with a brief overview of the initial discoveries in reorientation, and will highlight how Marcia Spetch's research has advanced our understanding of reorientation. In particular I will discuss: a) the complexities of using geometric cues for reorientation; b) the role of short-term and long-term experiences on reorientation strategies; c) comparisons in reorientation across several species; d) Marcia Spetch's lasting contribution to the field.

1.1. *The first puzzle piece: of rats and toddlers*

Over 30 years ago, Cheng (1986) studied rats searching for food in rectangular enclosures with unique feature cues (odor, color, pattern, etc.) at each corner (see Fig. 1). The rats searched in the enclosure until food was found, and then during feeding the rat was removed, disoriented, and placed back in the enclosure. Something remarkable happened. On half of the trials, the rats returned to the exact place where food had been found. But for the other half, the rats headed to the diagonally opposite corner in the rectangular room. What odd behavior from the rat. However, the diagonal corners are rotational equivalents, and share the same geometric properties. For example, if the rat had been eating at a corner with a long wall to the left, then there are actually two corners of the rectangle that have this same property. To explain the seemingly sub-optimal pattern of responding, Ken Cheng proposed that the reorientation system of rats was modular. The geometric properties of the environment were suggested to support the orientation system, and other aspects of the environment such as odors, colors, or the number and pattern of lights were discarded on working memory versions of the task (Cheng, 1986). This system was proposed to be evolutionarily adaptive since the geometric properties of the environment are stable (the wall of mountains is always on the North side of the city) whereas the features may change throughout the

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* Correspondence to: Mount Royal University, Department of Psychology, 4825 Mount Royal Gate SW, Calgary, Alberta, Canada T3E 6K6.
E-mail address: atwyman@mtroyal.ca.

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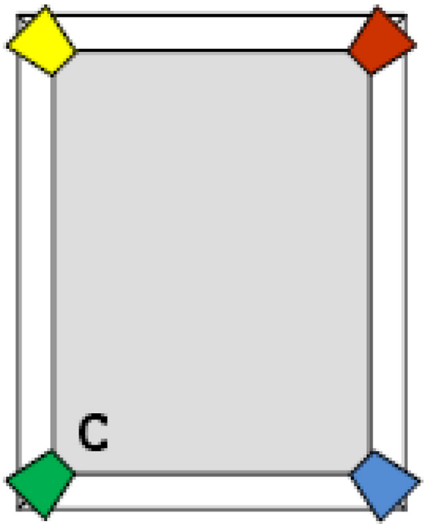

Fig. 1. The Standard Reorientation Paradigm. Rats searched for food in this enclosure containing both geometric and feature cues. The correct location (C) can be determined by either geometry (such as to the left of a long wall, which would results in food 50% of the time) or by feature cues (such as the green panel that smelled of peppermint).

day (such leaves blowing across a field in the fall, or the shadows and lights that shift during the day) and the seasons (the same field may looks quite different in August versus January in many geographic locations, such as the prairies of Alberta) (Gallistel, 1990). Furthermore, when reorientation was first examined in humans, children under the age of six performed similar to the rats. Even young toddlers could use the geometric properties of the environment to reorient and yet failed to use a giant red wall to do so (Hermer and Spelke, 1994, 1996). As visual creatures, we find it hard to believe that children would ignore something as obvious as a uniquely colored wall. And in fact, for adults, we quite easily use both feature and geometric cues to reorient (Hermer and Spelke, 1994, 1996). From the modularity perspective at the time, it was proposed that our spatial language allows us to overcome our innate geometric module for reorientation and enables us to be more flexible thinkers than young children and non-human animals (Kinzler and Spelke, 2007). Currently, the modularity account of reorientation is still thriving. While less emphasis has been placed on language, the modularity view has increased in the scope of by researchers supporting this claim. In the modularity-plus-language account, the adult human mind is viewed as integrated. Currently, a two-step model of reorientation recants this stance. It has been proposed that in any reorientation task, there are two components: a) reorient: find your heading direction; and, b) find a goal location. Any instances of feature use have been attributed to the goal localization system for all species and all ages of organisms. Only geometric cues are proposed to support true reorientation (see Lee and Spelke, 2010; Lee, 2017). This position has seen a recent resurgence in support within the reorientation literature, as well as by the broader research community (Ferrara and Landau, 2015; Julian et al., 2018).

1.2. The second puzzle piece: of chicks and pigeons

At first, it seemed that the reorientation puzzle was going to be fairly simple to solve: rats and non-human animals use stable geometric cues to re-gain a heading direction, while adults flexibly use feature and geometric cues for this task, mediated by their mastery of spatial language. Or in a modern version, all species use geometric cues for reorientation and feature cues in a separate system to find a goal location. This potential solution has a few problems, even from early on, when examining birds. In the first reorientation study of a bird, Vallortigara et al. (1990) discovered that chicks can encode and rely on both geometric and feature cues in reorientation. Surprisingly, in situations of conflict (moving the feature cue from one corner to a geometrically incorrect corner for the test trial), chicks prefer the feature cue over the geometric cue. Thus, at least as far as chicks are concerned, the reliance on geometric cues is not widespread throughout the animal kingdom. Marcia Spetch and her long-time collaborator, Debbie Kelly, showed us that this was also true for pigeons. They discovered that pigeons can use both geometric and feature cues for reorientation (Kelly et al., 1998). And perhaps even more surprisingly, with remarkable flexibility. Pigeons were trained to reorient in a rectangular environment with unique feature panels in each corner. After training, subjects were given a conflict test. Pigeons that had been trained in the compound condition (feature panel-plus-rectangular-room) followed the training feature panel to a geometrically incorrect corner, and thus relied quite heavily on the feature cue. In contrast, pigeons that had received pre-training in an all-white rectangular room (only geometric cues available), followed by the compound training (feature panel-plus-rectangular room), divided their search on the conflict trials between the two geometrically equivalent corners and the featurally correct corner. When offered both geometric and feature reorientation cues, pigeons tend to rely more heavily on feature cues for reorientation. But previous experience with a geometric reorientation cue can cause the birds to rely more evenly on the two reorientation cues.

