COGNITIVE SCIENCE
A Multidisciplinary Journal

Cognitive Science 42 (2018, Suppl. 3) 923–936

ISSN: 0364-0213 print / 1551-6709 online
DOI: 10.1111/cogs.12575

First Direct Evidence of Cue Integration in Reorientation: A New Paradigm

Alexandra D. Twyman,[1] Mark P. Holden,[1] Nora S. Newcombe

Department of Psychology, Temple University

Received 6 August 2015; received in revised form 7 September 2017; accepted 25 September 2017

Abstract

There are several models of the use of geometric and feature cues in reorientation (Cheng, Huttenlocher, & Newcombe, 2013). The adaptive combination approach posits that people integrate cues with weights that depend on cue salience and learning, or, when discrepancies are large, they choose between cues based on these variables (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Newcombe & Huttenlocher, 2006). In a new paradigm designed to evaluate integration and choice, disoriented participants attempted to return to a heading direction, in a trapezoidal enclosure in which feature and geometric cues both unambiguously specified a heading, but later the feature was moved. With discrepancies greater than 90 degrees, participants choose geometry. With smaller discrepancies, integration appeared in three of five situations; otherwise, participants used geometry alone. Variation depended on direction of feature movement and whether the nearest corner was acute or obtuse. The results have implications for contrasting adaptive combination and modularity theory, and for future research, offering a new paradigm for reorientation research, and for testing cue integration more broadly.

Keywords: Geometric module; Adaptive combination; Spatial orientation; Reorientation; Integration; Spatial memory

1. Introduction

The spatial world is rich in cues to where things are and how to navigate, including both information deriving from internal cues (e.g., proprioception or kinesthesis) and information deriving from the external world (e.g., landmarks, geometric boundaries, and gradients). One area of controversy in spatial cognition research has concerned the use of two classes of external cues, geometry and features, in cases where organisms are

Correspondence should be sent to Alexandra D. Twyman, Department of Psychology, Temple University, Weiss Hall 1701 North 13th Street, Philadelphia, PA. E-mail: atwyman2@unl.edu

[1]Presently at the University of Nebraska-Lincoln, 1400 R Street, Lincoln, NE 68588.

disoriented and internally generated spatial cues are not useful. Two competing theoretical perspectives are modularity and adaptive combination accounts of how reorientation occurs. In modularity accounts, only geometric information guides reorientation. In adaptive combination theories, both geometric and/or feature cues can be used to guide search, depending on factors such as cue salience and individual learning history. Furthermore, they can be integrated depending on these factors.

In the first study of spatial orientation, Cheng (1986) found that rats failed to use feature cues (such as color, odor, or number of lights) and instead relied on the geometric configuration of the room (e.g., long wall on left), which only led to a food reward half of the time. To explain this suboptimal behavior, Gallistel (1990) argued that ignoring features and relying on geometry (i.e., using a geometric module) might be adaptive because the features of the environment (e.g., shadows or leaf color) are more likely to change than the geometry. Indeed, when humans were tested, there were parallels between the behavior of rats and young children (Hermer & Spelke, 1994, 1996). When toddlers performed the reorientation task in a small room with three white walls and one red wall, the children completely ignored the salient feature and searched instead equally often in the two geometrically equivalent corners (corners across the diagonal of the room). Around 6 years of age, when children start producing the terms “left” and “right,” they became able to reorient and return to the correct corner (Hermer-Vasquez, Moffet, & Munkholm, 2001). Thus, Hermer-Vazquez, Spelke, and Katsnelson (1999) argued that young children share a geometric module for reorientation with other non-human species that later becomes punctured by spatial language. While this was an intriguing account of the development of the reorientation system, and an interesting view of reorientation across species, there have been numerous empirical findings that cast doubt on this explanation (see Twyman & Newcombe, 2010, for a review of the developmental findings), and some have gone as far as to suggest abandoning the modularity approach (Cheng, 2008). As such, new theories and models of the reorientation data have emerged to explain the expanding dataset (reviewed by Cheng et al., 2013), as have new variations of the modularity position, including a two-step revision suggested by Lee and Spelke (2010b).

