Thinking outside of the box: Transfer of shape-based reorientation across the boundary of an arena

CrossMark

Matthew G. Buckley [a,*], Alastair D. Smith [b], Mark Haselgrove [b]

[a] Department of Psychology, Durham University, Science Site, Durham, DH1 3LE, UK
[b] School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK

ARTICLE INFO

ABSTRACT

The way in which human and non-human animals represent the shape of their environments remains a contentious issue. According to local theories of shape learning, organisms encode the local geometric features of the environment that signal a goal location. In contrast, global theories of shape learning suggest that organisms encode the overall shape of the environment. There is, however, a surprising lack of evidence to support this latter claim, despite the fact that common behaviours seem to require encoding of the global-shape of an environment. We tested one such behaviour in 5 experiments, in which human participants were trained to navigate to a hidden goal on one side of a virtual arena (e.g. the inside) before being required to find the same point on the alternative side (e.g. the outside). Participants navigated to the appropriate goal location, both when inside and outside the virtual arena, but only when the shape of the arena remained the same between training and test (Experiments 1a and 1b). When the arena shape was transformed between these stages, participants were lost (Experiments 2a and 2b). When training and testing was conducted on the outside of two different-shaped arenas that shared local geometric cues participants once again explored the appropriate goal location (Experiment 3). These results provide core evidence that humans encode a global representation of the overall shape of the environments in, or around, which they navigate.

© 2016 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

* Corresponding authors.
   E-mail addresses: matthew.buckley@durham.ac.uk (M.G. Buckley), alastair.smith@nottingham.ac.uk (A.D. Smith), mark.haselgrove@nottingham.ac.uk (M. Haselgrove).

1. Introduction

In order to navigate efficiently, organisms must maintain a sense of direction within the environment. If an organism becomes lost for any reason, a process of reorientation must occur in order for it to know the direction of travel. For instance, when emerging from an underground train station, it is necessary to reorient in order to know the direction in which to walk to work. For nearly 30 years, there has been an ongoing and influential debate surrounding the manner in which human and non-human animals learn about the *shape* information that is provided by the boundary walls of an environment, and its relative importance in reorientation behaviour (for recent reviews see: Burgess, 2008; Jeffery, 2010; Pearce, 2009). A wide range of species, with different evolutionary paths, have been observed to use the shape information that is provided by the boundaries of an environment during reorientation, including ants (Wystrach & Beugnon, 2009), fish (Sovrano, Bisazza, & Vallortigara, 2002), chicks (Vallortigara, Zanforlin, & Pasti, 1990), mountain chickadees (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005), pigeons (Kelly, Spetch, & Heth, 1998), rats (Hayward, Good, & Pearce, 2004), rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001), as well as children (e.g. Hermer & Spelke, 1994, 1996) and adult humans (Redhead & Hamilton, 2007, 2009). Whilst these findings demonstrate that the shape information provided by the boundary walls of an environment acts as a useful cue for reorientation, there has been considerable discussion about how animals encode shape information (for a review see: Cheng, Huttenlocher, & Newcombe, 2013).

The origin of this debate can be traced back to the seminal work of Cheng (1986), who trained rats to find food buried within a rectangular arena, each corner of which contained a unique landmark. The rats quickly learned to dig in the corner that was baited with food; however, they also frequently dug in the corner that was diametrically opposite the baited corner (see also: Margules & Gallistel, 1988). As the baited corner and the diametrically opposite corner are geometrically equivalent, it appeared that the rats were relying on the shape of the environment to locate the buried food, rather than the unambiguous landmark cues. When discussing these findings, Cheng and Spetch (1998) claimed that the animals were using the broad shape of the environment to reorient and, on the basis of his results, Cheng (1986) proposed that the shape information provided by the boundary walls of an environment is processed in a dedicated geometric module that encodes a global representation of the shape properties of an environment (see also: Wang & Spelke, 2002, 2003). A similar proposal was made by Gallistel (1990), who noted that, whilst animals frequently use non-geometric landmark cues to guide some navigational behaviour, when disorientated, they rely almost exclusively on the global geometric properties of an environment to re-establish orientation.

The notion that organisms reorient using a global representation of the shape of the environment has, however, not gone unchallenged. As noted by Pearce, Good, Jones, and McGregor (2004), it is possible to explain the findings reported by Cheng (1986) by assuming that, instead of encoding a global representation of the shape of the environment, rats learned the location of the buried food on the basis of local-shape information. According to this analysis, organisms encoded only the local-shape information that predicted the location of a goal, such as the sight of a short wall to the left of a long wall. Crucially, the corner diametrically opposite this baited corner was geometrically identical, also being formed of a short wall to the left of a long wall. Rats reorienting on the basis of local-shape information in Cheng's experiment, therefore, would also be expected to visit the diametrically opposite corner.

In support of local theories of shape encoding, a number of shape-transformation experiments have demonstrated that organisms transfer search behaviour that is based on both the relative lengths, and angles, of conjoining walls between environments that have different global shapes. For instance, Lew et al. (2014) trained adult humans to navigate to a hidden goal in, say, the corner of a rectangle-shaped virtual environment where a short wall was to the left of a long wall, after which a test trial was administered in a kite-shaped virtual environment that was built from the same walls as the rectangle-shaped environment. During this test trial, participants spent more time in (Experiment 1), or visited first (Experiment 4), the corner of the kite-shaped arena that shared the same local-shape cues as the rewarded corner of the rectangle-shaped arena (see also: Buckley, Smith, & Haselgrove, 2015; Esber, McGregor, Good, Hayward, & Pearce, 2005; Pearce et al., 2004; Poulter,

Kosaki, Easton, & McGregor, 2013). Similarly, humans trained to locate a goal in a parallelogram-shaped virtual environment preferentially searched in the acute corners of a rhombus-shaped virtual environment in a subsequent test (Lubyk, Dupuis, Gutierrez, & Spetch, 2012: see also Tommasi & Polli, 2004). The results of these shape-transformation experiments appear inconsistent with theories that emphasise global-shape encoding. If participants were only using a representation of the global-shape of the training environment to locate the goal, then this would be of little help in a test environment of a different shape. Instead, the results of these shape-transformation experiments are more amenable to an explanation based on encoding of local-shape cues, where organisms encode segments of the environment that are associated with the goal location (Pearce, 2009; Pearce et al., 2004).

Although theories based on local-shape cues (e.g. Pearce, 2009) provide an explanation for the transfer of behaviour between different shaped environments, it has been argued that, in fact, the transfer of behaviour between kite- and rectangle-shaped environments can be explained by a global-shape property of the environment, namely, the principal axis. The principal axis is colloquially known as the long axis, and passes through the centre of any shape (see Cheng, 2005). In a rectangle, the principal axis connects the centre of each short wall and, in a kite, it runs from the acute corner to the obtuse corner. Cheng and Gallistel (2005) suggested that animals can extract the principal axis of the shape of the environment, and use this to align global representations of the shapes in which they navigate. The behaviour of participants in the Lew et al. (2014) study could be explained if participants travelled to the corner that was the furthest to the right of the principal axis in both training and test arenas. In both a rectangle- and kite-shaped environment, travelling to the furthest wall to the right of the principal axis would lead the animal to the corners which shared the same local geometry of a short wall to the left of a long wall.

Experiments conducted with non-human animals have failed to find evidence to support the use of the principal axis during reorientation (Kelly, Chiandetti, & Vallortigara, 2010; McGregor, Jones, Good, & Pearce, 2006). It has, however, been demonstrated that adult humans can use the principal axis to guide reorientation. For example, Bodily, Eastman, and Sturz (2011) trained participants, in a trapezium-shaped virtual environment that comprised three equally sized short walls and one long wall, to find a goal located at the obtuse corner that was on the right side of a principal axis. Participants were then placed in a rectangle-shaped environment, where they preferentially searched in the corners of the rectangle where a short wall was to the left of a long wall. As the walls either side of the goal location in the trapezium-shaped training environment were the same size, and because there were no obtuse corners in the rectangle-shaped test arena, local-shape information could not have been driving this behaviour. Instead, it was suggested that the preference shown by participants in the rectangle-shaped test arena was driven by them travelling to corners that were on the right side of the principal axis, as it was this side of the principal axis that was rewarded during training (see also: Sturz & Bodily, 2011). In similar shape-transformation experiments, adult humans have been observed to preferentially use local-shape information over the principal axis (Bodily et al., 2011), but the opposite preference has also been observed (Sturz, Gurley, & Bodily, 2011). Whether local-shape information is preferred over information provided by the principal axis of environments, or vice versa, appears to depend on the size of the environments (Sturz, Forloines, & Bodily, 2012), the field of vision (Sturz, Kilday, & Bodily, 2013), and the relative length of walls (Sturz & Bodily, 2011).