Kelly and Spetch (2004a,b) extended this line of work from the 3 dimensional (3D) search space to a 2 dimensional (2D) computer reorientation task with pigeons and adult humans. One of the novelties of this transformation of the task was that pigeons and human adults could be tested using the exact same experimental method and procedure, making sure that similarities or differences found across species was due to the underlying reorientation task, rather than variations in the apparatus or procedure. When tested in this fashion, both species were able to use proximal and distal feature cues for reorientation. Both species automatically encoded the geometric cues even if not explicitly required for the task (although the human adults did find geometry learning a little bit difficult). Beyond the interesting finding of the similarity in responding of pigeons and adults, the task itself has had interesting applications. Recently, Kelly and Spetch's task has been used to investigate hemispheric asymmetry in split-brain patients when real-life and virtual reality tests were difficult to administer (Prete et al., 2018). Additionally, the 2D computer version of the task paved the way for further exploration of reorientation in computer tasks, an important step for fMRI investigations of the of reorientation in humans (Sutton et al., 2012). Thus, the 2D computer task was important for the data collected, but has also been a foundational study that has allowed for the exploration of the neural underpinning of reorientation systems in humans.

Together, these sets of experiments with birds demonstrated from even early on in the reorientation literature, that flexibility would be required to explain the puzzle of reorientation. These sets of findings have been problematic for modularity accounts of reorientation. And, they are a key pillar of an alternative theoretical account of reorientation: adaptive combination theory (Newcombe and Huttenlocher, 2006). Briefly, from this perspective, potentially any cue can be used to support reorientation, and their relative use will depend on factors such as cue salience and reliability as well as previous experience (Twyman and Newcombe, 2010; Twyman et al., 2018). In sum, Marcia Spetch's research with pigeons has demonstrated that geometric cue use is not a dominant strategy throughout the animal kingdom. And importantly, at least for pigeons, chicks, and people, that the system is flexible and adaptable.

2. Breaking down rectangles: how do geometric cues support reorientation?

In the first reorientation experiments, researchers were trying to understand if the global shape of the room (geometry) was the only cue that could enable reorientation, or if other cues such as a discrete feature panel or a uniquely colored room wall, could be used to guide reorientation (Cheng, 1986; Hermer and Spelke, 1994; Kelly et al., 1998). This question has yet to be conclusively answered, with proponents of modularity theory arguing that only boundaries aid reorientation (Lee, 2017) and proponents of adaptive combination theory stating that both geometric and feature cues are integrated in spatial memory (Twyman et al., 2018). However, "geometry" is an umbrella term that encompasses many types of environmental cues, such as wall length, distance between walls, or corner angle, just to name a few. Marcia Spetch has spent almost 20 years exploring what it means for a cue to be geometric and inspiring others to think more deeply about the horizontal and vertical dimensions of space.

2.1. Global geometric cues: wall length, height, and visibility

One of the most noticeable aspects of rectangle enclosures is that they have four walls. Recent research has investigated just how these walls might support reorientation. Are the walls encoded as a relative size cue, or as an absolute length? Can wall height as well as wall length guide reorientation? Is it the relative lengths of the walls themselves that support reorientation, or the distance between the walls that does so? And does the wall have to be opaque, or could a transparent wall still be used for reorientation? These questions are discussed in the following sections.

2.1.1. Is wall length a relative or absolute geometric cue?

In reorientation studies, the geometric cue is often an enclosed rectangle. Kelly and Spetch (2001) were one of the first research teams to explore if the differential wall lengths were encoded in absolute distances or as relative cues. In their experiment, pigeons were trained to reorient in a large 100 x 200 cm rectangular enclosure. In the test trials, the size of the walls were reduced to particular sizes to see if the pigeons rely on the absolute wall length (such as left of the 100 cm wall) or if they relied on relative encoding (left of the shorter wall). If the arena was reduced to two-thirds of its original size, reorientation was unaffected. As the enclosure was made even smaller to a 50 x 100 cm size, the relative wall lengths flipped, in essence creating a conflict between the absolute wall length (left of the 100 cm wall) and the relative wall length (now, to the left of the shorter wall). In this conflict situation, pigeon relied more heavily on the relative geometric cue, but pigeons responded far less consistently in the conflict test (60% of choices to the relative geometric corners) than they had during the two-thirds reduction condition (83% to the relative geometric corners). The authors suggest that this may have been because the conflict enclosure was so small that pigeons tended to pick the first corner that was quite close to their entry point due to the room size. Or I'd like to suggest, that perhaps pigeons could have been encoding the room size both in absolute as well as relative distances. Another possibility is that the geometric cues themselves might be altered depending on the size and context of reorientation, explored in the next section. Regardless, exploration of relative versus absolute cue is in reorientation is an interesting question that warrants further exploration across species and throughout the lifespan.

