Transfer of spatial search between environments in human adults and young children (*Homo sapiens*): Implications for representation of local geometry by spatial systems

Adina R. Lew[1], Barrie Usherwood[1], Frantzeska Fragkioudaki[1], Varvara Koukoumi[1],
Shamus P. Smith[2], Joe M. Austen[2] and Anthony McGregor[2]
1. Lancaster University, UK, 2. Durham University, UK

Lew, A. R., Usherwood, B., Fragkioudaki, F., Koukoumi, V., Smith, S. P., Austen, J. M., & McGregor, A. (2014). Transfer of spatial search between environments in humans adults and young children (*Homo sapiens*): Implications for representation of local geometry by spatial systems. *Developmental Psychobiology*, *56*(3), 421-434,

Abstract

Whether animals represent environmental geometry in a global and/or local way has been the subject of recent debate. We applied a transfer of search paradigm between rectangular- and kite-shaped arenas to examine the performance of human adults (using virtual environments) and children of 2.5 to 3.5 years (using real arenas). Adults showed robust transfer to a congruent corner in a kite-shaped arena, following training in a rectangular-shaped arena in two paradigms modelled on those used with rats and young children respectively. In contrast, the children showed no evidence of transfer of search, despite above chance performance in the rectangular arena, and above chance performance in a study where search occurred in the kite arena only. The pattern of findings suggests global aspects of environmental geometry may be used to re-establish heading, and that the matching of elements of local geometry in new global contexts may be an advanced developmental achievement.

Keywords: Spatial navigation; Geometric module; Reorientation; Spatial development; Spatial cognition; Local geometry

---

The authors would like to thank Iona Symington and Cassandra Gilbert for assistance with data collection for Study 1; also Athanasia Provi and Apoorva Kering for interobserver agreement coding on Studies 2 and 3 respectively. We are grateful to all the students, parents, and children that participated in the studies.

Correspondence concerning this article should be addressed to Adina R. Lew, email: a.r.lew@lancaster.ac.uk; telephone: +44 (0)1254 593696; facsimile: +44 (0)1524 593744, or Anthony McGregor, email: anthony.mcgregor@durham.ac.uk; telephone: +44 (0)191 3343277; facsimile: +44 (0)191 3343241

The mechanisms by which diverse species represent spatial relations in the environment in support of adaptive behavior have been vigorously debated (e.g. Pearce, 2009; Jeffery, 2010). One influential theory, the *geometric module* hypothesis (Gallistel, 1990; Wang & Spelke, 2002), posits that in order to reorient after a loss of heading direction, animals match the whole shape of an environment with that stored in memory, where shape is given by bounded walls or macro-environment contour. Support for such an assertion comes from data showing that a variety of animals base their search for a remembered goal location on environmental geometry following inertial disorientation, sometimes at the expense of unambiguous featural information provided by landmarks or colored walls (reviews in Lew, 2011 and Tommasi, Chiandetti, Pecchia, Sovrano & Vallortigara, 2012). The clearest demonstration of this reliance on environmental geometry comes from the original canonical version of the reorientation task in which disoriented rats searched for the remembered location of food at correct and geometrically equivalent locations in a rectangular arena, despite the presence of distinctive landmarks that could have provided unambiguous locational information (Cheng, 1986; Margules & Gallistel, 1988).

One challenge to the geometric module hypothesis comes from computationally instantiated models by Miller and Shettleworth (2007, 2008; see also Dawson, Kelly, Spetch & Dupuis, 2010). Miller and Shettleworth provide an analysis of the reorientation task, in which the term “reorientation” is a misnomer, because no recourse is made to a specialised spatial system for maintaining a sense of orientation within an environment. Instead, non-visible spatial goals can be located by association with visible environmental cues, following associative and operant learning principles. In the Miller and Shettleworth model, the environment is parsed into discrete elements, such as a coloured wall or a corner with a particular local geometry (e.g. long wall on the right, short wall on the left). Using associative learning principles, together with an alteration of probabilities for selecting particular places as goal locations as learning progresses, the model predicts both successful goal localisation in a featureless rectangular environment (up to rotational ambiguity), as well as the over-riding of a feature such as a colored wall in favor of geometry.

Experimental evidence with rats (Esber, McGregor, Good, & Pearce, 2005; McGregor, Jones, Good, & Pearce, 2006; Pearce, Good, Jones, & McGregor, 2004) and chicks (Kelly, Chiandetti, & Vallortigara, 2011; Tommasi & Polli, 2004), added to the plausibility of theoretical models such as those of Miller and Shettleworth (2007) arguing for local rather than global processing of environmental geometry, without re-establishment of being necessary for goal localisation. For example, Pearce et al. (2004) trained rats to find a hidden escape platform in a corner of a rectangular pool, before transferring them to a kite-shaped pool formed by the two long and two short sides of the rectangular pool. The rationale for this experiment was that if rats in the rectangular arena were using the whole shape of the environment to reorient in order to locate the goal, there should be no transfer of search to a new, kite-shaped arena. If however, they were associating the local geometry of a corner with the goal, then transfer of search would be expected. The rats showed a preference for swimming towards the right-angled corner of the kite that was congruent with the goal location in the rectangle (e.g. long wall to the right of a short wall), as opposed to the incongruent right-angled corner despite the change in the overall shape of the environment, suggesting they based their search on local geometric properties. In response to these findings, Cheng and Gallistel (2005) suggested that the transfer of search could have occurred due to the coding of the goal location in terms of the principal axis of the rectangle, a global geometric property (e.g. the corner to the right of the long axis of the rectangle becomes the corner to the right of the long axis of the kite shape). McGregor et al. (2006) demonstrated that transfer of search in a shape where principal axis and local geometry use could be dissociated, conformed with use of local geometry rather than principal axis coding (see Kelly, Chiandetti, & Vallortigara, 2011 for equivalent findings of transfer of search based on local geometry in chicks, together with discussion in Sturz and Bodily, 2011a and Kelly, Durocher, Chiandetti and Vallortigara, 2011). In contrast to the findings with rats and chicks, human adults navigating in virtual environments can show flexible transfer based on local geometry or principal axis matching (see Bodily, Eastman, & Sturz, 2011, Sturz & Bodily, 2011b and Sturz, Gurley, & Bodily, 2011).

As Pearce et al. (2004) noted, however, demonstrating transfer of search does not preclude both global and local aspects of geometry being coded, with coding of local geometry being responsible for any transfer of search[1]. Some findings using the reorientation paradigm with young children are hard to accommodate without reference to global representations of the environment, casting doubt on operant associative models of reorientation task performance based on local geometry (Miller & Shettleworth, 2007, 2008). Lee, Sovrano and Spelke (2012) reported data that suggests that matching to local geometry does not underpin performance in the standard reorientation paradigm. When the walls of a rectangular enclosure were separated out to be equidistant from the central position of the child (e.g. the long and short walls of the rectangle form a square array), reorientation performance in 4-year old children fell to chance levels, in contrast to above-chance performance when four wall segments of equal length were arranged in a rectangular array relative to the central position. These results suggest that the rectangular array was important for the re-establishment of heading, which allowed the children to succeed on the task. They also suggest that the children were unable to simply form goal-wall-length associations within the 4 trials used in the task, which would have permitted them to solve the task with the walls of unequal length without reorientation being necessary. Lew, Gibbons, Murphy, and

---

[1] We thank an anonymous reviewer for clarifying that logically there are two separable components contained within the original geometric module hypothesis as proposed by Gallistel (1990). The first is that animals re-establish heading in order to solve the reorientation task, and the second is that they use global aspects of environmental shape for this re-establishment of heading. It is thus possible that the assertion that re-establishment of heading is part of the task is correct, but that a local aspect of environmental geometry can be used for this process. However, the evidence reviewed would suggest that both re-establishment of heading, and the use of more global aspects of arena geometry for this process, are involved in the performance of young children, at least in the types of arenas that have been studied to date.