The two-step modularity account of reorientation arose from data demonstrating that children easily used extended surfaces to reorient, but they could not use surface features on the boundaries or objects inside the search spaces to reorient. More specifically, children were asked to find stickers hidden within columns or boxes within cylindrical rooms. In the first experiment, young children retrieved stickers from an equilateral triangular array of hiding locations, with one unique (red) and two identical (blue) goal boxes following disorientation (Lee, Shusterman, & Spelke, 2006). When the sticker was hidden in the unique box, children were able to retrieve the target. In contrast, when the sticker was hidden in an ambiguous (blue) container, the children divided their searches between the two blue containers. In theory, if features were used for reorientation, then children should have been able to use the unique red box to reorient, which they failed to do. The authors interpreted these data to suggest that features could guide search for a hidden object, but not for reorientation. In a second series of experiments, children searched for stickers hidden in columns that varied in their location (adjacent to the room boundary or inside the search space) and their dimensions (2D or 3D) (Lee & Spelke, 2010a). Children retrieved the stickers when the columns were 3D and abutting the room walls, but not when the columns were 2D flush with the wall or 3D inside the space. Based on the findings reviewed above, Lee and Spelke (2010b) suggest a two-step modularity claim. "We propose, following Cheng and Gallistel's original theory, that human and animals navigate by: (a) an automatic process for analyzing the shape of the extended surface layout (b) an attention-dependent process for locating objects relative to perceptible nearby beacons" (p. 182). This two-step account of reorientation is the most extreme modularity position to date in the reorientation literature. In the modularity-plus-language position from the 1990s, adults were argued to have developed a more sophisticated integrated representation of space (compared to non-human animals and young children), which was achieved through the production of spatial language. In the current modularity account, all species, regardless of age, first reorient based exclusively by the geometry of the space. And then in a second separate step, participants can then use features and other cues to find a goal location. As we will explain next, this interpretation could account for almost all feature use in the reorientation literature as part of the goal-finding system.

There are many alternative models and explanations of reorientation data, including adaptive combination theory proposed by Newcombe and Huttenlocher (2006), instantiated recently in a computational model of the human reorientation data (Xu, Regier, & Newcombe, 2017). From this perspective, multiple sources of information are combined in memory to guide optimal behavior, including for spatial reorientation tasks. Each relevant environmental cue is assigned a given weight that depends on salience (which affects cue reliability) and learning (which determines the validity of the cue, as well as potentially affecting reliability of encoding). And then these weights are used to guide optimal behavior, such as spatial reorientation. One of the strengths of this approach is that the system is flexible and can account for many of the complex facts of reorientation, to which we will now turn. Geometry is more likely to be used in small spaces and features more likely to be used in large spaces, for children (Learmonth, Newcombe, Sheridan, & Jones, 2008), adults (Ratliff & Newcombe, 2008), fish (Sovrano, Bisazza, & Vallortigara, 2007), chicks (Chiandetti, Regolin, Sovrano, & Vallortigara, 2007; Sovrano & Vallortigara, 2006; Vallortigara, Feruglio, & Sovrano, 2005), and pigeons (Kelly, Spetch, & Heth, 1998). Additionally, short-term experience with a feature cue changes the behavior of young children (Twyman, Friedman, & Spetch, 2007), human adults (Ratliff & Newcombe, 2008), and pigeons (Kelly & Spetch, 2004). And rearing environment changes weighting of geometry and features, at least for some species, including convict fish (Brown, Spetch, & Hurd, 2007) and mice (Twyman, Newcombe, & Gould, 2013), although perhaps not chicks (Chiandetti & Vallortigara, 2008, 2010). Adaptive combination theory has been able to explain and predict these empirical research findings. However, there has yet to be direct evidence for the integration of geometric and feature cues in spatial memory. Existing work has evaluated choice between features and geometry in cases where conflict is compelled by the use of distinct hiding locations (e.g., Ratliff & Newcombe, 2008), but due to limitations with the traditional reorientation paradigm, we have been unable to directly answer the question of integration.

This paper aims to address this gap by testing for integration of feature and geometric cues using a new reorientation paradigm, adapted from a suggestion made by Cheng and Newcombe (2005). There are two key aspects to the new paradigm that allow for detection of integration, if it occurs. First, participants no longer select from discrete hiding locations, but rather start at a given head direction, are disoriented, and then are asked to return to their original starting position. Thus, participants can respond at an intermediate location between the two cues. Second, the search environment has been constructed so that geometric and feature cues both unambiguously specify a heading direction, making these cues comparable. Rather than the traditional rectangle (where there are two geometrically equivalent corners), the search space was a geometrically unambiguous trapezoid. Both humans (Sturzl, Gurley, & Bodily, 2011) and pigeons (Nardi & Bingman, 2009a,b; Nardi, Nitsch, & Bingman, 2010) have been shown to use the geometry of this shape for reorientation. Additionally, the paradigm used in this experiment is also important for evaluating the role of features in reorientation. In the traditional reorientation paradigm, there is a reorientation and a search component to the task. Therefore, the two-step account of spatial reorientation (Lee & Spelke, 2010b) can attribute any and all instances of feature use to the search for a target process, rather than for reorientation.