2.1.2. Does geometric cue salience change across scales of space?

As mentioned previously, adaptive combination theory proposes that as cue salience increases, then participants also increase their reliance on that particular cue. And yet, relatively little research in reorientation has specifically altered cue salience. There are a series of studies on the room size effect in reorientation that I'd like to take a minute to discuss. I think that it is particularly relevant to one of the hot-button issues of the last few years, namely the replication crisis. When the reorientation behavior of young children was first examined, there was disagreement between Elizabeth Spelke's research group and Nora Newcombe's research group if children could in fact use features to reorient (Hermer and Spelke, 1994; Learmonth et al., 2001). The two research groups were not replicating each other's results. As a consequence, the methods were examined in detail and it was discovered that one possibility could be a difference in size of the enclosures. The area available to participants was much smaller for participants in Elizabeth Spelke's lab than in Nora Newcombe's lab. When the size of testing enclosure was examined, it was discovered that this variable was important, and that young children could use features to reorient in large spaces, but had more challenges with smaller environments (Learmonth et al., 2008). The room size effect has now been studied with human adults, children, and a wide-range of species (reviewed in Twyman and Newcombe, 2010), and the same theme has emerged. Geometric cues are relied upon more heavily in small spaces and feature cues more heavily in larger spaces. However, it is difficult to say exactly why. Is it that the feature becomes more salient as room size increases? Or, and perhaps at the same times, does the geometric cue become less salient as the room size increases? In any case, out of a failure to replicate, important findings emerged. As we will turn to next, Marcia Spetch and her collaborators have developed an experimental technique that sheds light on the issue of cue salience.

Marcia Spetch and Weimen Mou (Mou et al., 2014) collaborated on a set of experiments examining the properties of geometric cues in smaller proximal spaces and larger distal spaces. In this task, adults first had to learn a virtual map of object locations within a city as well as the direction of places outside of a city. Four corner posts anchored a rectangular reorientation space. When pointing to objects in the smaller space, participants only required two additional posts per side for reorientation, whereas for the distal space, participants now required 34 posts per side (like a fence) for reorientation. To the best of my knowledge, this is the first demonstration that increasing the size of a search space necessitated a stronger geometric cue to support reorientation. Additionally, one could measure the geometric cue salience by computing the percentage of the wall length covered by the posts (0% = an imaginary line, 100% = a wall). An experimental paradigm like this can be used to test the cue salience predictions of adaptive combination theory.

2.1.3. Can wall height support reorientation?

I don't know if you often look up, but since writing this paper, I've found that my writing room has a few cobwebs in it, since I rarely look up. Spetch and her collaborators have considered this empirically, and have asked if vertical geometric cues (wall height) can be used in addition to horizontal geometric cues (wall length) for reorientation. In a recent set of experiments with people, participants were asked to reorient in a rectangular enclosure that also varied in wall height along opposite pairs of walls. Participants encoded both wall length and height. When the horizontal and vertical geometric cues were placed in conflict, people did not show a preference for one geometric cue over the other (Du et al., 2016a). Interestingly, children can also use vertical wall heights for reorientation, but this ability does not emerge until about four-years-of-age (Qingfen et al., 2015). This is a notable finding, since it has been extensively argued that geometric reorientation systems are fully developed early in life, from 18 to 24 months, (Hermer and Spelke, 1994; Lee, 2017), and yet it appears that some types of geometric cues might undergo development (such as vertical geometric cues). In addition to people, Spetch and her collaborators have also asked if pigeons are able to use vertical geometric cues for reorientation. The answer seems to depend on the salience of the cue (Du et al., 2016b). Pigeons performed a reorientation task in a standard rectangular enclosure that was modified so that two walls were shorter in height than the other two walls. In the first version of the task, the walls were either 40 or 80 cm tall, and results showed that the pigeons had encoded the horizontal wall length, but not the height. When the wall height was lowered to 20 and 40 cm respectively, pigeons were able to use the vertical geometric cue. The pigeons had encoded both the horizontal (wall length) and vertical (wall height) cues, but in conflict tests, relied more heavily on the horizontal geometric cue. This may have more to do with the relative salience of the horizontal and vertical geometric cues, rather than an inherent preference by pigeons for one cue over the other. Flight is an important part of daily life for pigeons, which requires paying attention to height (can I clear that fence?). In a similar fashion, fish too, often move up and down in the water column throughout their day. Thus, it remains a question for future studies to investigate how important vertical and geometric cues are to each species, or if cue salience operates similarly depending on salience for mobile organisms, or if vertical height is psychologically and functionally equivalent to horizontal length. Regardless, children, adults, and pigeons can use wall height as well as wall length for successful reorientation.

2.1.4. Is the distance between walls or the relative lengths of the walls used for reorientation?

Since Kelly and Spetch's (2001) investigation of relative versus absolute wall encoding of the geometric cue, researchers focused more attention on the question of whether features could guide reorientation. Recently, there has been a resurgence of interest in exactly how the four walls of a rectangular enclosure guide reorientation. In a rectangular room, pairs of walls vary in relative length (the longer wall or the short wall), but they also vary in distance from each other. For example, the north and south wall might be 6-feet apart, while the east-west walls are only 4-feet apart. This question was investigated in a pair of developmental studies with preschoolers discussed below (Lee et al., 2012a; Yousif and Lourenco, 2017).

In the first study, Lee et al. (2012a,b) conducted a reorientation experiment comparing with partial walls that varied either in distance from each other (but equal length) or in length (but equal distance). In the wall distance condition, the wall length was held constant (for example 5-feet long), but the distance between walls differed for the north-south walls (such as 10-feet apart) and the east-west walls (such as 5-feet apart). Preschoolers had no trouble reorienting in this condition. In the second condition, the wall distance was held constant (such as 20-feet between the north-south *and* the east-west walls) while the partial wall segments varied in length (such as a 5-foot segment versus a 10-foot segment). In this condition, performance went down to chance (Lee et al., 2012a). A similar pattern of findings was found for Zebra fish (Lee et al., 2013). Thus, it was argued that only certain geometric cues could guide reorientation. In particular, the distances between extended surfaces could guide reorientation for children and non-human animals (but crucially not relative wall length). And this property of the reorientation system was argued to be powerful enough to facilitate reorientation based on distance illusions (Lee et al., 2012b). In adults, experience with symbolic representations like spatial language and maps enables human adults to use both distance and length as geometric reorientation cues (Dillon et al., 2013; Spelke et al., 2010).