Bremner (2010) additionally found that young children only succeeded on the reorientation task in symmetrical arenas (a rectangle or isosceles triangle), with irregular quadrilateral or triangular arrangements leading to chance levels of performance. Symmetry is by definition a global property of an environment, and therefore this finding is hard to accommodate within an account of reorientation performance that focuses solely on local geometry. It may be that the axis of symmetry of the arena facilitates re-establishment of heading following disorientation.

One theoretical approach within a cognitive mapping framework that may account for both local and global geometry being coded is that proposed by Döeller, King and Burgess (2008; also Döeller & Burgess, 2008; see also White & McDonald, 2002). Döeller et al. (2008) proposed that a hippocampal mapping system, based on latent learning principles, codes place using distal cues for orientation and distance from boundaries for location specification. In parallel, a striatal system, based on action-outcome associations, codes the relation between a goal and discrete landmarks or boundary segments (see also Bullens, Nardini, Döeller, Braddick, Postma, & Burgess, 2010 for evidence of the two systems in development).

It is tempting to suggest that global environmental geometry is required to re-establish heading in the standard reorientation paradigm when no distal landmarks are available (see Knight, Hayman, Ginzberg, & Jeffery, 2011), whereas striatal systems underpin goal-to-local-geometry associations, leading to transfer of search phenomena. One difficulty with this account is that rats with hippocampal lesions are unable to learn the reorientation task, either in a rectangular pool or a circular pool containing a rectangular array of identical landmarks (McGregor, Hayward, Pearce, & Good, 2004; Pearce et al., 2004). In contrast, they can learn the relation between a goal and a single landmark at a constant distance and direction from the goal (Pearce, Roberts, & Good, 1998), and can also learn the reorientation task in a rectangular pool with walls of different colors (Pearce et al., 2004).

The pattern of findings in rats and children reviewed above could be accounted for in different ways within the parallel memory systems framework. One possibility is that hippocampal systems are required even for coding segments of space, and the geometric relations between landmarks or boundaries within those segments (McGregor et al., 2004; Pearce et al., 2004). In order for striatal systems to be effective, some distinctive feature of the boundary segment or discrete landmark (e.g. color, shape or odor) is required. Another possibility is that associations between segments of boundaries or arrays and goal locations can be formed within striatal systems, but with far greater difficulty than with more discrete objects, or objects that do not require the processing of local geometry in extended space. Thus, paradigms that investigate transfer of local geometry between environments may be tapping into questions concerning the extent to which hippocampal representations of an environment can be fractionated into constituent elements (including extraction of principal axes), or the types of cue that striatal systems are able to utilize.

The present research is the first to address the question of whether transfer of search can be observed in young children, employing similar paradigms to those used in other species. If associations between the goal location and local geometry underlie successful performance on the reorientation paradigm in children (Miller & Shettleworth, 2007, 2008), then children should transfer search between rectangular and kite-shaped arenas, as they generally show above chance performance in the standard reorientation task (e.g. Lee et al., 2012, Lew et al., 2010). If, however, transfer of search relies on alternative mechanisms, such as fractionation of hippocampal representations or the build-up of associations within striatal systems, then young children may fail to show transfer of search, despite above chance performance in the reorientation task.

In Study 1 we used a virtual environment task modelled on that of the rodent transfer of search paradigm (Pearce et al., 2004) to establish whether human adults show transfer of search under these conditions. The subsequent experiments examined the ability of children to search in the correct location for a hidden object following transfer (Study 2) and no transfer (Study 3) between environments. Finally, Study 4 acted as a control experiment with human adults navigating in virtual environments, where the paradigm was modelled closely on that used with children in Study 2, to ensure that procedural differences could not account for any differences between adult and child performance found in Studies 1 and 2.

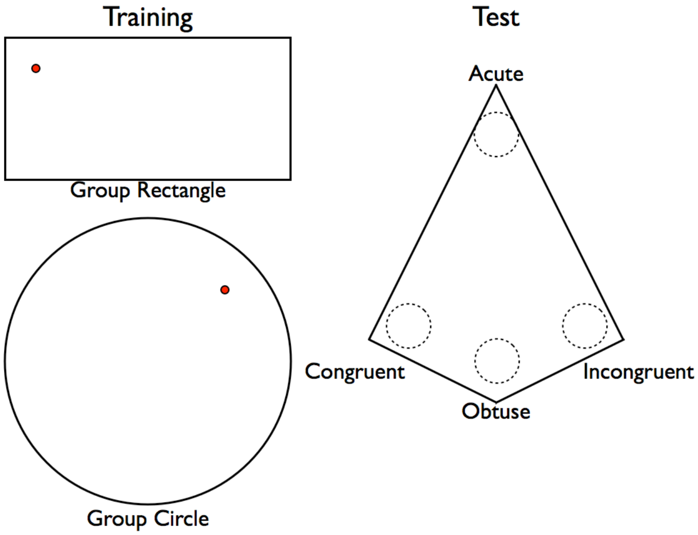

Figure 1. Schematic representation of the computer-generated arenas in Study 1. The arenas used during training for Groups Rectangle and Circle are shown on the left side of the figure, along with the location of the invisible hidden goal. All participants were tested in the kite, shown on the right side of the figure, in the absence of the goal. Time spent in invisible circular zones in each corner of the kite was recorded over a 60-s period.

Study 1

In Study 1 adult participants were trained to navigate to an invisible goal location in a computer-generated spatial learning task. In the experimental condition participants were trained first to locate the hidden goal in one corner of a rectangular arena. To ensure only cues provided by the shape of the arena could be used to return to the goal location there were no cues visible outside the arena, and the arena walls and floor were uniformly colored and lit. In addition, the start location on each training trial varied, so a fixed route from the start location to the goal could not be learned. Following training a test trial was conducted in a kite-shaped arena, which was made up of the same four walls as the rectangle, as shown in Figure 1. Should learning in the first phase of training be based solely on global shape matching then this representation will be of little use in the test trial and participants should be expected to search randomly in the arena. Alternatively, if participants learned the location of the goal with reference to some local aspects of the arena's shape then they should be expected to search in the right-angled corner in the kite that shares the local geometric properties of the corner that contained the goal during training in the rectangle, regardless of the global changes to the arena's shape. A second group was included that was trained to locate the hidden goal in a circular arena. Learning based on the shape of this arena was not expected to transfer to the test trial in the kite, thus providing a control condition with which to compare performance of participants in the experimental condition.

Method

Participants

Forty University undergraduates participated (20 males), with a mean age of 20.1 years (*SD* = 1.3 years; range 18 - 22 years). Participants were assigned randomly to one of two training conditions, each containing 10 males and 10 females. In the experimental condition, Group Rectangle, participants were trained in a rectangular arena, and in the control condition, Group Circle, participants were trained in a circular arena. All participants had normal or corrected-to-normal vision, were competent computer users, and were not paid for taking part. The study received ethical approval from the University's Psychology Ethics Sub-Committee and complied with both the American Psychological Association's and the British Psychology Society's ethical guidelines.