With our new paradigm, there is no longer a search component to the task. And therefore, if any evidence is found for feature use, it must be attributed to the reorientation system. Participants are first given practice during training starting a set heading direction, being disoriented, and then asking to return to the start direction. After training with the stable feature and geometric cues, we tested participants in four different situations in which the feature was moved: (1) a small distance toward the nearest corner, (2) a small distance away from the nearest corner, (3) a medium distance away from the nearest corner, and (4) a large distance onto a novel wall. Since the response space is a continuous area, participants can make a response based on the feature or geometric cue in isolation, or they can respond at an intermediate position between the positions suggested by the two cues. Adaptive combination theory predicts that participants will integrate geometric and feature cues (shown by searches at an intermediate position between the positions specified by the geometric and feature cues) in cases where the choices are not in stark opposition. When there is a large discrepancy between feature and geometric cues, participants should choose between the conflicting cues (Cheng et al., 2007). We speculated that the switch from integration to choice might occur at 90 degrees, based on Ratliff and Newcombe (2008) and also on data on combining or choosing between landmarks and dead reckoning (Zhao & Warren, 2015).

Additionally, the adaptive combination model of spatial cognition predicts that participants will balance the relative weights of potential cues based on their salience. The use of the trapezoid search space is particularly well suited to test this aspect of adaptive combination theory because there are acute and obtuse corners, which, based on previous research, vary in salience. To elaborate, in a reorientation experiment with domestic chicks, subjects were trained to find food at either an acute or an obtuse corner of a parallelogram. When tested in a rhombus, chicks had encoded the acute and obtuse corners. Interestingly, when tested with a mirror image of the training parallelogram, which pits the corner type (acute or obtuse) with trained wall length (e.g., left of the long wall), differences were found for each corner. Chicks that had been trained with an acute corner selected the acute corner in the mirror image test, while chicks that had been trained with an obtuse corner selected the corner that matched the wall length with training. Thus, for chicks, acute corners are more salient than obtuse corners (Tommasi & Polli, 2004). Similar results were found with rats in a water maze task. A discrete landmark overshadowed geometric information at an obtuse corner of a rhombus, but not at the acute corners. Thus, for rats, acute corners appear to be a more salient geometric cue than obtuse ones (Kosaki, Austen, & McGregor, 2013). Similar results are found with people in a reorientation experiment comparing global and local geometric cue use. Participants were asked to reorient within a rectangular array of corner posts (the overall shape provided a global geometric cue). The corner posts were hinges that could be set to either 50° or 75°. In conflict tests pitting the local (corner angle) and global (rectangular shape) cues against each other, the local cue was selected for the 50° condition, but not the 75° condition. Thus, in reorientation experiments with people, smaller corner angles are more salient than wider corner angles (Reichert & Kelly, 2011). In the present research, the trapezoidal search space contains two acute and two obtuse corners that vary in their geometric salience. Thus, according to the adaptive combination model, we predict that the corner angle (a geometric cue) will be more heavily weighted in conditions of high geometric salience (acute corner) than at a lower salience (obtuse) corner.

2. Methods

2.1. Participants

Participants were 43 women and 40 men. An additional 10 participants were excluded, 2 due to technical error and 8 for failing to attend to the task (defined as more than three standard deviations below the mean accuracy score on the six training trials). Remaining participants were an average of 20.71 (SD = 2.50) years of age and ranged between 18 to 38 years old. Participants were randomly assigned to one of four conditions, defined by location of the target direction with respect to the two acute (high geometric salience) corners and the two obtuse (low geometric salience) corners (see Trained Heading Direction below). The sample was ethnically diverse: 61% Caucasian, 16% African American, 7% Hispanic, 5% Asian, 2% Indian, and 8% Other. The Institutional Review Board approved all procedures.