Yousif and Lourenco (2017) pointed out that there was a confound in the previously discussed set of experiments. Specifically, the tests of relative wall distance and length with the partial walls created the global shape of a rectangle in one condition and a square in the other, which could quite easily be mentally connected according to the Gestalt principles of closure and completion, which even human infants do quite easily. In a set of experiments, Yousif and Lourenco replicated the initial Lee et al. (2012a,b) findings. Then, for each of the partial walls, they capped the walls with small horizontal tabs (| vs. I) to reduce the global processing of shape. This small modification allowed preschoolers to reorient with wall length or with wall distance as reorientation cues. Furthermore, if the position of the partial walls are modified so that the walls are still different distances from each other, but that the global shape is a square, then suddenly reorientation is impaired. Thus, the geometric properties of wall length and wall distance, can both be used to support reorientation for children, and are both influenced by the global geometric shape. These findings suggest that wall length and distance are psychologically equivalent, and that geometric cues interact with each other during reorientation. Future experiments can explore this question in non-human animals.

2.1.5. Do you have to be able to see the walls at all?

This question has only been recently asked, so there has yet to be a definite answer. In a series of experiments with transparent and opaque walls, Gianni et al. (2018) asked this question with young children. The geometric cue was a standard rectangle, but the walls were either transparent or opaque. In almost all of the developmental studies of walls as a reorientation cue, the walls support reorientation (Twyman and Newcombe, 2010). Surprisingly, it was not until about 5–7 years-of-age that children could use the transparent walls. The younger children were able to use opaque walls, but failed to reorient if the walls were clear Plexiglas. This suggests that if you decrease the salience of the geometric cue, by making it harder to see, then walls can fail to support reorientation, at least for human children. Additionally, since transparency varies on a scale from 0% (opaque) to 100% (invisible), then this could be a particularly fruitful paradigm to use to test the effects of cue salience within the adaptive combination framework. The initial findings are tantalizing, and future research can determine more about the relative roles that vision, motion, height, etc. play in reorientation across development and across species.

2.1.6. Summary of extended surfaces as a reorientation cue

Walls are an often-used geometric cue for reorientation. In the last few years, we have learned quite a bit about what aspects and how walls support reorientation. The distance between walls as well as the relative lengths of the walls can both be used by children to support reorientation. And the walls themselves appear to be encoded as relative lengths, rather than as an absolute size for pigeons. Pigeons, children, and adults can all use wall height as well as wall length, but the ability to use wall height undergoes development in children. Similarly, adults and older children can reorient even if the walls are transparent, but for children under five, the walls must minimally have opaque sections. Thus, at least two aspects (wall height and wall visibility) of geometric cues undergo development in people. Now that we know more about the geometric properties of walls themselves, we will discuss how the walls interact with local geometric cues: corner angles.

2.2. Local geometric cues: corner angles

Another notable aspect of a rectangular room is that the walls intersect at corners. In the rectangular spaces, these corners are all set to 90°, so it is not a useful reorientation cue. However, these local geometric cues might support reorientation. The next sections disiscuss how local corner angles interact with the global geometric wall cues as well as feature cues.

2.2.1. How does global wall length interact with local corner angle geometric cues?

A few experiments have compared the relative use of corner angles and wall lengths such as the pair of experiments conducted by Spetch et al. with pigeons (Lubyk and Spetch, 2012) and people (Lubky et al., 2012). For both studies, participants started training in a parallelogram that contained two types of geometric cues: relative wall length and local corner angle (60 vs. 120 °). After training, each cue was tested in isolation (a rectangle for the wall length test and a rhombus for the corner angle test) and it was found that both pigeons and people had encoded both geometric cues. In a reverse parallelogram conflict test, both pigeons and people relied more heavily on the local geometric cue (corner angle) rather than the relative wall length cue. Thus for reorientation in fully enclosed spaces, corner angle seems to be an important reorientation cue. It remains to be seen how general this finding may be, for both birds and mammals. In a reorientation experiment with domestic chicks, the subjects could also use corner angles or wall length for reorientation (Tommasi and Polli, 2004). However, when the cues were placed in conflict, corner salience (unlike pigeons or people in the previous experiments), and relative cue use depended on the salience of the local geometric cue. Chicks went to a corner consistent with the local geometric cue if the previously trained corner had been high in salience (an acute corner). In contrast, chicks went to the corner consistent with wall length if the previously trained corner had been low in local geometric salience (an obtuse corner). When adults were asked to reorient in a rectangular array of corner posts, rather than a full-enclosed space, set to either 50- or 75-degrees, participants failed to encode the global shape (a rectangle) and only the men had encoded the local geometric corner angles (Reichert and Kelly, 2011). There are a few reasons why participants may have done poorly in this situation. Extracting the geometric shape from arrays appears to be more challenging than from fully enclosed spaces (Lee, 2017). And the difference between the local corner angles was less pronounced (only 25 °) than in the previously discussed experiments (60 °). Overall, corner angles are salient geometric cues that often trump wall length. For some species and some conditions, the corner angle seems to have to be more salient (e.g. an acute corner) to fully dominate the wall length geometric cue.

2.2.2. How do local corner angle cues interact with local feature panel cues?

In a series of experiments, Marcia Spetch et al. compared the relative use of corner angle with a feature panel in human adults and pigeons (Lubyk et al., 2013). The reorientation apparatus was either a fully enclosed diamond or an array of corner angle posts that would make a diamond if one mentally connected the corners, but in the end, results were comparable for each apparatus. Each of the opposite corner angles was set to pairs of 60 or 120 ° and the correct corner was marked with a blue feature panel. Both pigeons and people had encoded the corner angles as well as the feature cue. However, on conflict tests, slight difference emerged. For people, there was a sex-difference. The women relied more heavily on the feature cue while the men divided their searches between the geometric and feature choices. In contrast, for piegons, sex-differences were not found. Rather, the salience of the corner angle influenced responding. At the acute corner (high salience), pigeons relied on the local corner angle in conflict situations, while a more even reliance on the local geometric and feature cue was observed for the obtuse (low salience) corners. Thus, in line with adaptive combination theory, cue salience appears to alter reorientation strategy.