Apparatus

Three-dimensional computer-generated virtual environments (VEs) were created via an open source virtual reality toolkit (Maverik, Advanced Interfaces Group, 2008). The VEs were viewed from a first-person perspective and movement within them could be controlled using the arrow keys on a keyboard. Assuming subjective eye level to be 1.6 m, from which other distances could be determined, the walls of the arenas were 2 m high. With movement within the arenas programmed at 2 ms^{-1}, the subjective wall lengths in the rectangular arena were 10 m x 5 m, and the diameter of the circular arena was 10 m. A 0.3-m diameter hidden goal was located in each of these VEs and its position remained static in each arena for all trials. For Group Rectangle the hidden goal was always positioned 1.6 m from one of the corners of the rectangle that was made up of a short side to the left of a long side. The goal was equidistant from the two walls on a line that bisected the corner. For Group Circle the goal was always positioned 1.6 m from the wall on a line from the center of the arena that bisected the north and east cardinal points of the arena, although there were no cues present for participants to determine direction within, or outside, the arena. The VE in the final test trial was kite-shaped, composed of the same short and long walls as the rectangular arena, with two right-angled corners. One of these corners possessed the same local geometric properties as the one that contained the hidden goal for Group Rectangle during training, with the short wall to the left of the long wall. No goal was present in the kite-shaped arena, but time spent searching in each of four invisible circular zones, with diameters of 1.6 m, each located 1.6 m from the corners of the kite on a line that bisected the corner, could be recorded (see Figure 1). The walls in all VEs were uniform red, the ground grey and the sky blue. No cues were visible outside the enclosed arenas.

Figure 1 about here

Design and Procedure

All participants received 12 training trials in either the rectangle (Group Rectangle) or circle (Group Circle) before a final test trial in the kite arena. The task during training was to learn the location of the hidden goal and navigate to it, after which the trial terminated. These escape latencies were recorded automatically by the computer program. Participants were introduced to the arena from one of four release points on each trial. In the rectangular arena the release points were the midpoints of each of the four walls, facing the wall. In the circular arena the release points were the cardinal points of the arena, again, facing the wall. Each release point was used four times, in a pre-determined random order such that each release point was used once every four trials. Participants were required to navigate to the goal location, which was always located in the same corner, using the arrow keys on a computer keyboard. The up and down keys moved the participant forwards and backwards, respectively. The left and right keys caused the participant to rotate left or right. If the goal was not located within 60 s a tall red column appeared at its location in the arena and the participant was required to walk into the column to end the trial. The goal was not made visible if the participant navigated to the goal location within 60 s. When the goal was located the message ‘goal found’ appeared on the screen alongside a count down from five seconds until the next trial began. Once at the goal location the forwards and backwards keys were disabled although the participant was still able to rotate left and right to view the arena from this location.

Following the final training trial participants immediately received the test trial in the kite. Participants were not informed that the test trial was different to the preceding trials, although after participation had ended, they were asked if they had noticed any change in the final trial. All participants noticed the change. However, in the test trial, in addition to the overall shape of the arena differing from that in training trials, the goal was also removed, and the trial terminated automatically after 60 s. The release point was the center of the arena with the participant facing in a randomly determined direction. The time spent in zones in each of the corners of the arena was recorded automatically by the computer program.

Results and Discussion

Performance during training was assessed by comparing individual mean escape latencies in four-trial blocks. The mean escape latencies over four trials were taken because the distance from the release point to the goal varied among trials. Between four-trial blocks, however, the mean distance to the goal was equated. The upper panel of Figure 2 shows the performance of men and women in both conditions during training.

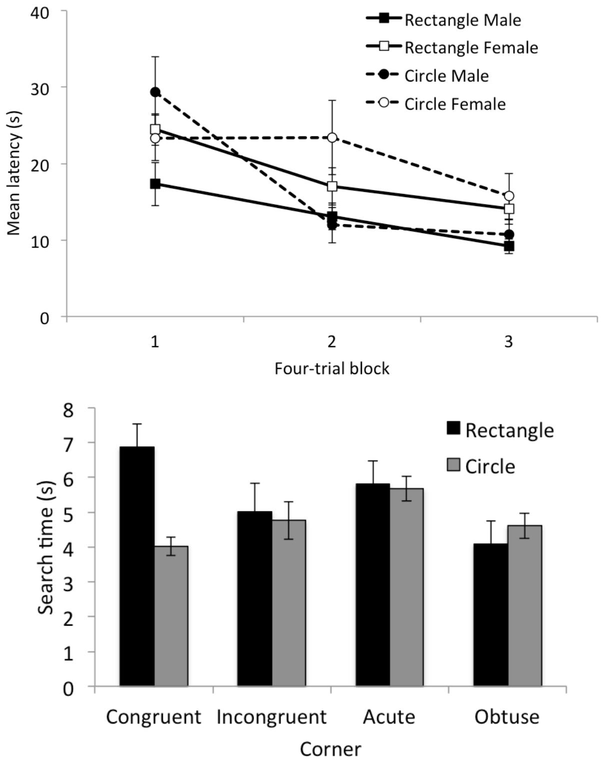

Figure 2. The mean escape latencies (± SEM) for men and women in the two training conditions in Study 1 (upper panel) and the mean times (± SEM) spent in the zones in each corner during the test trial in the kite-shaped arena, depending on training condition (lower panel).

Although there were differences among the genders and conditions, by the end of training the escape latencies were similar and relatively short. A three-way mixed Analysis of Variance (ANOVA) of individual mean escape latencies for each of the three four-trial blocks, with training condition and gender as between-subjects variables, revealed main effects of gender, F (1, 36) = 4.52, p = .040, η_p^2 = .112, and block, F (2, 72) = 22.17, p < .001, η_p^2 = .473, and a three-way condition x gender x block interaction, F (2, 72) = 4.71, p = .012, η_p^2 = .073. Analysis of simple main effects for this interaction revealed that while men in the rectangle condition were faster to locate the goal in block 1 of training than those in the circle condition, F (1, 36) = 6.81, p = .013, η_p^2 = .159, there were no other differences between conditions, Fs (1, 36) < 2.15, ps > .15, η_p^2s < .059, including in the final block of training. In addition, women in the circle condition were slower in block 2 of training (M = 23.40 s) than men in the same block (M = 11.95 s), F (1, 36) = 6.95, p = .012, η_p^2 = .162, but there were no other differences between men and women, including in the final block of training, Fs (1, 36) < 2.83, ps > .1, η_p^2s < .073. Finally, although there was an effect of block for women in both conditions, Fs (2, 35) > 3.32, η_p^2s > .159, and for men in the circle condition, F (2, 35) = 15.24, p < .001, η_p^2 = .466, there was no overall effect of block for men in the rectangle condition, F (2, 35) = 2.07, p > .1, η_p^2 = .106. Pairwise comparisons for these participants, however, revealed faster escape latencies in block 3 (M = 9.20 s) than in block 1 (M = 17.33 s). No other main effects or interactions were significant, Fs < 2.41, η_p^2s < .063. Training, therefore, resulted in faster escape latencies in both conditions and for both genders, with little difference between the groups by the end of training.