2.2. Apparatus

The key components of the apparatus are highlighted in Fig. 1. The enclosure was a trapezoidal room with an area of 9.57 m^2 (103 sq. ft.). The short wall was 2.13 m (7 ft.) long, the two diagonal walls were 3.20 m (10.5 ft.) long, and the long wall was 4.27 m (14 ft.) long. The angles of the obtuse and acute corners were 110° and 70°, respectively.

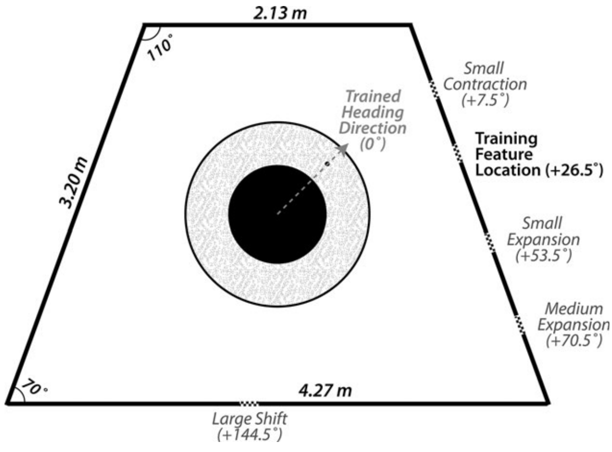

Fig. 1. An overview of the reorientation enclosure and the location of the feature cue for each of the test trial types. The feature cue was mounted flush onto the studs of the apparatus.

One of the diagonal walls of the enclosure pivoted and opened at an obtuse corner to serve as a door. This wall was secured from the outside of the space with clamps so that all of the corners were identical in appearance when it was closed. The walls were covered with a uniform light pink canvas and the ceiling was a uniform orange cotton-spandex blend. The floor of the enclosure was covered with a uniform gray carpet. The feature was a black and white checkerboard patterned strip of laminated paper mounted flush with the enclosure wall. The feature strip spanned the height of the enclosure (221 cm or 87 in.) and was 15.24 cm (6 in.) wide.

The response area was a centrally placed inflatable swimming pool with a circumference of 180 inches (457.2 cm) and a height of 11.5 inches (20.21 cm). The pool was inflated and filled with sand to a depth of 2 inches (5.08 cm). A table top painted uniform black, 30 inches (76.2 cm) in diameter, was placed in the middle of the sand. Thus, there was a narrow channel of sand surrounding the platform where the participants stood; it served as the response area. A flexible measuring tape was fixed to the outer wall of the swimming pool. The measuring tape was visible to the experimenter from the outside of the space, but not to participants standing on the platform. The external lights were extinguished and the enclosure was illuminated from the interior with four small (11.11 cm (4 3/8 inches) wide × 12.7 cm (5 inches) high) 35 watt lamps on the floor, one in each corner of the room.

2.3. Design and procedures

Once participants provided informed consent, they were led into the enclosure with the feature strip already mounted in the randomly assigned training location (described below) and asked to stand on the table top in the middle of the pool. They were shown two spikes, one of which had already been placed in the sand. Participants started in line with this spike and were given the second spike to hold. Participants were disoriented by spinning in a circle with their eyes closed in both directions and at variable speeds on a cue from the experimenter. During this time, the experimenter removed the original spike from the sand and obscured any cues. After disorientation, participants were invited to open their eyes and return to the initial heading direction. Participants were asked to place their spike in the response area and the experimenter took a photograph of where the spike had been placed. Participants were not given feedback.

To ensure that participants were truly disoriented before responding, each trial contained a disorientation check. Before spinning, participants were asked to remember a particular light that changed on every trial. Once the disorientation procedure was completed, participants were asked to stop with their eyes closed and to point to the light. Participants were rarely correct, but when they were, the disorientation process was repeated.

Participants were given six training trials in all, beginning with a block of four training trials, followed by two test trials, and then two further training trials (to refresh participants' memory for the correct heading direction) and the final two test trials. After the initial four training trials were completed, and before each test trial, participants were asked to leave the trapezoid and to perform a different task. This allowed a second experimenter to return to the trapezoid enclosure and covertly move the location of the feature strip.

2.3.1. *Trained heading direction*

Participants were randomly assigned to one of four training conditions, approximately corresponding to each of the corners of the room. In each condition, the correct heading direction (defined as 0°) was located along a diagonal wall with the nearest corner 9.5° in one direction (i.e., left/right) and the feature panel placed 26.5° away from the correct heading in the other direction. In order to compare across different trials, the feature direction was always defined as a positive value (e.g., +26.5°), and the corner direction remained constant at −9.5°.