2.2.3. How do global wall length, local corner angle, and a feature panel interact to support reorientation?

Recently, my colleagues and I designed a real-world experiment with human adults to look at cue integration of feature and geometric cues (Twyman et al., 2018). The reorientation space was a fully enclosed trapezoid. Participants started facing a certain direction, were disoriented, and then asked to return to their initial heading. There were two geometric cues to guide reorientation (wall length and corner angle) and one feature cue that was a 2D narrow floor-to-ceiling feature stripe along one of the walls. The relative use of the feature cue depended in part on the salience of the local geometric cue. When participants started in a location near an acute corner (high salience), they were more likely to rely on the geometric cues. In contrast, if they had started near an obtuse corner (low salience), they were more likely to return to a heading direction that integrated feature and geometric cues Thus, in this reorientation task, human adults behave quite similarly to Lubyk et al.'s pigeons. When corner angle and feature panels are both available, the salience of the corner angle influences the relative dependence on geometric and feature cues for successful reorientation. Furthermore, since this experimental procedure examines heading direction directly, it is strong evidence that feature cues do in fact support reorientation for human adults (problematic for the two-step account). Future research will be needed to determine if this is the case for children and non-human animals.

2.2.4. Summary of corner angle as a local geometric cue

Despite only occupying a small portion of the room, the local geometric cue of corner angle is a powerful reorientation cue for people, pigeons, and chicks. In the presence of either physical (an enclosure) or imputed (an array) wall length geometric cues, the corner angle is often relied on more heavily by pigeons and people. For chicks, the salience of the corner angle influences its relative use in combination with wall length. For the more salient angles, local cues are weighted more heavily (acute angles), whereas for less salient angles (obtuse), the wall lengths are weighted more heavily. When local geometric (an angle) and a local feature cue (a panel) can both support reorientation, both cues are encoded and support reorientation. Their relative dependence fluctuates depending on the species, the sex, and the salience of the local geometric cue (acute vs. obtuse). Despite a corner angles tiny size, it is an influential reorientation cue.

3. Short- and long-term environmental effects on reorientation strategy

3.1. Long-term environmental effects on reorientation

Rats rely heavily on geometric cues for reorientation (Cheng, 1986; Batty et al., 2009b). Along with other researchers in the field, Spetch wondered if this might be in part due to the upbringing of the lab rats. Typical laboratory rats are often raised in geometrically rich environments with lots of rectangles (the enclosure), triangles (nest boxes), and corner angles. The feature environment in quite impoverished by contrast, nothing like the rich smells, tastes, and odors of the natural world. Thus, could the reliance of rats on geometric cues be an artifact of an upbringing in a geometrically rich environment? Spetch sought to answer this question through several studies with different species. The first was to examine the reorientation behavior of mountain chickadees that had been caught from the wild. The chickadees were placed in rectangular training arenas with a blue feature wall. After the birds had learned the task, the chickadees revealed on the follow-up tests that the feature had overshadowed the geometric cue, a rare finding in the reorientation literature. Thus, it seemed, at least initially, that rearing conditions might have a huge impact on reorientation behavior (Batty et al., 2009a). A few years later, with a few tweaks to the reorientation procedure, Spetch and her collaborators again compared the performance of wild-caught mountain chickadees with wild-caught and laboratory-reared black-capped chickadees. Remarkably, there were slight differences in reorientation even for animals that shared the same genus (*Poecile*), albeit of different species (*atricapillus* for the black-capped and *gambeli* for the mountain chickadees). All of the black-capped chickadees demonstrated that they had encoded the geometry of the rectangle on the task, even when not required, and by contrast, some, but not all, of the mountain chickadees had encoded the geometry as well. Thus, the overall findings for wild-caught mountain chickadees suggests that although the effect might not be quite as strong as first thought, the feature-rich rearing of the natural world does seem to increase dependence on feature cues while decreasing reliance on geometric cues. And perhaps most surprisingly of all, that there are difference within a genus since geometry was a less preferred cue for the mountain chickadees than the black capped chickadees (Batty et al., 2009a).

As a complementary line of investigation, Marcia Spetch extended the wild-caught experiences question into a controlled rearing experiment with convict cichlid fish (Brown et al., 2007). In this investigation, fish were housed in either a rectangular or a circular tank from their first days of life for a period of four months. After rearing, training commenced in a rectangular arena with a feature cue, followed by post-training tests that investigated which cues were used for reorientation. The fish showed remarkable sensitivity to their rearing environment, especially if you consider that the rearing enclosures are still quite sparse compared to the natural world. The circular reared fish were faster to acquire feature information. In incidental tests of geometry, the rectangular reared fish demonstrated increased accuracy compared to the circular reared fish. And, in conflict tests that pitted geometric and feature cues against each other, the circular reared fish increased their choices to the featurally correct corner compared to the rectangular reared fish. Thus, it seems that in controlled rearing experiments, at least for convict cichlids, the rearing environment alters their relative use of geometric and feature cues. My colleagues and I conducted a similar rearing experiment with mice and additionally asked the question if a subject had to be exposed to the different environments during development, or if merely spending an extended period in the enclosure might change the reorientation strategies of adult subjects (Twyman et al., 2013). Specifically, we randomly assigned young (from birth) and adult (sexually mature) mice to be housed in either a geometrically rich (rectangle enclosure with a triangular nest box) or a featurally rich (circular enclosure with a blue wall on half of the enclosure, circular nest box) for a period of two months. Perhaps not surprisingly, the reorientation strategies of mice were altered by their home environments, and this was more strongly the case for the young mice than the adult mice. For the young mice, like convict cichlids, the circular reared mice were faster to acquire the feature task. Similar to the mountain-chickadee wild-caught experiments (Gray et al., 2005, 2009a,b), the young mice reared in the circular environment failed to encode the geometry of the room if it was not explicitly required for the task (failed incidental encoding of geometry test). The adult mice who had been housed in the circular enclosures for two months also failed incidental geometry tests, which may suggest that environmental experiences, even later in life, may shift our reorientation strategies. Taken together, it appears that convict cichlids and mice are sensitive to long-term environmental conditions.