To determine the extent to which participants learned the location of the goal during training with reference to the local geometric properties of the arena, the final test trial, in which the goal was removed, was conducted in a kite-shaped arena. Search times were recorded in the corner of the arena with the equivalent local geometric features as those in the corner of the rectangle in which the goal was located (with a short wall to the left of a long wall). This corner is termed the congruent corner, and the mirror-opposite right-angled corner was defined as the incongruent corner. The remaining corners are referred to as the obtuse and acute corners. The search times in each corner for participants that received training in either the rectangle or the circle are presented in the lower panel of Figure 2. As expected, those participants in the circle condition showed no preference for the congruent corner in the kite over the incongruent corner, while those that were trained in the rectangle preferred the congruent to the incongruent corner. A two-way mixed ANOVA of individual times spent in each corner zone, with condition as the between-subjects variable, supported this observation with a corner x condition interaction, F (3, 108) = 4.65, $p = .004$, $\eta_p^2 = .114$, and a significant main effect of corner, F (3, 108) = 3.44, $p = .020$, $\eta_p^2 = .087$. Analysis of simple main effects revealed an effect of corner for the rectangle condition, F (3, 34) = 6.08, $p = .002$, $\eta_p^2 = .349$, but not for the circle condition F (3, 34) = 1.98, $p > .1$, $\eta_p^2 = .149$. Pairwise comparisons for the rectangle condition showed that more time was spent in the congruent corner than the incongruent or obtuse corners, ps < .05, but that there was no difference between times spent in the congruent and acute corners. In addition, more time was spent in the acute than the obtuse corner, $p < .05$. There were no other differences. For the circle condition more time was spent in the acute corner than the congruent corner $p < .05$, but there were no other differences. The comparison between training conditions revealed more time spent in the correct zone in the rectangle condition than in the circle condition, F (1, 34) = 16.09, $p < .001$, $\eta_p^2 = .309$, but no other differences between the conditions, Fs < 1, η_p^2s < .010. No other main effects or interactions were significant, Fs < 1.62, ps > .2, η_p^2s < .043.

Therefore, participants trained to locate a hidden goal in one corner of a rectangle in a computer-generated navigation task transferred their spatial behavior to a rearranged shape that shared some local geometric properties with the rectangle. They spent more time searching for the goal in the congruent corner than in the mirror-opposite right-angled corner. However, there was no difference between time spent in the congruent and acute corners. A similar pattern of results was observed by Pearce et al. (2004) who trained rats to locate a submerged platform in one corner of a rectangle before being transferred to a kite-shaped arena. While Pearce et al. claimed that rats learned to turn to a corner at a particular end of a long wall during training, in a manner consistent with a stimulus-response association (Hull, 1932), they could not rule out the possibility that entries to the acute corner in the kite were the result of an unconditioned preference for that corner. An alternative explanation for Pearce et al.'s results was that rats in the first phase of training had learned to identify the corner containing the platform by means of a global parameter of the arena's shape, the shape's principal axis. Cheng and Gallistel (2005; see also Gallistel, 1990) suggested that the pattern of results observed by Pearce et al. was consistent with rats transferring their behavior from the rectangle to the kite based on the two arenas' principal axes. Although McGregor et al. (2006) and Kelly, Chiandetti, and Vallortigara (2011) failed to find any evidence that animals learn locations based on an arena's principal axis, and Esber, McGregor, Good, Hayward, and Pearce (2005) offered similar results with an array of landmarks, Pearce et al. (2004) could not rule out the possibility using transfer between rectangular and kite-shaped arenas.

Our results using transfer between a rectangle and kite may suffer from the same confound. However, the reason for our pattern of results is clearer in the light of the behavior of participants in the circle condition. There was no reason to suppose that learning about the spatial properties of the circle, either in terms of principal axis or local geometry, should transfer to performance in the kite, so the slight preference for searching in the acute corner in this group, and the fact that there was no difference between the circle- and rectangle-trained participants in time spent in the acute corner, does indeed suggest some unconditioned preference for that corner. In fact, it was noted that the fullest view of the arena, with three out of the four corners visible, was achieved by standing in the acute corner. It is perhaps not surprising, therefore, that participants in both conditions should spend time in this corner. Preferences for acute corners may also occur in other species for diverse reasons, depending on task parameters (rats: Yaski & Eilam, 2008; chicks: Tommasi & Polli, 2004).

Nevertheless, the results of the experiment demonstrate that spatial learning in a rectangle transfers robustly to performance in a differently shaped arena in adult humans. These results are consistent with those of Bodily et al. (2011), and additionally show the value of control conditions in which no transfer is possible, to control for unlearned choice biases. Study 2 goes on to investigate transfer of search in young children.

Study 2

The purpose of Study 2 was to examine whether children display the same ability as adults to transfer search between arenas that share some local geometric characteristics. Children played a game with their parent to hide and find a photograph in one of the corners of a rectangular arena following disorientation by 3-4 slow turns with the eyes closed. In a test trial, after hiding the photograph the shape of the arena was changed while the child was being disoriented, before they had an opportunity to retrieve it.

Method

Participants.

Thirty-six children participated (23 males), with a mean age of 3.0 years (*SD* = 0.3 years; range 2.6-3.9 years). A further 15 children were tested but excluded due to failure to follow the hide-and-seek procedure (9), failure to close their eyes during the disorientation procedure (5), and uncodable responses (1). Parent and child volunteers were recruited through a database held at the Centre for Research in Human Development and Learning. The study was approved by the University's Psychology

Departmental Ethics Committee and complied with both American Psychological Association and British Psychological Society ethical guidelines.

Apparatus.

A rectangular enclosure made from a wooden frame covered with awning material was constructed with hinges, such that one corner could be opened fully as an entrance. Hinges were also used to allow the enclosure to be formed into a kite-shape. The enclosure was 1 m high and the side lengths were 1.95 m x 1.26 m. The kite shape had the same side lengths as the rectangle, and the side angles between the long and short sides were right angles. A continuous 15 cm tall hiding pocket was stapled to the bottom of the inner walls of the enclosure, in which a photograph could be hidden. The staples were painted the same dark grey as the fabric of the hiding pocket. The enclosure was set in a 2 m tall featureless cylindrical structure of 2.3 m diameter, with a central light source. Eight cameras were positioned outside the enclosure to record through regularly spaced peepholes. Two video recorders, time-locked together, and two split screen systems, allowed the eight camera views to be viewed and then analysed offline. Further details of the cylindrical enclosure and recording equipment can be found in Lew, Foster, Bremner, Slavin and Green (2005).

A digital camera was used to take a picture of the parent and child in the play room of the Centre, which was then printed and used as the hiding object in the reorientation task. The photograph was given to the participants as a souvenir after participation.

Design and Procedure.

All participants experienced two trials in the rectangular arena, and a final test trial in the kite-shaped arena. Ideally, more training trials would have been given but to reduce participant attrition training was kept to the fewest number of trials possible. The task involved a hide-and-seek game in which the parent hid a photograph in one of the corners of the rectangular arena, by slipping it into the hiding pocket at that corner. The hiding pocket was continuous round the bottom of the enclosure. Parents made sure their child was attending to the hiding, or let their child hide the photograph. Children were then disoriented by being turned round slowly 3-4 times with their eyes closed and covered. Disorientation lasted approximately 20 s. Parents either picked up their child to disorient them, or turned them round while they themselves also made slow circles round the child. Children were then asked to open their eyes and find the photograph. Parents were asked to be encouraging, but not to offer help of any kind until their child had made a search. If they did not find the photograph, to maintain motivation, children were allowed to continue searching, with the parent’s help, until it was found. The same hiding corner was used throughout the three trials for a particular child.