2.3.2. *Test trial types*

All participants were given four types of test trials, as shown in Fig. 1. For the small contraction test, the feature moved a small distance toward the trained heading direction. In each of the other test trials, the feature moved a small, medium, or large distance away from the trained heading (moving away from +26.5°). Almost all of the shifts were within the diagonal wall where the feature was located during training, except for the large expansion where the feature moved to a new wall. The precise location of the feature for each of the test trial types can be found in Table 1. The order of test trials was largely fixed, so that each test trial type would not contaminate the subsequent tests. That is, we predicted that if the shift was large enough, participants would notice the discrepancy and choose between the cues. We therefore fixed the order to proceed from the smallest to the largest shift. However, as there were two small shifts either toward or away from the trained heading, we randomized the order of these trials.

Table 1
The direction and magnitude of the shift of the feature for each of the test trial types

Trial Type	Training Location	Magnitude of Shift	Testing Location
Small contraction	+26.5°	−19°	+7.5°
Small expansion	+26.5°	+27°	+53.5°
Medium expansion	+26.5°	+44°	+70.5°
Large shift	+26.5°	+118°	+144.5°

Note. Shifts in the direction of the trained heading are represented by negative shift values and shifts moving farther away are represented with positive shift values. The magnitude of the shift in small contraction and expansion was determined by where the studs were located on the outside of the experimental apparatus so that the feature panel could be mounted flush with the wall.

3. Results

3.1. Data analysis

The trained heading direction was defined as 0°, and all of the data were coded in relation to this point. Since the data are collected on a circle, it is not appropriate to analyze the data with linear statistics. To illustrate, the mean of headings at 359° and 1° is clearly 0°, but the linear mean would be 180°. Rather, the data were analyzed with circular statistics. Specifically, we employed one-sample tests for the mean angle—which is analogous to a one-sample *t*-test for linear data (Zar, 2010). Similarly, we used the Watson-Williams test—which is equivalent to a two-sample *t*-test—to compare across corner angle types (i.e., acute vs. obtuse) and to compare across the sexes.

3.2. Training trials (Corner = −9.5°, Trained head direction = 0°, Feature = +26.5°)

During the six training trials, participants started facing a set heading direction (set to 0° for all participants), were disoriented, and then were asked to return to the original heading direction (0°). Responses for each of the six training trials are found below in Fig. 2. There was far more uncertainty in the heading direction on trial 1 (average of +4.80°), but accuracy quickly improved, with an average error of +0.61° for the remaining five training trials. Thus, participants' responses for these five trials did not significantly differ from the correct training heading of 0°, 95% CI [−1.36°, 2.57°], *ns*. There were no effects of sex or corner angle type on training bias, all $F(1, 81) < 1.1$, *ns*.

3.3. Test trials

During each of the test trials, the feature moved to a new position along the wall(s) of the enclosure. When the feature moved closer to the trained heading direction, the shift was coded as negative (−) and when the feature moved further away from the trained heading direction, the shift was coded as positive (+). The location of the feature during training and test trials is shown in Fig. 1.