There have been a few other rearing experiments worth mentioning with domestic chicks (Chiandetti and Vallortigara, 2008, 2010; Vallortigara et al., 2009) and with redtail splitfins (Sovrano and Chiandetti, 2017). In the experiments with chicks, no differences were found between the circular and rectangular housed chicks, yet the birds were only housed in their environments for 72 h before testing began on the juvenile subject, so it is difficult to determine if there would be rearing effects with chicks had they been raised for longer periods of time and tested as sexually mature chickens. In the experiment with redtail split fins, the fish were raised either individually (for 1 week or 1 month) or in a group (for 1, 5, or 10 months) and in either circular or rectangular tanks before testing. In the individually housed condition, there was an advantage for the rectangular reared fish on use of geometric cues, and this effect was not present at 1-week, suggesting that an extended period of time in the rearing environment is required before differences between the rearing groups are observed. Another interesting finding from the study was that as fish matured, they became faster at the task until 5 months of age. This is somewhat surprising considering that redtail splitfins are a precocious species that are developed enough to be free swimming at birth and receive relatively little parental care. There are oddities in the conflict tests that make it difficult to interpret the results of the rest of the experiments.

In conclusion, Spetch's wild-caught experiments with mountain chickadees and rearing experiment with convict cichlids have demonstrated that spending extended periods of times in altered or naturalistic environments changes reorientation behavior (Gray et al., 2005, 2009a,b; Brown et al., 2007). And rearing experiments with mice suggests that reorientation is particularly malleable early in development, but still possible after sexual maturity (Twyman et al., 2013). This may or may not be the case for domestic chicks (Chiandetti and Vallortigara, 2008, 2010; Vallortigara et al., 2009) or redtail splitfins (Sovrano and Chiandetti, 2017), and future experiments can shed light on this issue. What is striking for me about the rearing versus the wild-caught experiments is how subtle the difference are between our rearing groups (a rectangle versus a circle) considering how rich the natural world is for spatial information. There are many colors, changing shadows, smells, sounds, etc. that are rich in their feature information. Yet rearing differences are observed for both convict cichlids and for mice. Thus, it appears that the housing environment, particularly early in life, can alter reorientation behavior. We now turn to short-term experience effects.

3.2. *Short-term environmental effects on reorientation*

Marcia Spetch's wild-caught and rearing experiments have demonstrated that reorientation can be altered through environmental input. Can experiences over much shorter time-periods also alter reorientation? A recent experiment with homing pigeons suggests that this might be the case, although with a few possible confounds, caution should be taken relying solely on this experiment. Melhorn and Rehkaemper (2017) compared reorientation in homing pigeons with and without navigation experience. Using a paradigm similar to Kelly and Spetch (2004b), the experiment was conducted with a 2D rectangle on a computer touchscreen and there were unique landmarks at each corner of the rectangle. Overall, homing pigeons preferred landmarks as a reorientation cue, not surprisingly considering the previous findings with pigeons (Kelly et al., 1998; Kelly and Spetch, 2004b). But navigation experience influenced the integration of geometric and feature cues. Those pigeons with extensive homing experience more readily combined the geometric and feature cues, while the naïve birds had difficulty doing so. Thus, for homing pigeons, navigation experience appears to influence how geometric and feature cues were combined. Let's now turn to an even shorter time frame than either rearing experiments or navigation experience, let's look at the effect of only a few trials. As mentioned in the first paragraph introducing the reorientation paradigm, even from the first studies with pigeons, Marcia Spetch and Debbie Kelly demonstrated that a few trials altered reorientation (Kelly et al., 1998). If pigeons are given training with feature and geometric cues, then the subjects relied solely on the feature cue on the conflict tests. However, if pigeons were given pre-training with geometry only, then pigeons subsequently relied on both geometric and feature cue in conflict tests. Thus, for pigeons, previous experience with geometric cues influences reorientation strategy. Debbie Kelly has extended this finding to mice, where even the order of testing altered reorientation (Leonard et al., 2018). Thus, at least for pigeons and mice, only a few trials worth of experience with the reliability of a feature cue can alter how feature and geometric cues are used for reorientation.

Together with our collaborator Alinda Friedman, Marcia Spetch and I studied the role of short-term experience in 4- and 5-year-old children (Twyman et al., 2007). Prior to our study, it was believed that children under the age of six could not use feature cues for reorientation (Hermer and Spelke, 1994; 1996). We decided to conduct a series of short-training experiments with children under the age of six, too young to be able to produce "left" and "right" spatial terms. In the first experiment, we gave children a training session in an equilateral triangle with 3 uniquely colored walls. In this enclosure, there were no useful geometric cues and therefore children practiced using landmarks for reorientation. In isolation, children readily used the feature wall color for reorientation and many children passed the training phase in the minimum three required trials. During testing in a rectangle (a geometric cue) with a yellow feature wall (the feature), children were easily able to reorient, returning to the correct corner in 71% of the trials (versus 25% chance).