The hiding corner used was counterbalanced between the four corners of the rectangle. The first facing direction of the child (north, south, east or west, see Figure 3) was counterbalanced. The subsequent two facing directions occurred at cardinal points 90° from the first facing directions, in either a clockwise or anticlockwise direction (counterbalanced). Small, discrete numbers placed at the parent’s eye-level on the cylindrical enclosure indicated direction of facing on each of the three trials.

Children were familiarized to the surroundings and the experimenters in a playroom at the Centre. Parents signed consent forms during this period, and a photograph of the parent and child was taken and printed. Participants were then taken to the testing room, and the parent was shown the enclosure. The procedure was also rehearsed with the parent. Once the parent and child were in the enclosure, the door was closed, making the entrance indistinguishable from the other corners of the rectangle. The entrance curtain of the larger cylindrical enclosure was also closed, and recording initiated. The experimenters clapped and cheered when the child found the photograph, but otherwise did not make any sound. Once participation was over, the parent was asked about whether they had observed any peeking from their child during disorientation. Two of the 8 cameras were also angled upwards to record the child's face during disorientation, to check for covered eyes. The child was asked to choose a book as a thank you present for participation, and a contribution towards travel expenses was provided.

All trials were scored off-line by FF and VK. Location of search was defined by the first location at which the child touched the hiding pocket and looked inside. In the rectangle, these locations were defined as correct, rotational, near and far (Figure 3). In the kite, they were defined as acute, congruent, incongruent and obtuse (Figure 3). There were 3 instances in the rectangle where the child searched in the middle of a side, rather than near a specific corner. If this search was subsequently followed by a move towards a corner, then the search was coded as being at that corner. If no disambiguating behaviours occurred, the trial was excluded. More than one ambiguous trial resulted in full exclusion from the sample (this only occurred in Study 2 in one instance). An independent observer, naïve to the aims of the study, and to the actual hiding location of the photograph, viewed clips of all the trials starting from the end of disorientation. There were two disagreements that were resolved by discussion, with the final data set reflecting the outcomes agreed after discussion. Latency to search between the end of disorientation and first search, and whether any scanning occurred prior to search, were also recorded.

Results and Discussion

The mean percentage of search at each corner in the rectangle across the two trials in the rectangle is displayed in Figure 3. A comparison of correct + rotational searches against a chance level of 50% was conducted using a one-sample t-test. The performance of the children was above the chance level, $t(35) = 2.17$, $p = 0.037$, 2-tailed test. The correct and rotational search level of 62.5% is consistent with initial first and second trial performance in other studies (e.g. Lew et al., 2010). There was an equal proportion of search at correct and rotational corners, confirming that children were successfully disoriented. In the kite shape, there was no evidence that children favoured one corner over the other, χ^2 (36, 3) = 4.67, $p = 0.20$, 2-tailed. They did not concentrate their searches at the two right-angled corners (binomial, $p = 0.24$). Fourteen children searched in correct or rotational locations in both rectangle trials; of these, 5 searched in the congruent corner of the kite, 3 searched at the obtuse corner, 1 searched in the incongruent corner, and 4 searched at the acute corner. In order to check that children were not basing their search in the kite on the nearest corner to the absolute location of the photograph, due to insufficient disorientation, we checked the 14 trials in which children searched at the acute corner of the kite. In 8 cases, this search was in the incorrect side of the room to the photograph's actual location, suggesting children were indeed disoriented.

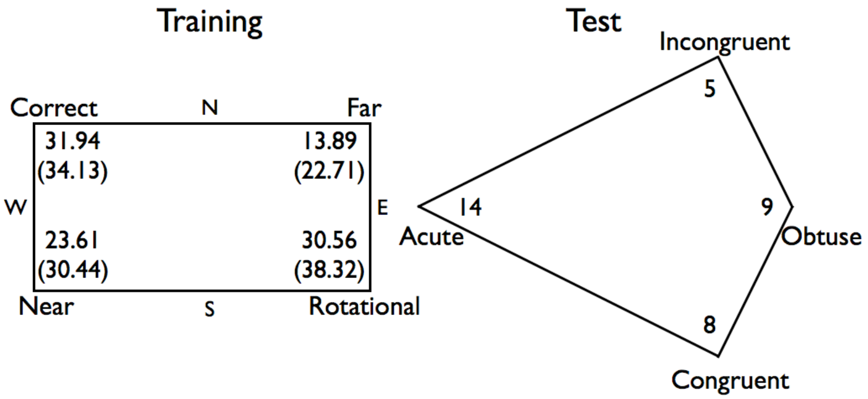

Figure 3. Mean percentage of search (*SD*) across trials 1 and 2 in the rectangular arena at each corner, and number of searches at each corner of the kite-shaped arena in Study 2. For ease of presentation, responses have been normalised so that different types of responses are shown in single corners, despite the counterbalancing of the actual position of the goal corner in the rectangular arena. *Note*. A second trial in the rectangle was missing for one participant due to failure to close the eyes sufficiently during disorientation.

We also investigated latency to search and whether scanning occurred between the end of disorientation and search. We reasoned that a greater latency and more scanning would be observed in the kite trial if children were reacting to the change of shape. In terms of latency to search, a within-subjects ANOVA with 3 levels yielded no significant difference between trials, F(1.4, 49.0) = 2.5, $p = 0.11$[1], $\eta_p^2 = .07$ (Greenhouse-Geisser correction for unequal variances applied). The means and SDs for trials 1-3 were 8.0 s (6.06 s), 5.4 s (3.1 s), 7.4 s (5.9 s) respectively. Seventeen children carried out at least one scan on trial 1, 14 children did so on trial 2, and 20 children carried out at least one scan in the kite. These differences were not significant (Cochran's Q, $p = 0.30$). Eleven children carried out at least one scan in both the rectangle and the kite. The overall level of scanning (approximately 50% of trials) was greater than the 8% reported by Huttenlocher and Vasilyeva (2003) in an isosceles arena. It is unclear if this reflects a genuine difference or whether the greater number of cameras available in the present research aided detection of scanning behaviour. The question arises as to whether children were insensitive to the shape change on the test trial, or whether latency and scanning are simply insensitive measures. We tend to favour the latter possibility, as

---

[1] One outlier with a Trial 1 with a latency of 77 s was excluded from the analysis.

several of the older children made spontaneous verbal remarks in the kite trial, the most memorable of which was that "the fairies had come to change things".

Unlike adults, the young children in Study 2 made no match between the correct corner in the rectangle, and the congruent corner in the kite shape. This may be an effect of exposure to the rectangle, in that both adults in the VE of Study 1, and the rats in Pearce et al. (2004) received many more training trials than is possible with young children. However, it is still unlikely that the greater than chance performance in the rectangular arena can be explained solely by local geometry-matching processes, particularly considering the insensitivity to angle-size matching, or side-length matching, shown by the children through searching all corners of the kite. One possible explanation for the apparently random search of the children in the kite-shaped arena, is that they cannot distinguish either corners or sides in this arena, due to its relative lack of familiarity compared to rectangular spaces. Thus their search patterns could not be interpreted in terms of disruption due to shape change. Rather, children simply search at random in a kite-shaped arena, whatever the circumstances.