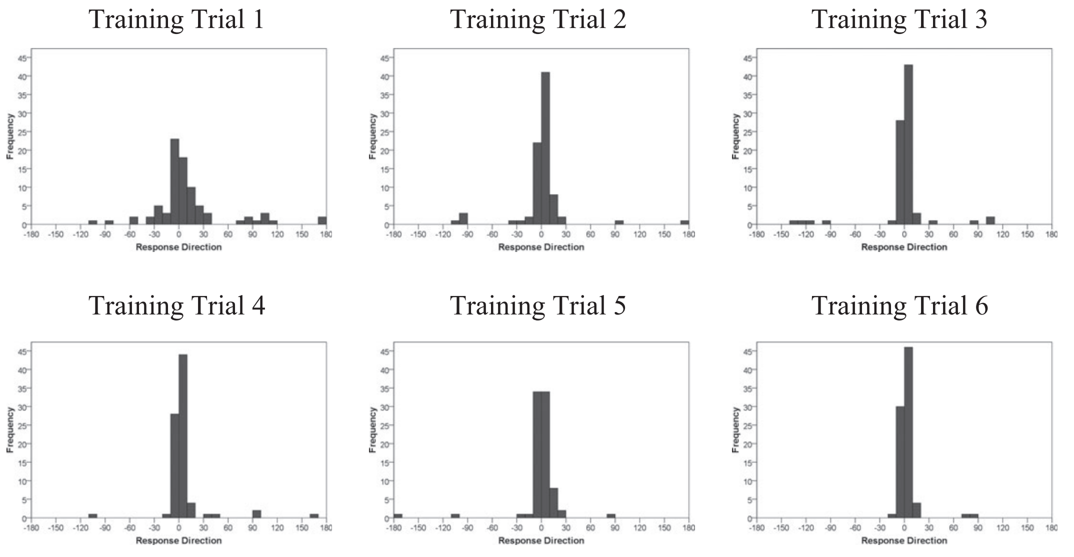

Fig. 2. Distribution of responses for the each of the six training trials.

3.3.1. *Small contraction (feature shifts −19°)*

Participants returned to the trained head direction and their responses did not differ significantly from 0°, M = +0.86°, 95% CI [−5.70, +7.42]. There were no effects of sex, corner angle type, or test order, all $F(1, 81) < 1$, *ns*.

3.3.2. *Small expansion (feature shifts +27°)*

Participant's responses depended on the corner angle type, $F(1, 81) = 5.83$, $p = .02$. When the trained heading direction was in the vicinity of a salient acute corner, participants continued to orient toward the trained direction, M = +2.60°, 95% CI [−4.08, +9.28]. However, when the trained heading direction was in the vicinity of a less salient, obtuse corner, participants oriented at an intermediate position between the geometric and feature positions, M = +12.92°, 95% CI [+7.48, +18.36], $p < .01$. There were no effects of sex or test trial order for either condition, all $F(1, 81) < 3.58$, *ns*.

3.3.3. *Medium expansion (feature shifts +44°)*

Participants oriented at an intermediate direction between the geometric and feature positions, M = +9.20°, 95% CI [+1.69, +16.70], $p = .02$. There were no effects of sex, corner angle type, or test order on the medium expansion test trials, all $F(1, 81) < 1$, *ns*.

3.3.4. *Large shift (feature shifts +118°, and onto a novel wall)*

Participants disregarded the shifted feature cue and oriented to the trained heading direction, M = +8.12°, 95% CI [−7.36, +23.61]. There were no effects of sex, corner angle type, or test order on the contraction test trials, all $F(1, 81) < 2.04$, *ns*.

To summarize the results, there were some cases when participants disregarded the new location of the feature and returned to the trained heading direction. In other instances, participants reoriented toward an intermediate direction between the geometric and feature cues. When this type of integration was observed, it was not the case that some participants used geometry and other participants used the feature to reorient. The 95% confidence intervals remained comparable in size when integration was and was not observed. Additionally, participants' responses are presented in Fig. 3, where there was no evidence of a bimodal or multimodal distribution.

4. Discussion

Since 1986, when Ken Cheng first demonstrated that hungry rats ignored feature cues that could have led to a food reward 100% of the time, and instead relied on a geometric cue that led to food only 50% of the time, there has been a great deal of empirical research on how organisms are able to regain their spatial position in the world following disorientation. This research is the basis for a vigorous debate concerning the organization of the mind: modular or integrated? Despite the theoretical importance of the debate, there has yet to be direct empirical evidence for integration of geometric and feature cues in a reorientation task, largely due to limitations of the method. The primary goal of the present research was to devise a new method that would allow us to observe cue