Since our training worked so easily, we then wondered if the feature training had to take place in the absence of useful geometric cues (such as with an equilateral triangle) or if just a few more trials in the rectangular enclosure with the feature wall would be sufficient. Typically, four trials are given to children in reorientation experiments. Therefore, we just gave the standard four trials in the first block, followed by four more trials in the second block. Children's reorientation changed from the first to the second block of trials. In the first block, children seemed to be relying on the geometric cue, responding 50% of the time to the geometrically correct corner by the feature wall, and 40% of the time to the all-white rotationally equivalent corner. In the second block of trials, children could now also use the feature wall – they were distributing 73% of their choices to the correct location, and only 21% of responses to the other rotationally equivalent corner. As a control, we also administered two blocks of four trials each in an all-white rectangular room. In the first block of trials, as expected, children responded equally (44% and 33%) to the two geometrically correct corners. Surprisingly, in the second block of trials, children were now responding more often to one of the geometric corners than the other (56% versus 15%). Upon closer inspection, we found that there was a small gap in the fabric at the base of the short wall where participants had increased their responding to the correct corner. And once we fixed the gap, then suddenly children reverted back to an even distribution of responses between the two rotationally equivalent corners in both blocks of trials. So even though we had not planned for a gap in the fabric (my fault), it led to an interesting set of findings. In these experiments, we demonstrated that even before children acquire spatial language, they flexibly use feature and geometric cues for reorientation if only given a few trials of practice in either the absence (equilateral triangle) or presence (rectangle) of useful geometric cues. Furthermore, even small features such as a gap in the fabric can guide reorientation if given a few trials of practice (the gap wasn't used in the first block, but was in the second). This data with the gap in the fabric was used by Noam Miller in part to develop his non-modular associative model of reorientation (Miller and Shettleworth, 2007). And that in turn prompted Spetch and her collaborators to develop their own non-modular simple neural network model (a perceptron) that generated many of the traditional reorientation findings (Dawson et al., 2010).

Overall, the rearing and training experiments reviewed above have demonstrated that reorientation is an important system for mobile organisms. Depending on our long-term experiences either in the wild or in controlled laboratory settings, our reorientation system will adjust the relative dependence on feature and geometric cues. And yet, our system adapts much faster than that. In just a few trials, the relative use of reorientation cues is altered for piegons (Kelly et al., 1998), mice (Leonard et al., 2018) and children (Twyman et al., 2007).

4. A mouse is not a rat: Reorientation strategies differ across strikingly similar species

Marcia Spetch's research was truly comparative in nature. For reorientation experiments alone, Spetch examined pigeons, convict cichlids, mountain and black-capped chickadees, rats, children, and adults. And many of her experiments directly compared at least two species at a time with the same experimental procedure. This allows for stronger direct comparisons across species. Together with her collaborators and other scientists studying reorientation, we have an enviably rich knowledge of reorientation across a wide-range of species. Below, I will discuss some of the similarities and differences across the animal kingdom.

4.1. Mammals

In the first reorientation experiment, Ken Cheng (1986) discovered that rats rely on geometric cues for reorientation in working memory versions of the task. This finding has sparked an intense theoretical debate surrounding the role of features for reorientation (for a review, see Twyman and Newcombe, 2010). What is interesting is that geometric cues appear to be quite salient for rats, even if the rats are still oriented (Batty et al., 2009a). By contrast, for mice, a species that fills a more similar ecological niche compared to many others used for the study of reorientation, features appear to be much more important. We know a little bit more about reorientation across the life cycle of the mouse than the rat. Early in life, mice more readily reorient via feature cues (Twyman et al., 2013), and as adults mice can use both geometric and feature cues for reorientation (Twyman et al., 2013; Fellini et al., 2006; Leonard et al., 2018), and as mice age, they become unable to use geometric cues (Fellini et al.). We are also starting to know more about reorientation across the lifespan of humans. As reviewed above, in childhood there is substantial growth and development in the use of both geometric and feature cues from initial use at 18–24 months to flexible proficiency integrating these cues as adults, generally speaking (Twyman et al., 2007). As people age, there is some deterioration in the use of distal feature cues at 70-years-of-age, and by 80-years-of-age, geometry is no longer encoded, just like for elderly mice (Siemens, 2017). At least for mammals, it would appear that mice and people are more similar in the reorientation behavior than rats and people, and perhaps even more similar than even mice and rats! It is interesting to speculate how the reorientation literature would look today if Ken Cheng had first picked up a mouse rather than a rat for our field's first study of reorientation.

4.2. Birds

There is variability in how likely birds are to use geometry to reorient. Most species can use both features and geometric cues. Pigeons have shown us repeatedly, that they are sensitive to feature cues and often encode distal feature cues even when not required for the task (Cheng and Newcombe, 2005). By contrast, Clark's nutcrackers appear to be highly sensitive to geometric cues (Reichert and Kelly, 2015). And for chickadees, there are even differences for birds that share the same genus. Mountain chickadees readily use feature cues for reorientation and show reduced and inconsistent use of geometric cues. By contrast, black-capped chickadees quite readily use both geometric and feature cues for reorientation.