The shape-transformation experiments reviewed above demonstrate that humans can transfer search behaviour between environments based on local-shape information, or the principal axis of environments. This evidence has led a number of authors to question whether organisms encode a global representation of the entire shape of the environment (e.g. Pearce, 2009; Twyman & Newcombe, 2010) and, moreover, it has been argued that it is not necessary to assume animals acquire a global representation of the entire shape of the environment in which they navigate (e.g. McGregor et al., 2006; Pearce et al., 2004). It is important to note, however, that evidence from shape transformation experiments that implicates reorientation on the basis of local-shape information, or the principal axis of environments, does not constitute evidence against the possibility that animals can also reorient using a representation of the global shape of the environment. For instance, in the first stage of the experiment conducted by Lew et al. (2014), it is possible that participants used both the local and the global-shape properties of the rectangle-shaped environment to travel to the hidden goal. At test, however, the global representation of the rectangle-shaped training environment would be

incongruent to the, now, kite-shaped test environment. Consequently, any global representation encoded by participants during training would be of little worth in guiding behaviour during test, thus, forcing them to reorient on the basis of the local-shape or principal-axis information that were preserved between the training and testing environments. Given this argument, there is little evidence against claims that organisms reorient using a global representation of the shape of the environment (Cheng, 1986; Gallistel, 1990). At the same time, however, there is surprisingly little behavioural evidence to support these claims, which is somewhat surprising given their continued discussion in the spatial literature (e.g. Burgess, 2006, 2008; Gallistel & Matzel, 2013; Lew, 2011; Spelke & Lee, 2012; Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012). Despite the relative lack of evidence for encoding of a global-shape representation, people's real-world behaviour suggests a motivation to use a global representation of the shape of the environment. For example, when working within, around, or upon a building, maintenance workers frequently consult a blueprint, or plan view, of the building in order to acquire a global representation of its shape.

Part of the problem in providing evidence for the notion that organisms encode a global representation of the shape of their environments is that it is difficult to design an environment whereby responses based on a global-shape representation can be dissociated from responses based upon local-shape cues. To assess if organisms reorient using a representation of the global shape of the environment, it is necessary to preserve the overall shape of the environment between training and testing, whilst also arranging a situation where theories based on local and global-shape cues predict differing behavioural responses. One manner in which this might be achieved is by training participants on the inside of an arena, before conducting a test trial on the outside of the same-shaped arena. As noted by Lourenco and Huttenlocher (2007), local-shape information is viewpoint dependent (i.e. it is encoded egocentrically). For example, consider a participant that is trained to travel to the inside corner of a kite-shaped arena where a short wall is to the left of a long wall. When placed on the outside of the same arena, the view of the rewarded corner is a short wall to the right of a long wall. As the relative lengths of the left- and right-sided walls are reversed from training, responding only on the basis of relative wall lengths would not lead the participant to the outside of the corner rewarded during training. In contrast, a representation of the global shape of the environment is viewpoint independent (i.e. it is encoded allocentrically). The overall shape of an environment does not change depending on whether the walls are viewed from the inside or the outside. Consequently, responding on the basis of a representation of the global shape would lead the participant to the outside of the corner rewarded during training.

To the best of our knowledge, only one study has conducted an inside-to-outside manipulation before. In an experiment conducted by Lourenco, Huttenlocher, and Vasilyeva (2005), 2-year old infants watched an experimenter hide a toy in a corner of a rectangle-shaped box that was located in a circular enclosure. During this phase of the experiment, infants were either placed on the inside, or outside, of the rectangular box. Once the toy was hidden, infants were disorientated, and asked to find the toy from the alternative side of the arena (i.e. outside or inside, respectively). Providing the disorientation procedure occurred following the translation between inside and outside, infants were able to relocate the toy. Interestingly, infants were unable to relocate the toy if disorientation preceded the translation between inside and outside. It is, however, rather difficult to interpret these results in terms of what shape representations children may have been using to guide search behaviour. As the authors note, when outside of the rectangular box, its walls were sufficiently low that infants could view every corner of the box from one position. Consequently, when on the outside of the box, participants would still have access to the spatial information about the inside of the box. This being the case, it is not possible to dissociate whether responses were being made on the basis of a global- or local-shape representation.

In the experiments reported here, we conducted inside-to-outside manipulations using virtual environments, with adult human participants, in order to assess the extent to which representations of global-shape, local-shape, and the principal axis are relied upon during reorientation. This is a deviation from traditional reorientation designs, which have largely focussed on reorientation within an environment. That there has been little focus on the study of how organisms reorient around bounded environments, or transfer their search behaviour between one side of an environment to the other (e.g. from the inside to the outside of a building), has been an important omission for at least two reasons.

First, humans regularly navigate around the boundaries of large environments in order to find a goal (such as when attempting to find the appropriate entrance to a sports stadium), and also transfer their search behaviour across environmental boundaries (such as when trying to locate a hole on the inside of a building having drilled into it from the outside). Second, our theories of shape-based reorientation (e.g. Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990; Pearce, 2009; Pearce et al., 2004) are limited by experiments conducted only in the context of participants reorienting within a bounded space. By transferring participants from the inside to the outside of an arena (or vice versa), our novel task provided the first insight into whether these theories can explain reorientation on the outside of an arena. In addition, because our task involves an unexpected shift in viewpoint, it was also uniquely placed to examine if the representations used for reorientation are allocentric in nature.

Participants in Experiments 1a and 1b were trained to navigate to a right-angled corner where, for example, a short wall was to the left of a long wall on one side of either a kite- or a rectangle-shaped arena (Experiment 1a: inside; Experiment 1b: outside). Following this training, participants received a test trial conducted on the alternative side of the same-shaped arena (Experiment 1a: outside; Experiment 1b: inside). As noted previously, the relative lengths of the left- and right-sided walls are reversed under these circumstances. Theories of reorientation based on local-shape cues that are formed explicitly in terms of relative wall lengths do not expect participants to navigate to the goal corner (e.g. Pearce, 2009; Pearce et al., 2004). Reorientation that is based upon a global representation of the shape of the environment, however, would lead participants to the goal corner (e.g. Gallistel, 1990). In Experiments 2a and 2b, participants were again trained to navigate to a particular corner on one side of, say, a kite-shaped arena, before receiving a test trial conducted on the alternative side of a rectangle-shaped arena. As the global shape of the training and test environments differed, participants could not navigate to the goal corner, at test, on the basis of a representation of the global-shape of the environment (e.g. Gallistel, 1990). Consequently, this manipulation assessed if participants could navigate to a previously rewarded corner on the basis of only the principal axis of the shapes (Bodily et al., 2011; Cheng & Gallistel, 2005). Finally, in Experiment 3, we trained participants to navigate to a hidden goal on the outside of a kite-shaped arena before testing their search behaviour on the outside of a rectangle-shaped arena (or vice versa). This experiment assessed whether reorientation around the outside of these shapes was consistent with previous observations from shape transformation experiments that have been conducted on the inside of these shapes (e.g. Lew et al., 2014).

2. Experiments 1a and 1b

In Experiment 1a, participants were trained to find a hidden goal that was positioned at one of the right-angled corners on the inside of either a kite- or rectangle-shaped virtual environment. Following this training, participants were given a single test trial in which, unbeknownst to the participants, there were no hidden goals. During the test trials, participants were placed on the outside of the same-shaped arena in which they were trained, and allowed to search for 120 seconds. If, during the test trial, participants were reorienting on the basis of a global representation of the shape of the environment (Gallistel, 1990), they should spend more time searching near the corner that previously contained the hidden goal (see Fig. 1). Theories of reorientation based solely on encoding of relative wall lengths (Pearce, 2009; Pearce et al., 2004), however, expect that participants would spend more time searching near the corner that did not previously contain the goal (see Fig. 1). Human participants trained to find a goal in the acute or obtuse corners of a parallelogram-shaped virtual environment have been observed to transfer learning based on relative wall lengths to a rectangle-shaped virtual environment (Lubyk et al., 2012), but it remains to be determined if learned relative wall length information will transfer from a convex to a concave corner, and vice versa, as predicted by local-shape theories.

Experiment 1b followed the same logic, and was conducted to assess if moving from the outside to the inside of an environment would produce comparable effects to moving in the opposite direction. In Experiment 1b, participants were trained to find a hidden goal on the outside of a kite- or rectangle-shaped environment, before being tested on the inside of the same shape for 60 seconds in the absence of any hidden goals. Again, participants were predicted to search in different corners of the test arena
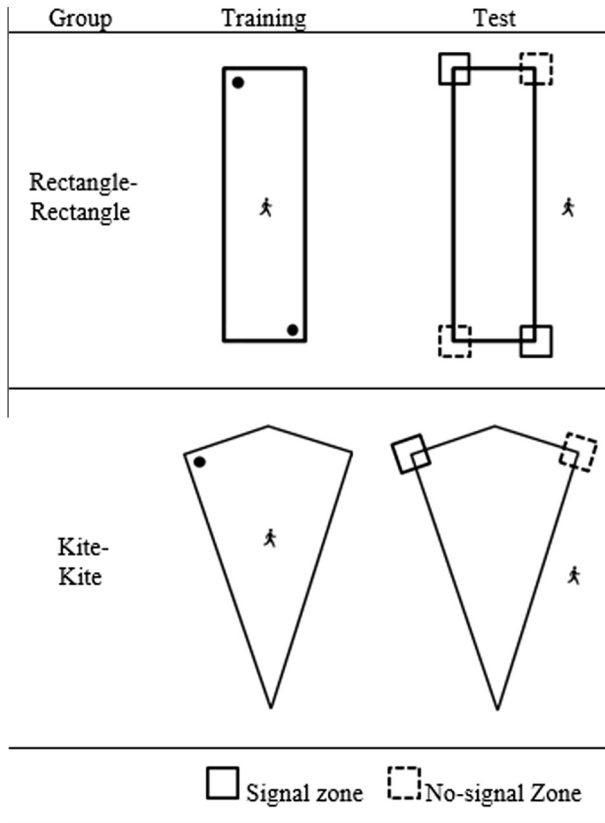
Fig. 1. Schematic views of the training and test environments of Experiments 1a. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

depending on whether they were reorienting using a global representation of the shape of the environment, or on the basis of local-shape information (Fig. 2). In Experiments 1a and 1b, the hidden goals that participants were searching for were a Wi-Fi and mobile (cell) phone signal, respectively. Searching for such signals has considerable face validity for young participants, and fits well with the allocentric nature of our task because these signals can realistically be present both on the inside and the outside of an arena, despite having an origin on only one side.