Lee et al. (2012) found that 2-year-old children were successful at relocating a goal in a rhombus-shaped environment, where the goal remained in the same location across 4 test trials (Hupbach & Nadel, 2005, found that only 4-year-olds were successful in a working memory version of the task). In addition, 2-year old children can search at rates higher than chance in an isosceles triangle arena, where both angle and side length differ, (Huttenlocher & Vasilyeva, 2003; Lew et al., 2010). Given these results, we would predict that children should be able to locate a goal in a kite-shaped arena at above-chance levels, and thus the disruptive effect of the shape change in Study 2 cannot be accounted for by general random search in a kite-shaped arena. In Study 3, children were tested in a kite-shaped arena only, for three trials, to determine whether performance was above chance. The photograph was hidden only in the right-angled corners.

Study 3

Study 3 was included to ensure children were capable of learning the location of a hidden photograph within a kite-shaped arena. Above chance performance in this task would suggest the failure of children to transfer search between environments in Study 2 was not the result of a general failure to discriminate corners within a kite.

Method

Participants.

Twenty children participated (10 males), with a mean age of 2.8 years (*SD* = 0.3 years; range 2.3 - 3.6 years). A further 2 children were tested but excluded due to unwillingness to follow the hide-and-seek procedure, or failure to close their eyes during the disorientation procedure, on more than one of the three trials. The study gained departmental ethical approval.

Apparatus.

The apparatus was the same as that for Study 2. The kite-shaped arena was used throughout the three trials of the study.

Design and Procedure.

The children were tested on the reorientation task within the kite-shaped arena for 3 trials. The hiding location was the same throughout the three trials for each child. Half the children saw the photograph hidden at the right-angled corner of the kite-shaped arena at the north end, and the rest of the children saw it hidden in the right-angled corner at the south end. All other procedural details were the same as those described for Study 2. A second independent observer, naïve to the aims of the study and to the actual hiding location of the photograph, observed all the trials. There were no disagreements with respect to coding search location.

Results and Discussion

The percentage of children searching at each of the corners of the kite-shaped arena is displayed in Figure 4, and the number of searches across the three trials is displayed in Table 1. Four, 1-sample t-tests (2-tailed) were conducted on the percentage of search at each corner across the 3 (or 2) available trials against a chance level of search of 25%. There were significantly more searches at the correct location than would be expected by chance, $t(19) = 2.49$, $p = 0.02$. Search at the obtuse corner and the opposite corner did not differ from chance. There were significantly fewer searches at the acute corner than would be expected by chance, t(19) = 2.39, $p = 0.03$.

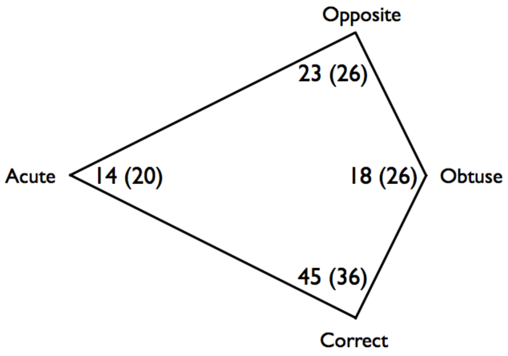

Figure 4. Mean percentage of search (*SD*) across trials 1-3 in the kite-shaped arena at each corner in Study 3. Responses have been normalised so that different types of responses are shown in single corners, despite the counterbalancing of the goal location between the two right-angled corners of the kite.

Consistent with studies in an isosceles-shaped arena and a rhombus (Huttenlocher & Vasilyeva, 2003, Lee et al., 2012), children were able to locate the photograph successfully significantly more than would be predicted by chance alone. Actual accuracy of performance was quite low, however, perhaps reflecting the fact that the hiding locations were the two similar corners only, rather than all corners. Unlike Study 2, search levels at the acute corner were quite low, suggesting children can distinguish this corner from the others. The low rate of search at the acute corner additionally suggests that the search patterns of children in Study 2 were influenced by the shape change they experienced between hiding and search, rather than a natural preference that overrides the memory for the goal location.

Table 1. Frequencies of search in the corners of the kite arena in Study 3.

Trial	Correct	Opposite	Obtuse	Acute
1[1]	10	1	3	2
2	11	3	4	2
3[2]	3	9	3	3

[1] There was 1 missing trial due to failure to search without help, 2 missing trials due to failure to maintain the eyes closed during disorientation, and 1 missing trial due to ambiguous search in the middle of a wall.
[2] There were 2 missing trials due to failure to maintain the eyes open.

While the results of Study 3 preclude general random search in a kite arena as the explanation for children's lack of transfer of search in Study 2, the possibility remains that the difference between these young children and the adults of Study 1 can be accounted for by procedural differences between Study 1 and Study 2, including the children receiving fewer training trials in the rectangle in Study 2 compared with the adults in Study 1. In order to address this possibility, Study 4 reports a VE study with adults modelled as closely as possible to the child paradigm used in Study 2.

Study 4

For practical reasons it was decided to attempt to replicate the procedure of Study 2 with adults using a virtual navigation task, rather than in a real-world environment. Arguably this method makes memory performance more difficult than a real-world equivalent because of the absence of vestibular and proprioceptive information, as well as the narrower rendered field of vision on a computer screen (about 60 deg) compared with real vision (nearly 180 deg). Therefore any differences between the adults' performance in Study 4 compared with that of the children in Study 2 were unlikely to be the result of differences in task difficulty.

Method

Participants

Participants were 48 undergraduate or postgraduate University students. Thirty-two were female and the remainder male. The mean age was 20.1 years (SD = 2.50 years; range 17 - 27 years). Participants were reimbursed for their time either by payment of course credit or with a £5.00 shopping voucher.

Apparatus

A custom-built VE presented participants with a first-person perspective of the 3D arenas used in this study. This VE was displayed in 1024x768 resolution on a flat-screen monitor. Participants used the arrow keys on a standard keyboard to move around within the VE. Forward/backward movement speed, as well as left/right rotational speed, was kept constant throughout the study. Participants were able to move at a brisk walking pace of 6.5km/h and were able to complete a full 360° rotation in 4.8 seconds. Two arena shapes were used in this study, as in Study 2; participants were trained in a rectangular-shaped arena before being placed into the kite-shaped arena, which shared the same wall lengths. As in Study 1, eye level was assumed to be 1.6 m from the ground, from which other distances could be calibrated. The short walls of the arenas were 6.9 m in length, while the long walls were 10.8 m. This preserved the exact same wall-length ratio (1:1.56) as used in Study 2. At each intersection of two walls, and running the entire height of the walls, was a 7 mm wide square column. The column was black and served to highlight the corners of the arenas. The walls surrounding the arenas were 3.5 m high, assuming a participant height of 170 cm. Outside of these walls a uniform, light-blue sky was all that was visible to participants.

A target object was used to mark the goal location, a multi-colored beach ball of radius 22.5 cm . The position of this beach ball was set so that its center lay 48 cm from the intersection of two walls, on an imaginary line that bisected the corner. The height of the beach ball was such that its lowest point was flush to the ground. The environments were lit ambiently, with no directional light sources and no shadows. The VE recorded latency and choice information from all trials of the study.

Design and Procedure

The study was designed to match closely the procedure of Study 2. Participants received two training trials, followed by a transfer trial. Each trial consisted of two phases: an exposure phase during which the beach ball was present, followed by a test phase in which participants had to relocate the hidden beach ball.