4.3. Are reorientation cues used in the same way?

Let's add another layer of complexity. Suppose a two different species both demonstrate that they can use a geometric cue to reorient. Are they necessarily using the geometric cue in the same way? This issue was raised in a pair of studies by Barbara Landau and her colleagues on reorientation in children and adults with Williams syndrome. Initial studies asked if these individuals could use feature and geometric cues. And then, as we will discuss shortly, asked if they are used in the same way as typically developing individuals. For individuals with Williams syndrome, they are missing a small set of genes, 26 genes are deleted from chromosome 7q11.23, that results in profiles of strengths and weaknesses. They are often mild or moderately intellectually delayed, have quite proficient verbal skills, and often sever spatial impairments. Adults with Williams syndrome often perform on spatial tasks at the ability of a 4- to 6-year-old child. Initial reports of reorientation suggested that geometric processing was impaired for individuals with Williams syndrome (Lakusta et al., 2010). When participants were oriented but had to close their eyes and wait to search for a toy, they were able to find the toy correctly 92% of the time. As soon as participants were disoriented, they were only able to go to a geometrically correct corner 52% of the time (versus 50% chance) in a rectangle, but could return to the correct corner 52% of the time (versus 25% chance) if a feature wall was added to the rectangle. Thus, it initially appeared that the feature system was spared and geometric processing for reorientation was impaired by the deletion of one, several, or all of these 26 genes on chromosome 7. However, a more recent study in the same lab group demonstrated that this might not actually be the case. The reorientation room was all black, poorly lit, and participants searched behind fabric flaps that blocked off the room corners. The initial study also suggested some sensitivity to geometry, since in the feature condition, participant had distributed more of the errors to the geometrically correct corner than the other two geometrically incorrect corners. With these slight tweaks to the paradigm, it was found that individuals with Williams Syndrome could in fact use geometry to reorient, and if anything feature or cue combination processes might be impaired (Ferrara and Landau, 2015).

These authors wondered if the gene deletion might act more subtly. Specifically, would typically developing children and adults use feature and geometric cues any differently than children and adults with William's syndrome? They were able to answer this question by using the methods of Huttenlocher et al. In a reorientation task, experimenters watched not just which corners were selected, but how participants behaved between opening their eyes and moving to a corner. Rather than looking around with the head or torso, children headed directly to the target corner, or "bee-lined" there (Huttenlocher and Vasilyeva, 2003; Lourenco and Huttenlocher, 2006). This supported their claim that the global shape of the room guided reorientation. A similar procedure was followed in the currently discussed studies to observe how participants approached a target – direct or meandering? The geometric cue appeared to be used quite similarly for both typically developing children and those with Williams syndrome. Proficiency with the geometric cue didn't seem to change through development and participants headed directly to the geometric corners. In contrast, there were some observed differences for the use of feature cues to reorient. All children were able to use the feature cue. But for children with William's syndrome, feature use improved as the child's age increased. Typically developing children and adults head directly for the correct corner. While for children and adults with Williams syndrome, they take a meandering route before eventually picking the correct corner at above chance levels. Thus, at least for features, it seems that people in general are able to use features for reorientation. But individuals with Williams syndrome may be using the cue in a different way such as trying to image-match rather than a global representation of space like the typically developing participants. Do these animals, who both rely on geometry do so in the same way? Or for mice, pigeons and mountain chickadees who are proficient feature reorienters, do they rely on the feature cue in the same way?

5. How Marcia Spetch's research changed reorientation research

From the first few studies of reorientation in the late 1980s and early 1990s, it seemed like it was going to be easy to answer the question "how do we regain our bearings after we have become disoriented, how do we get our compass back?" Initially, it seemed as though children and non-human animals were able to do so by extracting the geometric properties of extended surfaces and then as adults, we were able to add feature information into our orienting system (Hermer and Spelke, 1994; 1996). From Debbie Kelly and Marcia Spetch's first study of reorientation with pigeons (Kelly et al., 1998), we learned that the story wasn't going to be quite that neat and tidy. Pigeons heavily relied on feature cues for reorientation, but could flexibly increase their reliance on geometric cues if pigeons had prior experience with geometric cues. And since then, Spetch and her collaborators have shown us that the answer is much more complex and interesting than first imagined. Her research has shown us that the use of certain types of geometric cues is far richer than first imagined. Many aspects of geometry can support reorientation, including the use of relative wall length of extended surfaces (Kelly and Spetch, 2001), relative distances between objects (Mou et al., 2014), the height of extended surfaces (Du et al., 2016a,b), corner angles at the intersection of walls and corner angles of posts (Lubyk et al., 2013). She has shown us that the relative use of classes of geometric cues appears to change across reorientation contexts (Mou et al., 2014), cue classes, saliences, and species (Lubyk et al., 2013). She has also shown us that many species can use feature cues to reorient, and the relative dependence on these cues is altered my many factors, such as the species, the salience of the geometric and feature cue, the experience of the animal in the short- and long-term (Lubky et al., 2012, 2013; Lubyk and Spetch, 2012; Gray et al., 2005, 2009a,b; Brown et al., 2007; Twyman et al., 2007; Kelly and Spetch, 2001, 2004a,b; Kelly et al., 1998). And she asked these questions with a variety of types of animals so that we have a more complete understanding of how reorientation occurs across animal kingdom.

Such a rich diversity of findings has allowed several theoretical models of reorientation, a more formal answer to the question "how do we reorient" to flourish. The original modularity claim has been through several iterations over the decades, and is still an influential theory today (Lee, 2017; Ferrara and Landau, 2015; Julian et al., 2018). As reviewed elsewhere (Twyman and Newcombe, 2010), there have been several alternative proposals to explain reorientation, including: a) the use of the principal axes or medial axis of space to determine heading; b) an image matching account were subjects compare a visual snapshot of the current and target location and minimize in a direction to minimize the discrepancy between the two; c) associative learning models of reorientation; d) a perceptron simple neural network model or reorientation; and e) adaptive combination theory. Each of these positions has been challenged by the results of Spetch's experiment and our theories and models are stronger because of it. I'm incredibly indebted to Spetch and her data to support and refine adaptive combination theory. The theory was first proposed by Newcombe and Huttenlocher (2006) and suggested that potentially any cue in the environment can be used to support reorientation, but the relative use of a cue will depend on factors such as a priori bias for certain species, the type of rearing environment, short-term experiences with cue salience, cue reliability, and success. As you will have noticed, these are many of the questions posed by Spetch and her collaborators, and without her data, the foundational empirical support for adaptive combination theory would not exist. Regardless of one's theoretical position, Marcia Spetch's research in the area of reorientation has changed our understanding of the phenomenon, and we are grateful for the rich understanding of reorientation that she has given us across a wide-range of species.

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