2.1. Method

2.1.1. Participants

For Experiment 1a, 32 students were recruited from the University of Nottingham (26 female), aged between 18 and 28 years (mean = 20.78, *SD* = 2.54). For Experiment 1b, a further 32 students, aged between 18 and 41 years (mean = 21.28, *SD* = 4.46), were also recruited from the University of Nottingham (23 female). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

2.1.2. Materials

All virtual environments were constructed and displayed using Mazesuite (v2.1) software (Ayaz, Allen, Platek, & Onaral, 2008; www.mazesuite.com). The virtual environments, which participants
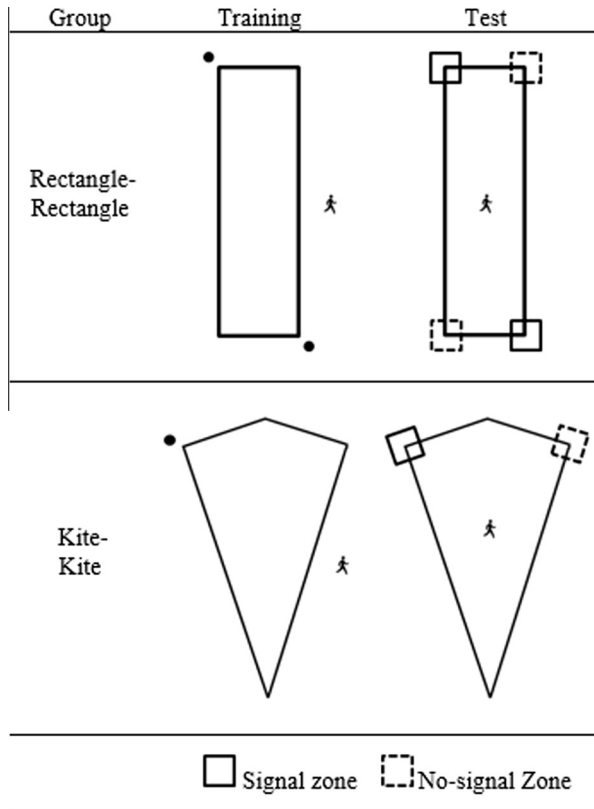
Fig. 2. Schematic views of the training and test environments of Experiments 1b. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

viewed from a first-person perspective with a field of view of 45°, were run and displayed on an Apple Mackintosh model A1224 (EMC2133) with a screen of 27.40 × 43.40 cm. Assuming a walking speed similar to that in the real world (2 m/s), the perimeter of both the kite and rectangular shaped arenas was 72 m, with the small walls being 9 m in length and the long walls 27 m. The height of both arenas was approximately 2.5 m. The kite was configured such that it contained two right-angled corners with the remaining two angles being 143.14° and 36.86°. The rectangle, necessarily, contained four 90° corners. The goals within the arenas were square-shaped regions (1.08 m × 1.08 m, invisible to participants) that were always placed 2.48 m away from the walls of the arena, along on a notional line that bisected the corner.

When participants were on the inside of the arena, a wooden texture was applied to the floor, and a uniform dark grey texture was applied to the ceiling. The walls of the arena were a cream colour which, using the 0–255 RGB scale employed by Mazesuite, were defined as 204, 178, 127. When participants were on the outside of the arena, a grass texture was applied to a 780 m × 780 m floor, and the sky was rendered as a uniform black expanse. As shown in Fig. 3, the uniform grassy plain on which participants walked extended towards a black horizon.

2.1.3. Procedure

After signing a standard consent form, participants were given a standard set of instructions (for Experiment 1a: Appendix A. For Experiment 1b: Appendix B). Participants sat not more than 50 cm
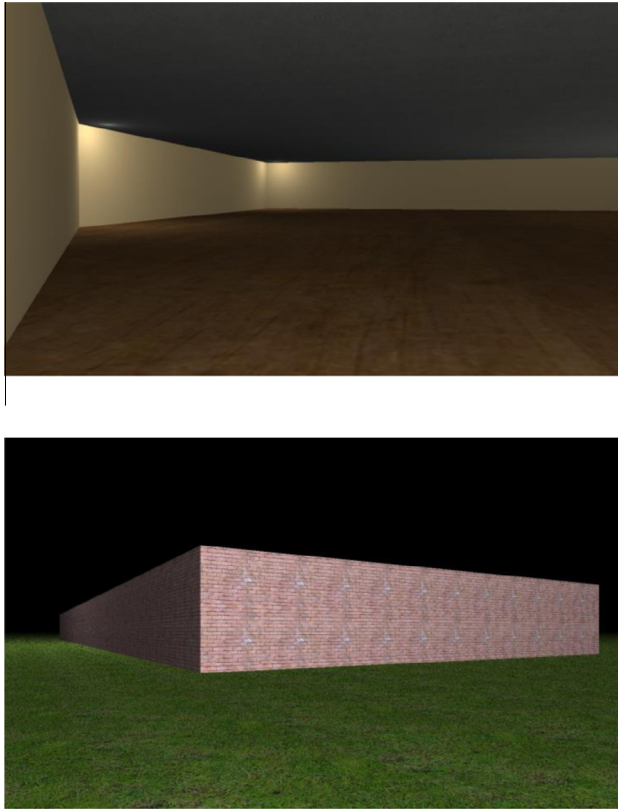
Fig. 3. Top: a screen shot of the inside of a kite-shaped arena. Bottom: a screen shot of the outside of a rectangle-shaped arena.

from the screen and, for each of the 16 acquisition trials that were administered, participants were required to navigate to the hidden goal by using the cursor keys. Presses on the "up" and "down" cursor keys permitted the participant to move forwards and backwards within the arena, respectively, while presses on the "left" and "right" cursor keys permitted the participant to rotate counterclockwise and clockwise within the environment, respectively. There was no time limit for any acquisition trials, thus, each trial ended only when the hidden goal was found. Once the hidden goal had been found, participants could no longer move within the arena and a congratulatory message (For Experiment 1a: *Wi-Fi Connected!* For Experiment 1b: *Signal Found!*) was displayed on screen using the default font and character size in Mazesuite. Participants pressed enter to begin the next trial.

The 32 participants recruited for Experiment 1a were split, equally, into two groups. Group rectangle-rectangle were trained inside a rectangle-shaped arena before receiving a test trial conducted on the outside of a rectangle-shaped arena and, likewise, group kite-kite were trained inside a kite-shaped arena before receiving a test trial conducted on the outside of a kite-shaped arena. During training, the location of the hidden goal, for both groups in the experiment, was counterbalanced such that eight participants within each group were required to navigate to a right-angled corner where a long wall was to the left of a short wall, whilst the remaining eight participants in each group were required to navigate to a right-angled corner where a long wall was to the right of a short wall. As with the kite-shaped arenas, we wanted to ensure that visits to the correct corner of the rectangle always resulted in finding the hidden goal. As the rectangular arenas contained two corners which shared the same geometric properties, it was necessary for each rectangular arena to contain two hidden goals. Experiment 1b was conducted in an identical manner, apart from the fact participants were trained on the outside of an arena before receiving a test trial conducted on the inside of an arena.

Participants trained inside of an arena travelled at 2 m/s during both acquisition and test trials (MazeSuite move parameter set to .005). Those trained inside of a kite-shaped arena began each trial at a point located halfway between the apex and obtuse corners, and the direction in which participants began facing was randomised for every trial. Participants trained inside a rectangle-shaped arena began each trial at the centre of the environment, again, facing in a random direction for every trial (see Fig. 4). Participants trained on the outside of these environments were required to traverse greater distances compared to those trained on the inside of an arena when learning the task. In order to not increase the length of time required to complete the task, participants trained on the outside of an arena travelled at 3.6 m/s during both acquisition and test trials (MazeSuite move parameter set to .009). Participants trained on the outside of either-shaped arena began each trial facing the centre of one of the four walls (see Fig. 4), and were located 3.15 m away from that wall, along a notional line running perpendicular to the wall. Each of the four walls served as a start location for four acquisition trials for each participant in Experiment 1b. As previously described, in both groups of the experiment, eight participants were required to navigate to a given corner of the arena. Of these eight participants, four received start locations in the order of ADBCDBCABDCACABD, whilst the other four received these start locations in reverse order.