All exposure phases occurred in the rectangular arena. The participant began in the center of the arena, facing the center of a long wall, with the beach ball located at a consistent corner throughout the three trials. The position of the beach ball remained the same for each participant, with the actual positions counterbalanced across participants. At the beginning of a trial the VE automatically rotated the participant through 360° in a clockwise direction over the course of 10 seconds, during which the participant had no control over their movement. The automatic rotation was to compensate for the relatively limited field of view afforded in the VE relative to a real environment.. Once the automatic rotation had completed, the participants were given 10 seconds during which they were allowed to rotate freely, but were unable to move from their central position. During this initial 20 seconds a message reading "Remember where the beach ball is" was displayed in the top-left of the screen. The message was then changed to "Touch the beach ball to proceed" and participants were given full control over movement and rotation. Once the participant had touched the beach ball, the screen went to black with the message "Please wait for next trial..." displayed in white text. After an inter-trial interval (ITI) of 20 seconds (the approximate time the disorientation phase lasted in Study 2), the test phase of the trial began.

During the test phases of all three trials, there was no beach ball present and participants had to visit the place in the arena where they thought the beach ball should be located. For the first two trials, the test phases occurred in the rectangular arena. Participants began the phase in the center of the arena, facing to the center of one of the four walls. The identity of this wall was counterbalanced between participants. The message "Relocate the beach ball" was presented on screen, and participants had free control over both rotation and movement from the outset of the test phase. A choice was determined by a participant being less than 135cm from the intersection of two walls. If the correct corner was entered, then the message "It's here! Well done!" was displayed on screen. For 5 seconds, the participant was then able to rotate, but not move, to learn more about the correct location. Should a participant approach an incorrect corner, they received the message "Not here, keep searching" and had to continue their search until the correct corner was entered. For the final trial, the test phase occurred in the kite-shaped arena. Forced rotation, followed by free rotation in the absence of movement, then occurred in the same manner as during the exposure phase of the first two trials, to ensure that participants could observe the whole arena before making a choice. This was accompanied by the message "Where should the beach ball be located?" Once this forced and free rotation had been completed, the onscreen message changed to "Move directly to where you think the beach ball should be" and participants were given full control over rotation and movement.

Results and Discussion

During the test phases of the first two training trials, participants chose the correct or rotationally equivalent corners significantly more frequently than the incorrect corners (trial 1: 40 versus 8; trial 2: 42 versus 6; binomial tests *p*s < .001), with no significant differences between correct and rotationally equivalent corners (57% of participants selected the correct corner first across the 2 rectangle trials). There were no differences between males and females in the percentage of trials in which they chose the correct and rotationally equivalent corners over the incorrect corners (males: 81.25%; females 87.5%; $t(46) = .75$, $p > .4$). The results demonstrate that adults were able to learn and remember the location of the beach ball during the exposure phases of the training trials in the rectangle.

Unlike the children in Study 2, adults were also able to discriminate the congruent corner in the kite test phase from the other corners χ^2 (3) = 17.2, $p < .001$. Post-hoc binomial tests showed that significantly more participants chose the congruent corner (24) than chose either the incongruent corner (5), obtuse corner (10) or acute corner (9), *p*s < .05.

The results demonstrate unequivocally that adults are capable of identifying a location based on local geometry, and that this effect does not rely on extensive training (see also Bodily et al., 2011, Sturz et al., 2011, and Doeller et al., 2008). Recent work with rats by Poulter, Kosaki, Easton, and McGregor (2013) has also demonstrated that transfer of search phenomena can occur in this species without the need for extensive training. Poulter et al. found that rats showed a preference for exploring a familiar object in a novel location based on local geometry after only a single exposure during familiarization. Research using techniques that go beyond behavioral measures are required in order to establish the brain systems underlying these different transfer of search phenomena, but it is clear that extensive training to build up S-R associations is not always required.

The results of Study 4 clarify that the failure of young children to transfer search relative to adults was not due to differences in training procedures. The implications of this finding, and those of the other studies, are considered further in the General Discussion.

General Discussion

One interpretation for the finding that adults show robust transfer of search between rectangular and kite-shaped virtual environments is that, as with rats, an environment can be parsed into local geometry segments (Pearce et al., 2004). Before such a conclusion can be accepted the possibility of transfer based on global shape parameters should be ruled out. Cheng and Gallistel (2005) discussed the possibility of transfer between environments based on generalization between responses made with respect to the principal axis of an environment, a parameter based on the global properties of the environment. Although McGregor et al. (2006) and Kelly et al. (2011) have failed to find any evidence in support of principal axis use in non-human animals, recent studies have shown adult humans to be capable of using the principal axis. Bodily et al. (2011) have shown adults' search in transformed arenas to be consistent with both global geometry in the form of principal axes, and local geometry in terms of the wall lengths and angles subtended by walls in individual corners. Further studies (Sturz, & Bodily, 2011; Sturz et al., 2011) have examined the circumstances in which global and local geometric learning takes precedence. However, as discussed in relation to the design of Study 1 earlier, our results are more consistent with learning based on local geometric cues. The inclusion of the circle-trained condition reduced the possibility that search in the acute corner of the kite by rectangle-trained participants was the result of navigation in the rectangle based on its principal axis.

However adults were able to show transfer of search between environments, the key findings of the current article are from Studies 2 and 3 suggesting that children were disrupted by the shape change, particularly in terms of higher search rates at the acute corner of the kite-shaped arena, relative to when children see the photograph hidden in one of the side pockets of the kite-shaped arena. An account of reorientation performance in the rectangle that focuses strictly on learning based on local geometric features (Miller & Shettleworth, 2007, 2008; review in Pearce, 2009) is not supported by the findings that children can show above chance performance in the rectangular arena, without transfer of search occurring in the kite-shaped arena. Study 4 additionally demonstrated that procedural differences between Study 1 and Study 2 could not account for children's failure to transfer search relative to adults.

In combination with the data from Lee et al. (2012) our results strongly suggest that local geometry matching between hiding and search plays little role in reorientation performance in children, with reestablishment of heading based on more global shape parameters being critical in this task. Successful transfer of search appears to rely on different spatial mechanisms relative to reorientation performance. It would also be hard to account for the pattern of search performance by children based on view-matching processes, in that it would not be predicted that search would occur at the acute corner in the kite-shaped arena, as happened in Study 2 after arena shape change, given the lack of match between this corner and the goal corner in the rectangle. View-matching processes based on minimising the difference between the current panorama and memorised panoramic snapshots of the goal location have been found to account for a range of findings concerning insect navigation, but the relevance of view-matching algorithms in mammalian spatial orientation has been questioned (Lee & Spelke, 2011; Stürzl, Cheung, Cheng, & Zeil, 2008; Twyman & Newcombe, 2010; Wystrach, Cheng, Sosa, & Beugnon, 2011).

Further research is required, perhaps using a combination of real and virtual arenas, to examine when in development successful transfer of search occurs, and the mechanisms that underlie such development. Research using the reorientation task shows an increase across development in performance, such that by 5-6 years of age adult levels of performance are obtained in simple enclosures (Hermer-Vasquez, Moffet & Munkholm, 2001). Shusterman, Lee, and Spelke (2011, also Hermer-Vasquez et al., 2001) argue that the attainment of correct spatial language, for example in use of left-right terms for sense relations, underpins the ability to combine featural and geometric information. Twyman and Newcombe (2010; also Twyman, Friedman & Spetch, 2007) question whether the acquisition of spatial language is causal in this case, or is reflective of greater ability to remember and integrate angular, length, distance and sense information in the context of navigation. It is likely that successful transfer of search will not occur until robust correct performance is observed when no change in global geometry occurs. Recently, Chiang (2013) found that 3-5-year-old children were better able to find a goal in an acute-angled corner of a simple isosceles-shaped table-top model room, compared to a similarly angled corner within a more complex shape. Performance improved across the age range studied within the isosceles model. This study did not examine transfer of search, but the results reinforce the view that children do not *a priori* fragment global geometry into constituent elements, only doing so, depending on task demands and the complexity of the environment, later in development.