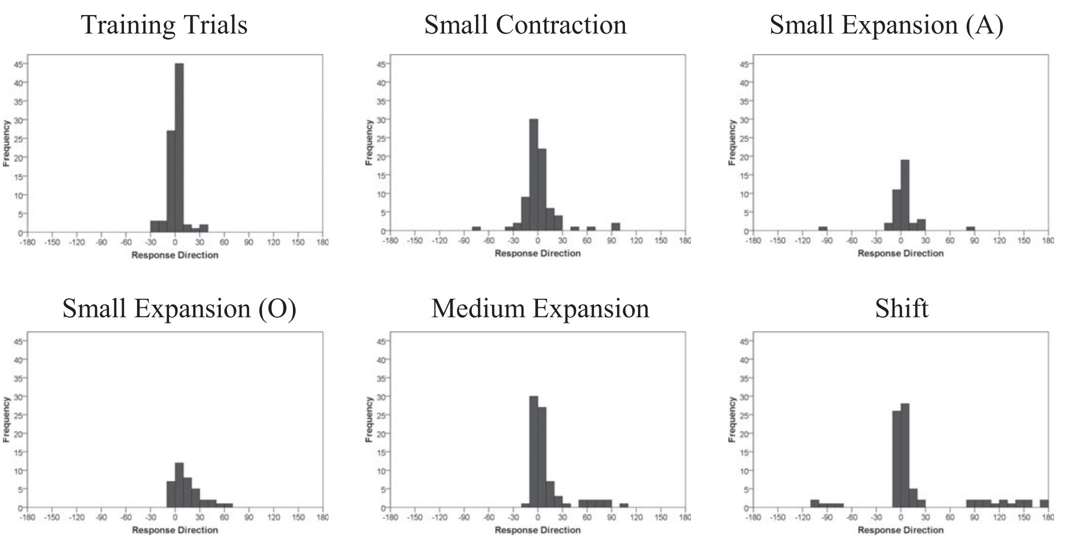

Fig. 3. Distribution of responses for the training trials (averaged across training trials 2–6) and each type of test trial. The data are collapsed across the acute (A) and obtuse (O) corners, except for the small expansion test where there were different response patters for each corner type.

integration, if in fact the mind is organized this way. In the standard paradigm, participants can respond to either a feature or geometric cue, but never at an intermediate position. This experiment used a continuous search space so that an integrated response was possible. In addition, the new paradigm consisted of a trapezoid-shaped room so that the feature and the geometry of the space both unambiguously specified a heading direction. Lastly, in the most recent version of modularity theory, the two-step account suggests that there are two components in reorientation experiments—a reorientation process guided exclusively by geometric cues and an object search process that can be guided by feature cues. Therefore, anytime features are used to solve a task, it is possible that the participant could have been using the feature cues in the object search component rather than the reorientation component. With our new paradigm, we have eliminated the object search part of the reorientation task. Thus, with our new paradigm, we found evidence of feature use; therefore, contrary to the two-step account of reorientation, 2D surface feature cues can be used by human adults to support successful reorientation. Next we will discuss the role of geometric cues, and evidence suggesting that geometric and feature cues are combined in spatial memory.

The findings from the novel paradigm support the importance of geometry, but not a modular account of how it is used. Geometry dominated when the feature moved a large distance onto a new wall, or a small distance toward a previously trained corner, or a small distance away from an acute corner. But in other cases, integration of geometry and features was observed. Neither the original modular account nor the Lee and Spelke (2010a,b) two-step revision predicts such a complex pattern. In the original modularity account, once language is acquired, adults should use feature and geometric cues all the time. For the two-step revision, adults should only use geometric cues. In both accounts, features are used in an all-or-none fashion. In contrast, variation is an essential aspect of the adaptive combination approach. First, with large movements of the feature, choice rather than integration is predicted by an adaptive combination account (Cheng et al., 2007). Second, in cases of smaller movements, where the nearest corner provides a marker against which to establish a heading direction, cue salience should influence integration. In our experiment, the corner angle varied in salience. For the acute corner, the angle is small and thus it is easier to pinpoint its exact direction in space. By contrast, the obtuse corner contains more uncertainty in direction since the obtuse corner is wider than the acute corner. When the feature moved toward a corner, or a small distance away from high salience geometric cues (acute corners), participants returned to a heading direction specified by the geometry of the room. When the feature moved a small distance away from low-salience geometric cues (obtuse corners), participants returned to an intermediate position between the geometric and feature cues. Third, in cases of larger movements, where precise head direction is likely less reliably coded in any case, then regardless of cue salience, participants responded at an integrated position between the geometric and feature cues and minimizing their overall errors. Thus, the data from the current project support the adaptive combination viewpoint.

This paradigm provides an avenue to address many remaining questions about integration and choice in reorientation. Clearly, future experiments could vary the heading directions, the corner angles, use more features than just one, and so forth, establishing better psychometrics and making more precise quantitative predictions. Such experiments might be easier to do in virtual reality, as long as consistent patterns of data are found across both real world and virtual reality settings. A particularly pressing need is to measure the accuracy and reliability of judgments based on the feature alone (i.e., a feature in a circle) and geometry alone (i.e., a trapezoid without features) to evaluate the Bayesian predictions quantitatively, focusing in reductions in variability of responses as well as bias effects on the mean responses. These future experiments could be used to test and refine the recently developed computational model of the human reorientation data (Xu et al., 2017). Future investigations could also vary where the feature is located in relation to the head direction. Currently, the head direction is more closely aligned with the corner than the feature cue. If the feature was aligned more closely with the head direction, then it is possible that feature use and cue integration might be strengthened (we thank an anonymous reviewer for this suggestion).