Having completed 16 acquisition trials, participants received instructions prior to the test trial (for Experiment 1a: Appendix A. For Experiment 1b: Appendix B). For participants in both groups of Experiment 1a, pressing enter began a 120 second test trial in which they were placed on the outside of an arena that contained no hidden goals. Participants began the test trial facing one of the four walls of the shape, and were again located 3.15 m from the centre of the wall. There were 4 possible start locations for the test trial, and each location was used twice in every set of eight participants previously described. For participants in both groups of Experiment 1b, pressing enter began a 60 second test trial in which participants were placed on the inside of an arena that contained no hidden goals. For tests conducted in a kite-shaped arena, participants began each trial at a point located halfway between the apex and obtuse corners and, in a rectangle-shaped arena, they began each trial at the centre of the arena. In both shapes, the direction in which participants began facing was randomised for every trial.

At the beginning of the test trial, it was necessary for participants in Experiments 1a and 1b to establish their orientation using the shape of their environment, before beginning to search for the, now absent, hidden goal. When on the inside of an environment, it is possible to establish orientation
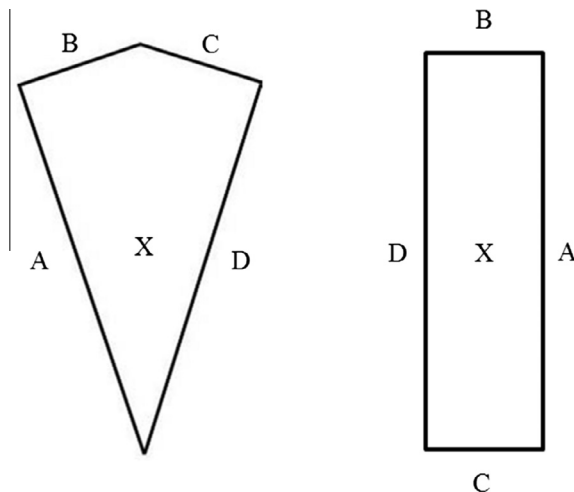
Fig. 4. Schematic diagrams of the environments used in the experiments. Letter X represents the location in which participants began each acquisition trial when trained to find a hidden goal inside of the environments, during Experiments 1a and 2a. Letters A, B, C, and D represent the locations in which participants began acquisition trials when trained to find a hidden goal on the outside of the environments, during Experiments 1b, 2b, and 3.

based on the shape of the environment by simply rotating around the *y*-axis to bring each consecutive wall into view. When on the outside of an environment, it is also necessary to view each consecutive wall in order to establish an orientation. This, however, this cannot be achieved by simply rotating around the *y*-axis. Instead, participants must travel along the *x*- and *z*-planes in order bring each wall into view and, consequently, establishing orientation when on the outside of an environment takes considerably longer compared to reorienting on the inside of an arena. In order to account for this, and ensure that participants tested on the outside of an environment had sufficient time to search for the absent hidden goal, we ensured that test trials conducted on the outside of an arena were 60 seconds longer than those conducted on the inside of an arena.

To measure behaviour during test trials, the time spent within 6.48 m × 6.48 m square search zones, which were centred on all points where a long and short wall met to create a right angled corner, was recorded. These search zones were orientated such that two of its edges were parallel to a long wall of an arena, and the remaining two edges ran parallel to a short wall of an arena (see Figs. 1 and 2). Signal zones were located at the right angled corners of an environment that had previously contained the hidden goal, and no-signal zones were located at the right angled corners of an environment that did not previously contain the hidden goal. Assessing spatial behaviour during extinction tests in such a manner is common in both animal (e.g. McGregor, Horne, Esber, & Pearce, 2009), and human (e.g. Redhead & Hamilton, 2009) experiments.

2.2. Results

In all the experiments reported here, we adopted an alpha level of .05 for each statistical test. For all *t*-tests, we report Cohen's *d* as a measure of effect size, and also report appropriate confidence intervals. For one-sample *t*-tests, we report the 95% confidence interval (CI) around the mean value observed for each experimental group, and for paired-samples *t*-tests we report the 95% CIs around the mean difference between two samples. Where data were subjected to analysis of variance (ANOVA), we used partial eta squared (η_p^2) to estimate the size of significant effects, and we report confidence intervals around this effect size to communicate uncertainty in the data (see: Lakens, 2013). According to Steiger (2004), if the confidence interval surrounding η_p^2 for a given effect excludes zero, the corresponding *p* value must indicate significance. This relationship, however, depends on calculating the appropriate confidence interval. In order to be consistent with the results obtained from analysis of variance (ANOVA) that uses .05 as the criterion for significance, it is necessary to calculate a 90% confidence interval around η_p^2. Calculating 95% confidence intervals around η_p^2 may lead to cases where an *F*-test returns a significant *p* value, but the confidence intervals for η_p^2 includes zero (Lakens, 2013).

2.2.1. Experiment 1a – acquisition (inside)

The top panel of Fig. 5 shows that the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal decreased across trials for both the rectangle-rectangle and kite-kite groups. A two-way ANOVA conducted on individual latencies to find the goal, with a between subjects factor of group (rectangle-rectangle or kite-kite) and a within subjects factor of trial (1–16), revealed a significant main effect of trial, $F(15,450) = 5.97$, $MSE = 2138.16$, $p < .001$, $\eta_p^2 = .17$ [.09–.19], confirming that participants found the hidden goal quicker as trials progressed. There was no main effect of group, $F(1,30) = 2.02$, $MSE = 2708.56$, $p = .17$, $\eta_p^2 = .06$ [.00–.23], however, the interaction between group and trial approached significance, $F(15,450) = 1.66$, $MSE = 2138.16$, $p = .056$, $\eta_p^2 = .05$ [.00–.06]. Simple main effects analysis revealed that this was driven by participants in the rectangle-rectangle group finding the goal quicker on trial 1 compared to participants in the kite-kite group, $F(1,30) = 6.49$, $MSE = 5267.38$, $p = .016$, $\eta_p^2 = .18$ [.02–.36]. There were no other differences between groups on any other trials, $Fs(1,30) < 3.46$, $MSEs < 24523.34$, $ps > .073$, $\eta_p^2 < .10$ [.00–.28].
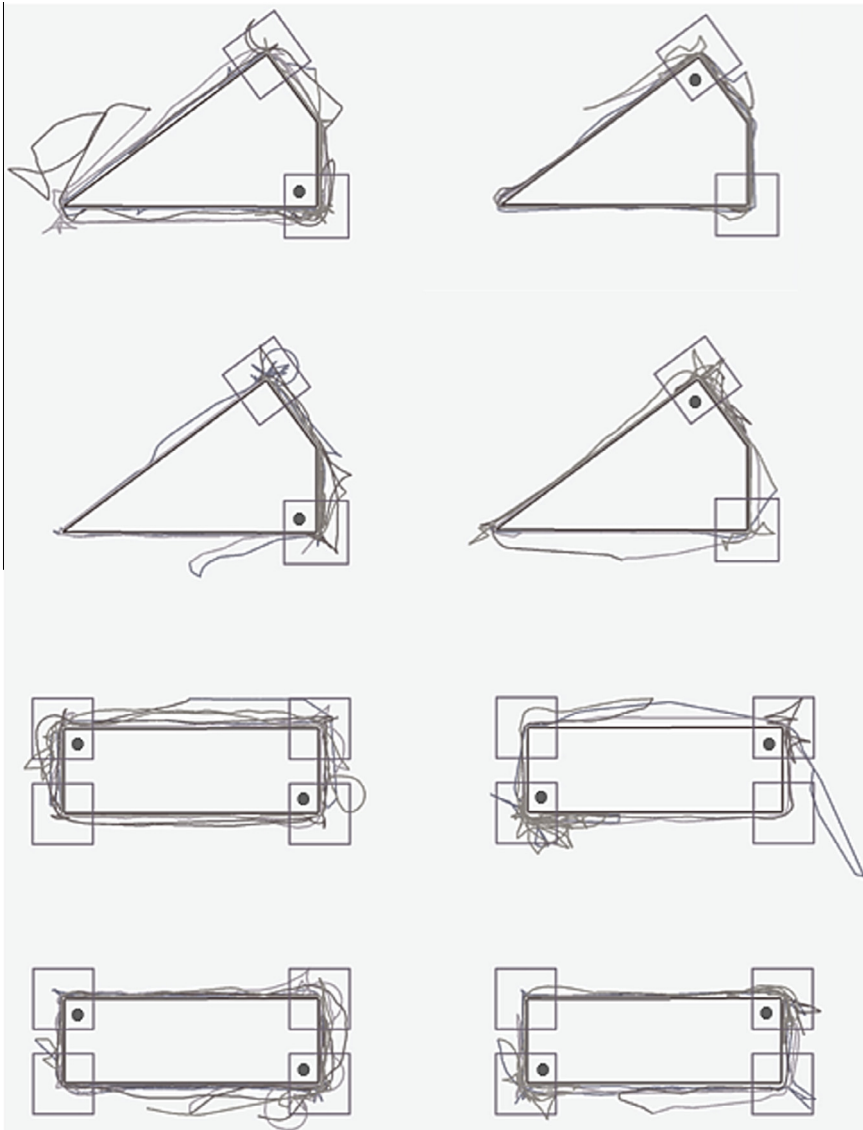
2.2.2. Experiment 1a – test trial (outside)