In summary, the transfer of search paradigm is a fruitful way of studying the systems underlying coding of local geometry in humans, both from developmental and comparative perspectives. The pattern of findings showing no transfer of search in young children, together with robust transfer in adults, suggests that the matching of elements of local geometry in new global contexts may be an advanced developmental achievement. It is unlikely that above-chance reorientation performance in the original arena can therefore be accounted for by local geometry-matching processes, as opposed to a re-establishing of heading utilising some aspect of global geometry. The question of which mechanisms are responsible for successful transfer of search based on local geometry requires further research, particularly with methods such as fMRI that can go beyond behavioral performance, with either hippocampal or striatal systems being potential candidates.

References

Advanced Interfaces Group (2008). MAVERIK virtual reality software. University of Manchester (UK). Retrieved June 2008 from http://aig.cs.man.ac.uk/maverik.

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011) Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition, 14*, 665-674.

Bullens, J., Nardini, M., Döeller, C. F., Braddick, O., Postma, A. & Burgess, N. (2010). The role of landmarks and boundaries in the development of spatial memory. *Developmental Science, 13*, 170-180. doi: 10.1111/j.1467-7687.2009.00870.x

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

Cheng, K. & Gallistel, R. C. (2005). Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi & Poli (2004). *Journal of Experimental Psychology: Animal Behavior Processes, 31*, 254-259. doi: 10.1037/0097-7403.31.2.254

Chiang, N. C. (2013). Influence of global shapes on children's coding of local geometric information in small-scale spaces. Learning and Motivation, 44, 16-30. doi: 10.1016/j.lmot.2012.03.002

Dawson, M. R. W., Kelly, D. M., Spetch, M. L., & Dupuis, B. (2010). Using perceptrons to explore the reorientation task. *Cognition, 114*, 207-226. doi: 10.1016/j.cognition.2009.09.006

Döeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the USA, 105,* 5909-5914. doi: 10.1073/pnas.0711433105

Döeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the USA, 105,* 5915-5920. doi: 10.1073/pnas.0801489105

Esber, G. R., McGregor, A., Good, M. A., Hayward, A., & Pearce, J. M. (2005). Transfer of spatial behaviour controlled by a landmark array with a distinctive shape. *The Quarterly Journal of Experimental Psychology, 58B*, 61-91. doi: 10.1080/02724990444000069

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

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.

Hull, C. L. (1932). The goal-gradient hypothesis and maze learning. *Psychological Review, 39,* 25-42.

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

Huttenlocher, J. & Vasilyeva, M. (2003). How toddlers represent enclosed spaces. *Cognitive Science, 27*, 749-766. doi: 10.1016/S0364-0213(03)00062-4

Jeffery, K. J. (2010). Theoretical accounts of spatial learning: A neurobiological view (commentary on Pearce, 2009). *The Quarterly Journal of Experimental Psychology, 63,* 1683-1699. doi: 10.1080/17470210903540771

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: do animals use global or local geometry strategies? *Biology Letters, 7*, 372-375. doi: 10.1098/rsbl.2010.1024

Kelly, D. M., Durocher, S., Chiandetti, C., & Vallortigara, G. (2011). A misunderstanding of principal and medial axes? Reply to Sturz & Bodily. Biology Letters, 7, 649-650. doi: 10.1098/rsbl.2011.0482

Knight, R., Hayman, R., Ginzberg, L. L., & Jeffery, K. (2011). Geometric cues influence head direction cells only weakly in nondisoriented rats. *Journal of Neuroscience, 31,* 15681-15692. doi: 10.1523/JNEUROSCI.2257-11.2011

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

Lee, S. A. & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic Bulletin & Review, 18,* 192-198. doi: 10.3758/s13423-010-0035-z

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

Lew, A. R., Foster, K. A., Bremner, J. G., Slavin, S., & Green, M. (2005). Detection of geometric, but not topological, spatial transformations in 6- to 12-month-old infants in a visual exploration paradigm. *Developmental Psychobiology, 47*, 31-42.

Lew, A. R., Gibbons, B., Murphy, C., & Bremner, J. G. (2010). Use of geometry for spatial reorientation in children applies only to symmetric spaces. *Developmental Science, 13*, 490-498. doi: 10.1111/j.1467-7687.2009

Margules, J. & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. Animal Learning & Behavior, 16, 404-410.

McGregor, A., Hayward, A.J., Pearce, J. M., & Good, M. A. (2004). Hippocampal lesions disrupt navigation based on the shape of the environment, *Behavioral Neuroscience, 118,* 1011-1021. doi: 10.1037/0735-7044.118.5.1011

McGregor, A., Jones, P. M., Good, M. A., & Pearce, J. M. (2006). Further evidence that rats rely on local rather than global spatial information to locate a hidden goal: Reply to Cheng and Gallistel (2005). *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 314-321. doi: 10.1037/0097-7403.32.3.314

Miller, N. Y. & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes, 33,* 191-212. doi: 10.1037/0097-7403.33.3.191

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

O'Keefe, J. & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford, UK: Clarendon Press.

Pearce, J. M. (2009). An associative analysis of spatial learning. *The Quarterly Journal of Experimental Psychology, 62*, 1665-1684. doi: 10.1080/17470210902805589

Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30,* 135-147. doi: 10.1037/0097-7403.2.135

Poulter, S.L., Kosaki, Y., Easton, A., & McGregor, A. (2013). Spontaneous object location memory is maintained following transformation of global geometric properties. *Journal of Experimental Psychology: Animal Behavior Processes*. Advance Online Publication. doi: 10.1037/a0030698

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

Sturz, B. R., & Bodily, K. D. (2011b). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin and Review, 18*, 848 – 854. doi: 10.3758/s13423-011-0111-z

Sturz, B., & Bodily, K. D. (2011a). Of global space or perceived place? Comment on Kelly *et al*. Biology Letters, 7, 647-648. doi: 10.1098/rsbl.2011.0216

Sturz, 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.

Stürzl, W., Cheung, A., Cheng, K., & Zeil, J. (2008). The information content of panoramic images I: The rotational errors and the similarity of views in rectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34,* 1-14. doi: 10.1037/0097-7403.34.1.1

Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews, 36,* 799-824. doi: 10.1016/j.neubiorev.2011.12.007

Tommasi, L. & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (Gallus gallus). *Animal Cognition, 7* 53-59. doi: 10.1007/s10071-003-0182-y

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

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

Wang, R. F. & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6,* 376-382.

White, N. M. & McDonald, R. J. (2002). Multiple parallel memory systems in the brain of the rat. *Neurobiology of Learning and Memory, 77*, 125-184. doi: 10.1006/nlme.2001.4008

Wystrach, A., Cheng, K., Sosa, S., & Beugnon, G. (2011). Geometry, features, and panoramic views: Ants in rectangular arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 37*, 420-435. doi: 10.1037/a0023886

Yaski, O. & Eilam, D. (2008). How do global and local geometries shape exploratory behaviour in rats? *Behavioural Brain Research, 187*, 334-342. doi: 10.1016/j.bbr.2007.09.027