Another interesting question is to investigate the reorientation response across the lifespan with age and particular types of experience. Much of the theoretical debate has concerned what children know about the world from a young age and how this changes with development. This experiment supports that human adults integrate geometric and feature cues, but it is unknown if young children or elderly adults would show the same pattern of spatial orientation. Previous research has demonstrated that short- and long-term experience alter the use of geometric and feature cues, and it would be interesting to determine if certain types of experience, such as independent way finding in indoor or outdoor environments, would influence development.

Acknowledgments

This research was supported by the National Science Foundation (grant SBE0541957 and SBE1041707). We would like to thank Caitlin Vossberg for her assistance in collecting and scoring data; Daniele Nardi for advice in the planning stages of this experiment; Susan Pense for preparation of the histograms; and for Temple University's RISC (Research in Spatial Cognition) group for the use of their meeting space to house our bulky apparatus.

References

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.

Cheng, K. (1986). A purely geometric module in the rats spatial representation. *Cognition*, *23*, 149–178.

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, *12*, 355–361.

Cheng, K., Huttenlocher, J., & Newcombe, N. S. (2013). 25 years of research on the use of geometry in spatial reorientation: A current theoretical perspective. *Psychonomic Bulletin & Review*, *20*, 1033–1054.

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1–23.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*, 625–637.

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.

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.

Chiandetti, C., & Vallortigara, G. (2010). Experience and geometry: Controlled-rearing studies with chicks. *Animal Cognition*, *13*, 463–470.

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

Hermer, L., & Spelke, E. (1994). A geometric process for spatial representation in young children. *Nature*, *370*, 57–59.

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition*, *61*, 195–232.

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.

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.

Kelly, D. M., & Spetch, M. L. (2004). Reorientation in a two-dimensional environement: II. Do pigeons (*Columba livia*) encode the featural and geometric properties of a two-dimensional schematic of a room? *Journal of Comparative Psychology*, *118*, 384–395.

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.

Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behavior Processes*, *39*, 126–139.

Learmonth, A., Newcombe, N. S., Sheridan, M., & Jones, M. (2008). Why size counts: Children's spatial reorientation in large and small enclosures. *Developmental Science*, *11*, 414–426.

Lee, S. A., & Spelke, E. S. (2010a). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*, 152–176.

Lee, S. A., & Spelke, E. S. (2010b). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, *206*, 179–188.

Lee, S. A., Shusterman, A., & Spelke, E. (2006). Reorientation and landmark-guided search in children: Evidence for two systems. *Psychological Science*, *17*, 577–582.

Nardi, D., & Bingman, V. P. (2009a). Pigeon (*Columba livia*) encoding of a goal location: The relative importance of shape geometry and slope information. *Journal of Comparative Cognition*, *123*, 204–216.

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.

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.

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.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Using geometry and features following landmark displacement. *Psychological Science*, *19*, 1301–1307.

Reichert, J. F., & Kelly, D. M. (2011). Use of local and global geometry from object arrays by adult humans. *Behavioural Processes*, *86*, 196–205.

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, *10*, 47–54.

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.

Sturzl, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in trapezoid-shaped enclosures: Implications for theoretical accounts of geometry learning. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*, 246–253.

Tommasi, L., & Polli, C. (2004). Reorientation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition*, *7*, 53–59.

Twyman, A. D., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology*, *43*, 1523–1530.

Twyman, A. D., & Newcombe, N. S. (2010). Five reasons to doubt the existence of a geometric module. *Cognitive Science*, *34*, 1315–1356.

Twyman, A. D., Newcombe, N. S., & Gould, T. G. (2013). Malleability in the development of spatial reorientation. *Developmental Psychobiology*, *55*, 243–255.

Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different size. *Developmental Science*, *8*, 393–401.

Xu, Y., Regier, T., & Newcombe, N. S. (2017). An adaptive cue combination model of human spatial reorientation. *Cognition*, *163*, 55–66.

Zar, J. H. (2010). *Biostatistical analysis* (5th ed.). Upper Saddle River, NJ: Pearson.

Zhao, M., & Warren, W. H. (2015). Environmental stability modulates the role of path integration in human navigation. *Cognition*, *142*, 96–109.