During the test trial conducted on the outside of the rectangle-shaped arena, paired-samples *t*-tests revealed that there were no significant differences in the mean number of seconds participants spent searching in the two signal zones, $t(15) = .172$, $p = .87$, $d = .04$ [−17.77–15.11], or the two no-signal zones, $t(15) = .918$, $p = .37$, $d = .22$ [−2.98–7.48]. In the following analysis, therefore, we collapsed
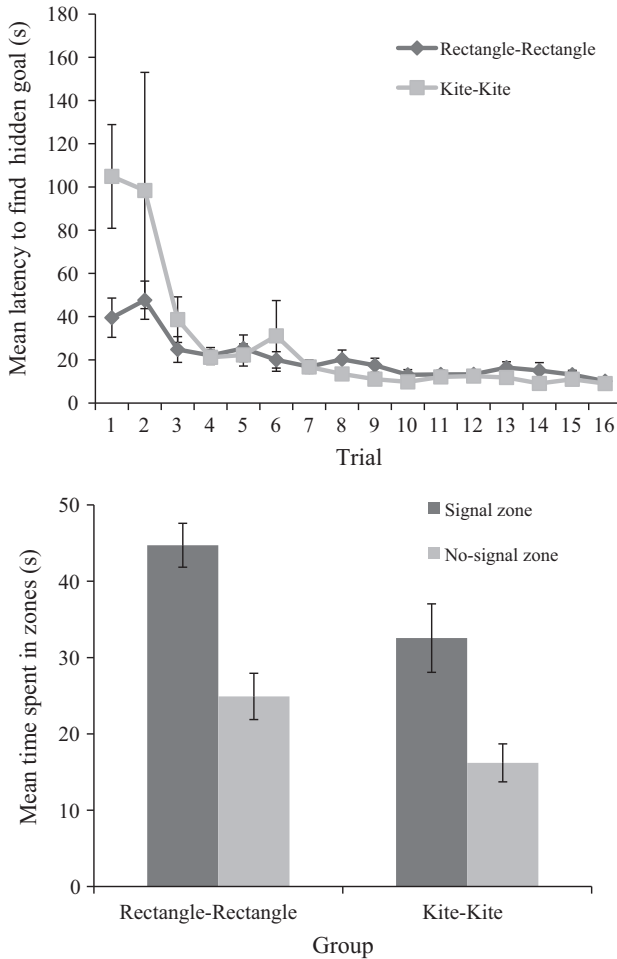
Fig. 5. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-rectangle and group kite-kite of Experiment 1a. Error bars show 1 ± standard error of the mean.

across both signal zones and also across both no-signal zones. The bottom panel of Fig. 5 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena. Participants in both the rectangle-rectangle and kite-kite groups searched for more time in the signal zone of the arena, compared to the no-signal zone (see Fig. 6 for individual paths traversed). A two-way ANOVA, with a between subjects factor of group (rectangle-rectangle or kite-kite) and a within subjects factor of zone (signal or no-signal), confirmed that participants spent more time in the signal zone, over the no-signal zone, $F(1, 30) = 22.93$, $MSE = 227.99$, $p < .001$, $\eta_p^2 = .43$ [.20–.58]. A significant main effect of group also revealed that participants in the rectangle-rectangle group spent more time in zones compared to participants in the kite-kite group, $F(1, 30) = 14.18$, $MSE = 122.79$, $p = .001$, $\eta_p^2 = .32$ [.10–.49]. There was, however, no significant interaction between group and zone, $F < 1$.

Whilst the ANOVA above demonstrates that participants in both groups preferentially searched in the signal over the no-signal zones, it is not possible to determine whether the time spent in the signal zone was different to that which would be expected by chance. In our task, it might be possible to determine the amount of time that participants would spend in the signal zone by calculating the percentage of the entire navigable space that is defined as the signal zone (.005%), and then assume that

Fig. 6. Individual paths travelled during test trials of Experiment 1a. Each image displays the paths travelled by 4 participants during the test trial conducted on the outside of the arena. Black circles indicate the goal location during training on the inside of the arena, and the search zones used to measure behaviour are super-imposed on each image.

participants would spend this proportion of time in the signal zone during the entire test trial (0.6 seconds). This definition of chance is, however, flawed as it requires that participants explore the entire navigable space randomly and equally. Instead, given that participants were trained to find a Wi-Fi hotspot at a corner inside of an arena, it should be expected that participants will search close to the corners of the arena when placed on the outside of the building. Consequently, it is much more appropriate to analyse whether participants spend more time searching at the exterior corner closest to the rewarded location during training, relative to other exterior corners of the environment. To perform this analysis, we expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1). As the size and number of signal

Table 1
Mean proportion of time spent in the signal zone as a proportion of time spent in all zones during the test trials of Experiment 1–3. Asterisk (*) indicate that that the mean proportion of time spent in the signal zone was significantly ($p < .05$) above the chance value of .5.

| Experiment	Shape transformation		Mean proportion of time (SD)
	Training	Test	
1a	Kite (inside)	Kite (outside)	.65 (.18)*
1a	Rectangle (inside)	Rectangle (outside)	.65 (.15)*
1b	Kite (outside)	Kite (inside)	.58 (.20)
1b	Rectangle (outside)	Rectangle (inside)	.63 (.15)*
2a	Kite (inside)	Rectangle (outside)	.53 (.14)
2a	Rectangle (inside)	Kite (outside)	.53 (.15)
2b	Kite (outside)	Rectangle (inside)	.47 (.10)
2b	Rectangle (outside)	Kite (inside)	.58 (.21)
3	Kite (outside)	Rectangle (outside)	.63 (.17)*
3	Rectangle (outside)	Kite (outside)	.60 (.13)*

and no-signal zones were equal at test, this calculation yielded a conservative chance value of .5. One sample t-tests conducted on individual mean proportions of time spent in the signal zone revealed that both the kite-kite, $t(15) = 3.340$, $p = .004$, $d = .84$ [.55–.74] and rectangle-rectangle, $t(15) = 3.834$, $p = .002$, $d = .96$ [.57–.73], groups spent significantly more time in the signal zone than would be expected by chance.

2.2.3. Experiment 1b – acquisition (outside)

The top panel of Fig. 7 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-rectangle and kite-kite groups. The latency to find the goal decreased across early trials for both groups, although the rectangle-rectangle group appeared to find the goal quicker than the kite-kite group throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between subjects factor of group (rectangle-rectangle or kite-kite) and a within subjects factor of trial (1–16), revealed a significant main effect of trial, $F(15,450) = 21.33$, $MSE = 5684.11$, $p < .001$, $\eta_p^2 = .42$ [34–45], confirming that participants found the hidden goal quicker as trials progressed. There was also a significant main effect of group, $F(1,30) = 79.40$, $MSE = 3064.04$, $p < .001$, $\eta_p^2 = .73$ [.56–.80], and a significant interaction between group and trial, $F(15,450) = 7.69$, $MSE = 5684.11$, $p < .001$, $\eta_p^2 = .20$ [.13–.23]. Simple main effects analysis revealed that participants in the rectangle-rectangle group found the goal quicker than participants in the kite-kite group on trials 1, 5, 6, 8–10, 12, and 16, $Fs(1,30) > 4.72$, $MSEs > 180.16$, $ps < .038$, $\eta_p^2 > .14$ [.004–.32].

2.2.4. Experiment 1b – test trial (inside)

During the test trial conducted on the inside of the rectangle-shaped arena, paired-samples t-tests revealed that there were no significant differences in the mean number of seconds participants spent searching in the two signal zones, $t(15) = 1.51$, $p = .15$, $d = .38$ [−.92–5.33], or the two no-signal zones, $t(15) = .580$, $p = .57$, $d = .15$ [−1.91–3.33]. In the following analysis, therefore, we collapsed across both signal zones and also across both no-signal zones. The bottom panel of Fig. 7 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena (see Fig. 8 for individual paths traversed). Again, participants in both the rectangle-rectangle and kite-kite groups preferentially searched in the signal zone of the arena, over the no-signal zone. A two-way ANOVA, with a between subjects factor of group (rectangle-rectangle or kite-kite) and a within subjects factor of zone (signal or no-signal), confirmed that participants spent more time in the signal, over the no-signal, zone, $F(1,30) = 17.16$, $MSE = 31.35$, $p < .001$, $\eta_p^2 = .36$ [.14–.53]. A significant main effect of group also revealed that participants in the rectangle-rectangle group spent more time in zones compared to participants in the kite-kite group, $F(1,30) = 7.21$, $MSE = 28.95$, $p = .012$, $\eta_p^2 = .19$ [.03–.38]. There was, however, no significant interaction between group and zone, $F < 1$.
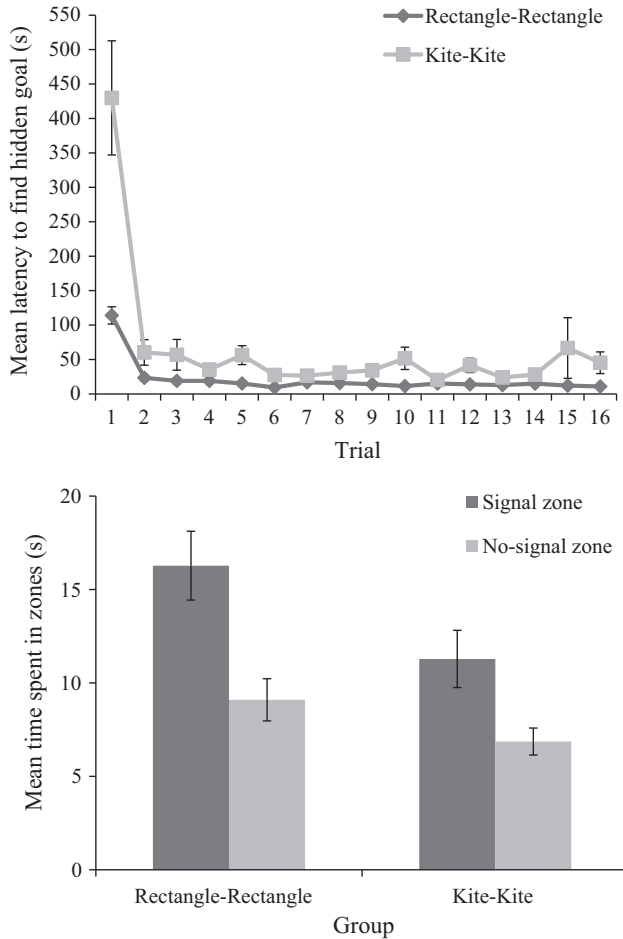
Fig. 7. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-rectangle and group kite-kite of Experiment 1b. Error bars show 1 ± standard error of the mean.

To assess performance at test to chance, we again expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1), and compared to a chance value of .5. One sample *t*-tests conducted on individual mean proportions of time spent in the signal zone revealed that rectangle-rectangle group spent significantly more time in the signal zone than would be expected by chance $t(15) = 3.302$, $p = .005$, $d = .83$ [.54–.71]; however, the kite-kite group did not spend significantly longer in the signal zone than would be expected by chance, $t(15) = 1.637$, $p = .12$, $d = .41$ [.48–.69].

2.3. Discussion

In Experiment 1a, participants were trained to find a hidden goal that was located at a distinctive corner inside either a rectangle- or kite-shaped arena. Following this training, participants were placed on the outside of the same shape for a test trial in the absence of the goal. Participants spent more time searching at the outside of the corner that contained the hidden goal from training, and
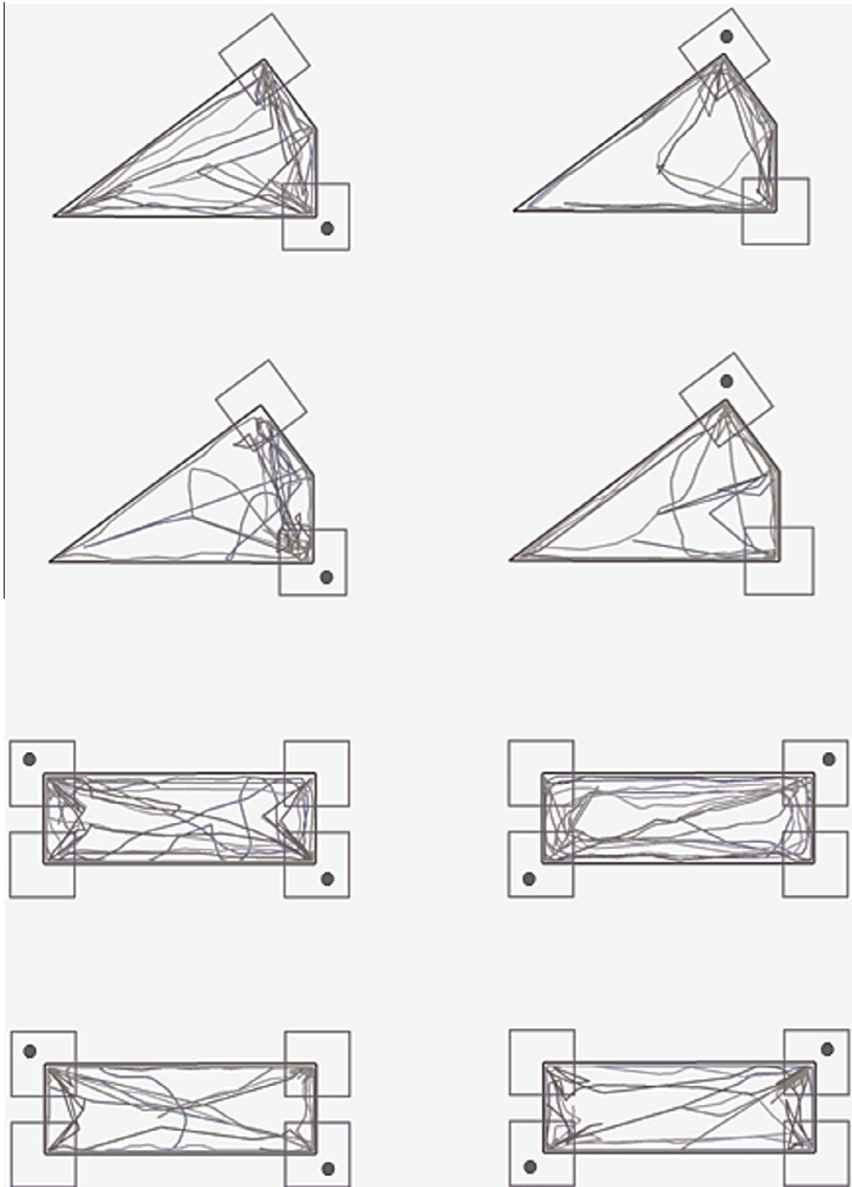
Fig. 8. Individual paths travelled during test trials of Experiment 1b. Each image displays the paths travelled by 4 participants during the test trial conducted on the inside of the arena. Black circles indicate the goal location during training on the outside of the arena, and the search zones used to measure behaviour are super-imposed on each image.

participants in both the rectangle-rectangle and kite-kite groups spent significantly more time in the signal zone than would be expected by chance. A similar pattern of results was also observed in Experiment 1b, when participants were first trained to find a hidden goal on the outside of a given shape before receiving a test administered on the inside of the same shape. Again, participants in both groups spent more time searching at the inside of the corner that contained the hidden goal from

training. It should be noted, however, that the preference for the signal zone at test in Experiment 1b was probably driven by participants in group rectangle-rectangle, who spent significantly more time in the signal zone than would be expected by chance. The proportion of time that participants in group kite-kite of Experiment 1b spent in the signal zone was numerically more than chance, but we note the lack of statistical significance to support this observation.

It is difficult to explain why group kite-kite failed to spend significantly more time in the signal zone than would be expected by chance. Previous reorientation tasks have observed that adult humans trained with a relatively restricted field of view (50°) failed to learn to navigate to a goal location in a trapezium-shaped environment (Sturz et al., 2013). Given the field of view in our experiments was 45°, it might be expected that this would have influenced learning in our task. It is, however, difficult to explain why a restricted field of view would only impact learning in group kite-kite of Experiment 1b, and not group rectangle-rectangle, or the two groups of Experiment 1a. In any case, the acquisition data for Experiment 1b clearly demonstrate that group kite-kite learned the task. Alternatively, it might be expected that the perceived size of the arena may have influenced task performance. Participants in Experiment 1b travelled faster than participants in Experiment 1a, which may have caused participants in Experiment 1b to perceive the arenas as smaller than their counterparts in Experiment 1a. It has been demonstrated that participants trained in small arena reorient on the basis of local-shape cues and the principal axis with equal preference (Sturz et al., 2012). It could, therefore, be the case that some participants in group kite-kite of Experiment 1b reoriented on the basis of global-shape information at test, whereas others navigated on the basis of local-shape information. It is, however, again difficult to understand why this would be the case for group kite-kite in Experiment 1b, and not group rectangle-rectangle. In addition, Sturz et al. (2012) found that participants trained in larger arenas preferentially reorient on the basis of local-shape information. If anything then, it would be expected that participants in Experiment 1a would display a weaker preference for the signal zone compared to chance, rather than participants in Experiment 1b as was observed here. Given this, the reason as to why group kite-kite failed to spend significantly more time in the signal zone than would be expected by chance remains to be determined.

The results observed in Experiment 1a and 1b are not consistent with the notion that participants were reorienting on the basis of local-shape information (e.g. Pearce, 2009; Pearce et al., 2004). If, for example, participants learned to navigate to the intersection of a short wall to the left of a long wall during training, then at test participants should spend more time exploring the corner of the alternative side of the arena that best matches this description. The results of Experiments 1a and 1b clearly demonstrated that this was not the case, as participants spent more time searching next to the corner where the short wall was to the right of the long wall. The current results, therefore, seem to be more consistent with the idea that a global representation of the shape of the environment is acquired during training. For example, if participants in the rectangle-rectangle group from Experiment 1a acquired a representation of the training environment (and the location of the goal within it) in a manner that is comparable to the sketch in the top-left of Fig. 1, then it is relatively straightforward to understand why participants would explore the top-left and bottom-right corners of the arena when placed on its outside, as these corners are closer to the position where the goal was located than any other external point.

3. Experiments 2a and 2b

In Experiments 1a and 1b, it is possible that participants acquired a global representation of the shape of the arena during learning, and referred to this representation at test in order to search for the goal. It is, however, possible that the global encoding is sparser than this. As noted in the introduction, Cheng and Gallistel (2005) suggested that organisms might extract the principal axis of environments, and it has been observed that adult humans are able to transfer behaviour between different shaped environments on the basis of the principal axis (e.g. Bodily et al., 2011; Sturz & Bodily, 2011; Sturz et al., 2011). Given these findings, it is necessary to evaluate the possibility that participants in Experiment 1a and 1b might have been travelling to the appropriate locations during test on the basis of the principal axis of the environments, rather than the global shape of the environments.

In order for reorientation based upon the principal axis to explain the behaviour observed in Experiments 1a and 1b, it is necessary to make two assumptions. First, it must be assumed that reorientation on the outside of an environment can be guided by the principal axis. To the best of our knowledge, previous research has only assessed reorientation based upon the principal axis from inside an environment, thus, the notion that the principal axis may be used to guide reorientation on the outside of an environment has not been examined before. Nevertheless, the principal axis of a shape mathematically extends both inside and outside of a shape, and so there is reason to expect that organisms might use the principal axis to reorient on the outside of an environment, despite the lack of evidence in support of this notion. Second, it also appears necessary to assume that participants in Experiments 1a and 1b encoded the principal axis in an allocentric framework. This notion is a departure from previous spatial theories in which information provided by the principal axis of shape is used in combination with a sense component; however, given the allocentric nature of our task it appears to be a necessary assumption. Consider training conducted in a rectangle-shaped environment, in which the hidden goals are in corners where the left hand wall is longer than the right hand wall. In order to explain learning of this goal location, it has previously been suggested that participants would identify the principal axis, and travel to corners of the left hand side of this axis (e.g. Cheng & Gallistel, 2005). Whilst this theory has had some success in explaining how adult humans transfer behaviour between the insides of different shaped environments (Bodily et al., 2011; Sturz & Bodily, 2011; Sturz et al., 2011), the egocentric nature of sense makes it difficult to explain the results observed in Experiment 1a and 1b. For instance, following training in a rectangle-shaped
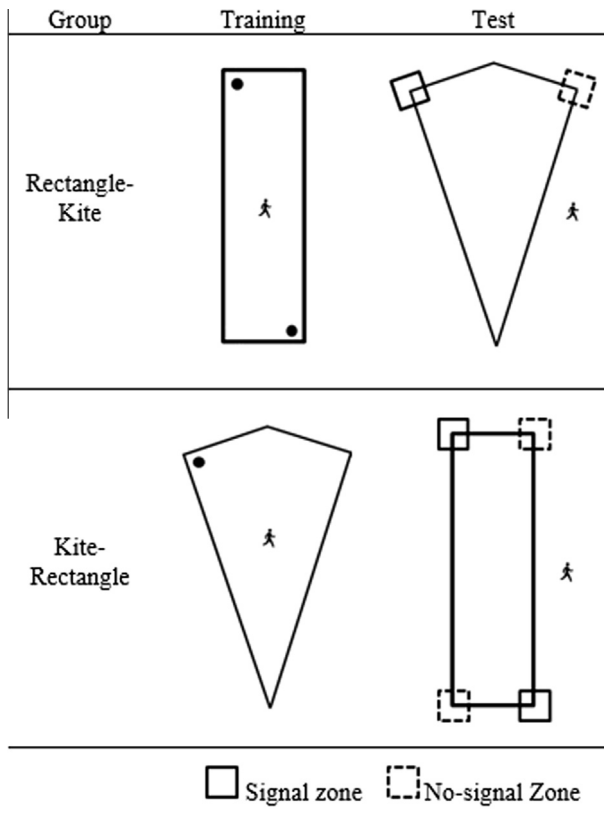
Fig. 9. Schematic views of the training and test environments of Experiments 2a. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

environment in Experiment 1a, participants were placed on the outside of the rectangle. Here, searching on the left hand side of the principal axis only predicts searching at the signal zone if participants turn left when facing away from the arena walls. If participants are facing towards the arena walls, then travelling to the corner on their left would lead to the no-signal zone. Given this, the only way that reorientation based upon the principal axis could reliably explain the preference for the signal zone that was observed in Experiment 1a would be if it were encoded in an allocentric manner.

The purpose of Experiments 2a and 2b was to evaluate the type of global-shape information that participants may have used to reorient in Experiments 1a and 1b, by changing the overall shape of the arena between training and test from a rectangle to a kite, or vice versa. In Experiment 2a, group rectangle-kite were first trained on the inside of a rectangle-shaped arena and then tested on the outside of a kite-shaped arena. Likewise, group kite-rectangle were first trained on the inside of a kite-shaped arena and tested on the outside of a rectangle-shaped arena. The same groups were also used in Experiment 2b; however, participants were trained on the outside of one shape before receiving a test trial inside the other shape (see Figs. 9 and 10). If participants reorient on the basis of the global shape of the environment (Cheng, 1986; Gallistel, 1990), then changing the shape of the arena between training and test should remove the preference for searching in one test zone over another that was observed in Experiments 1a and 1b. If, however, participants were reorienting on the basis of an allocentric representation of the principal axis of the environments in Experiments 1a and 1b, then a similar preference for the signal zone over the no-signal zone should be observed in Experiments 2a and 2b.
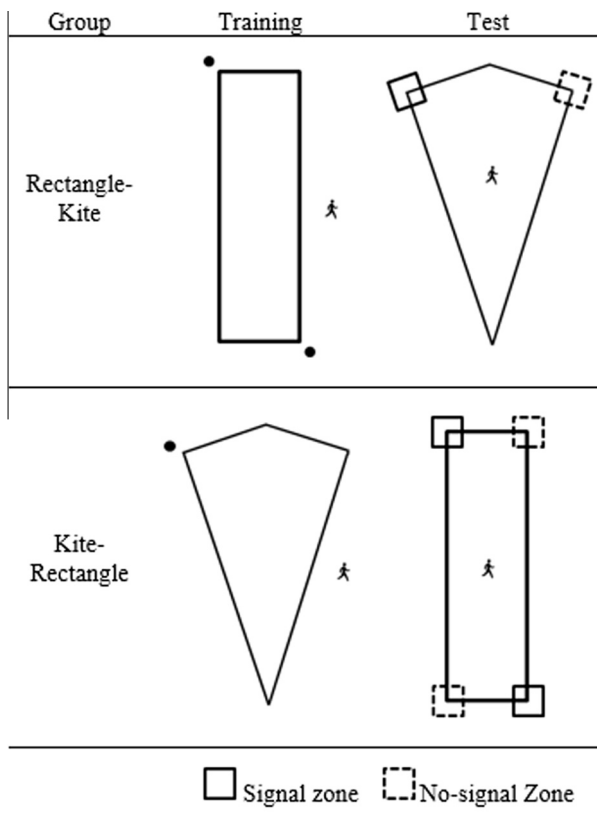
Fig. 10. Schematic views of the training and test environments of Experiments 2b. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

3.1. Method

Unless otherwise stated, the material and procedural details of Experiments 2a and 2b were identical to those reported for Experiments 1a and 1b.

3.1.1. Participants

For Experiment 2a, 32 students were recruited from the University of Nottingham (19 female), aged between 18 and 29 years (mean = 20.34, *SD* = 2.66). For Experiment 2b, a further 32 students, aged between 18 and 33 years (mean = 21.41, *SD* = 3.32), were also recruited from the University of Nottingham (20 female). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

3.1.2. Materials

For Experiment 2a, all materials were identical to Experiment 1a and, similarly, the material details for Experiment 2b were identical to those reported for Experiment 1b.

3.1.3. Procedure

Participants received identical instructions to those presented in Experiment 1. In group rectangle-kite, participants were trained to find a hidden goal that was always located at a particular corner of a rectangle-shaped environment, before receiving a test trial conducted with a kite-shaped arena. Likewise, group kite-rectangle were trained to find a hidden goal that was always located at a particular corner of a kite-shaped environment, before receiving a test trial conducted with a rectangle-shaped arena. For Experiment 2a, participants were trained inside of an environment and tested outside of an environment (see Fig. 9). In contrast, for Experiment 2b, participants were trained outside of an environment and tested inside of an environment (see Fig. 10). In both Experiments 2a and 2b, the training procedure, the test procedure, counterbalancing of the location of the hidden goal, the location in which participants began each trial, and the direction in which they were facing, were all identical to Experiments 1a and 1b, respectively.

To measure behaviour during test trials, the time spent within 6.48 m × 6.48 m square search zones, which were centred on all points where a long and short wall met to create a right angled corner, was recorded. These search zones were, again, orientated such that two of their edges were parallel to a long wall of an arena, and the remaining two edges ran parallel to a short wall of an arena (see Figs. 7 and 8). Signal zones were located at right angled corners that were the same side of the principal axis as the right angled corners that contained the hidden goal during training. No-signal zones were located a right angled corners on the opposite side if the principal axis.

3.2. Results

3.2.1. Experiment 2a – acquisition (inside)

The top panel of Fig. 11 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-kite and kite-rectangle groups. The latency to find the goal decreased across early trials for both groups, although the rectangle-kite group appeared to find the goal quicker than the kite-rectangle group on trial 1. A two-way ANOVA conducted on individual latencies to find the goal, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within subjects factor of trial (1–16), confirmed that participants became quicker to find the goal as trials progressed, $F(15, 450) = 12.39$, $MSE = 1011.39$, $p < .001$, $\eta_p^2 = .29$ [21–.32]. There was no main effect of group, $F < 1$, however, there was a significant interaction between group and trial, $F(15, 450) = 2.66$, MSE 1011.39, $p = .001$, $\eta_p^2 = .08$ [.02–.09]. Simple main effects analysis revealed that participants in the rectangle-kite group found the goal quicker than participants in the kite-rectangle group on trial 1 only, $F(1, 30) = 4.31$, $MSEs = 8699.87$, $p = .047$, $\eta_p^2 = .13$ [.001–.31].
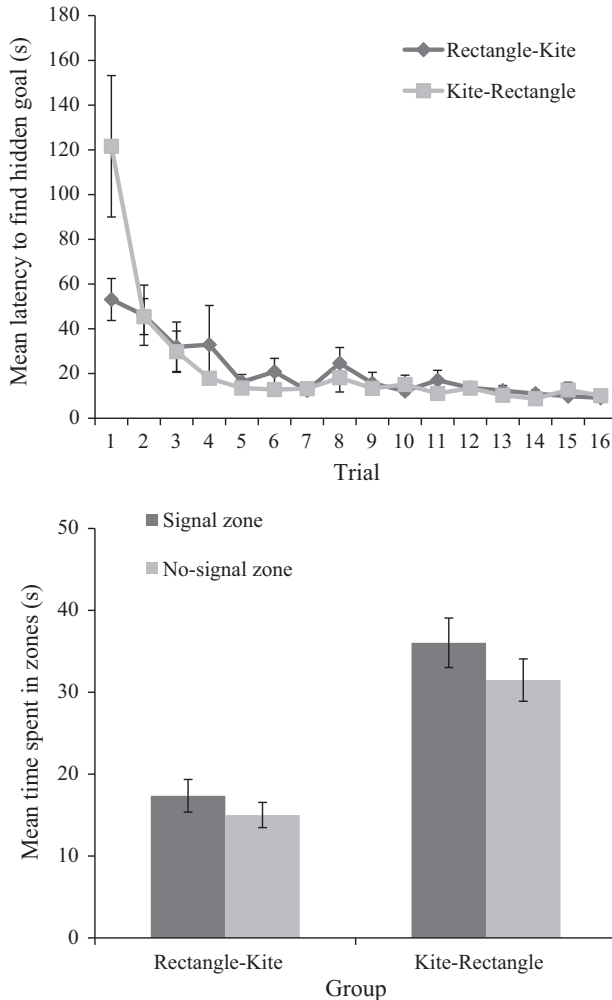
Fig. 11. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-kite and group kite-rectangle of Experiment 2a. Error bars show 1 ± standard error of the mean.

3.2.2. Experiment 2a – test trial (outside)

During the test trial conducted on the outside of the rectangle-shaped arena, paired-samples t-tests revealed that there were no significant differences in the mean amount of time participants spent searching in the two signal zones, $t(15) = .314$, $p = .76$, $d = .08$ [−6.06–8.15], or the two no-signal zones, $t(15) = .673$, $p = .51$, $d = .17$ [−4.11–7.90]. In the following analysis, therefore, we collapsed across both signal zones and also across both no-signal zones. The bottom panel of Fig. 11 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena (see Fig. 12 for individual paths traversed). Participants, in both the rectangle-kite and kite-rectangle groups, spent a similar amount of time searching in both zones during the test trial. A two-way ANOVA, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within-subjects factor of zone (signal or no-signal), revealed only a significant main effect of group $F(1,30) = 83.59$, $MSE = 59.20$, $p < .001$, $\eta_p^2 = .74$ [.57–.81], with participants in the kite-rectangle group spending more time in zones than participants in the rectangle-kite group. The main effect of zone was not significant, $F(1,30) = 1.61$, $MSE = 118.20$, $p = .21$, $\eta_p^2 = .05$ [.00–.21], nor was the interaction between zone and group, $F < 1$.
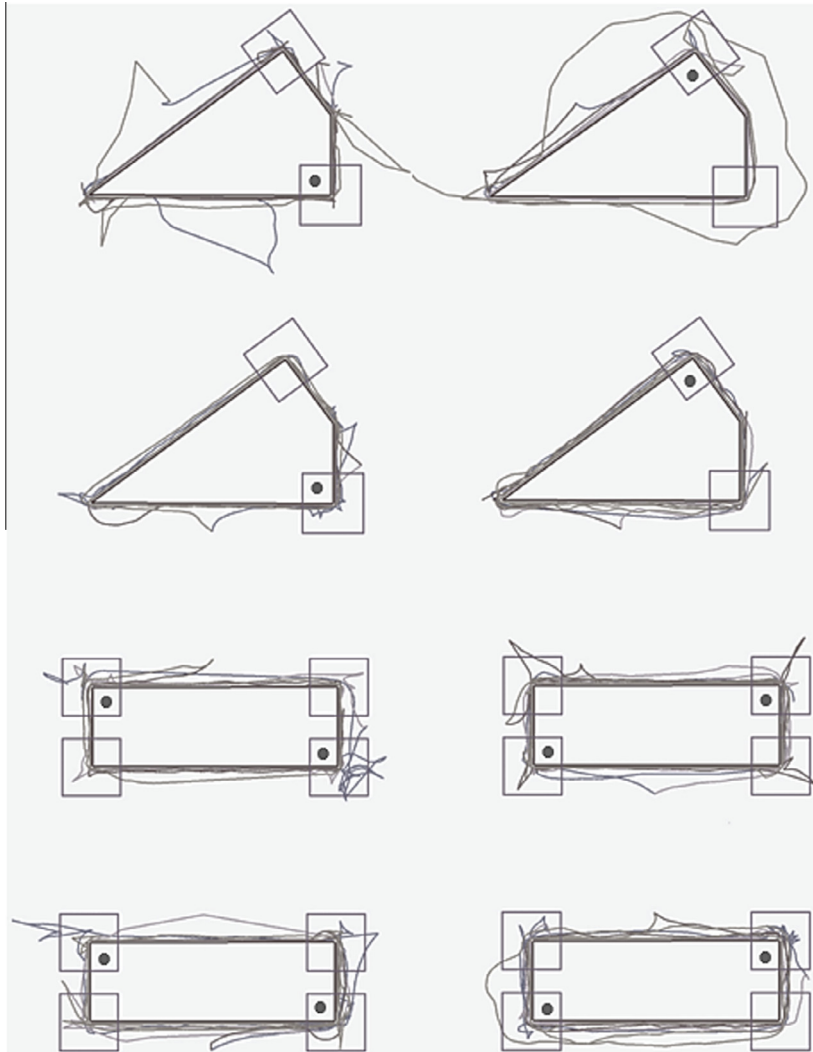
Fig. 12. Individual paths travelled during test trials of Experiment 2a. Each image displays the paths travelled by 4 participants during the test trial conducted on the outside of the arena. Black circles indicate the goal location during training on the inside of the arena, and the search zones used to measure behaviour are super-imposed on each image.

To assess performance at test to chance, we expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1), and compared this to a chance value of .5. One sample *t*-tests conducted on individual mean proportions of time spent in the signal zone revealed that neither the rectangle-kite, $t(15) = .869$, $p = .40$, $d = .22$ [.45–.61] or kite-rectangle, $t(15) = .879$, $p = .39$, $d = .22$ [.46–.60] groups spent significantly more time in the signal zone than would be expected by chance.

3.2.3. Experiment 2b – acquisition (outside)

The top panel of Fig. 13 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-kite and kite-rectangle groups. The latency to find the goal decreased across early trials for both groups, although participants trained with a rectangle shaped arena (group rectangle-kite) appeared to find the goal quicker than participants trained
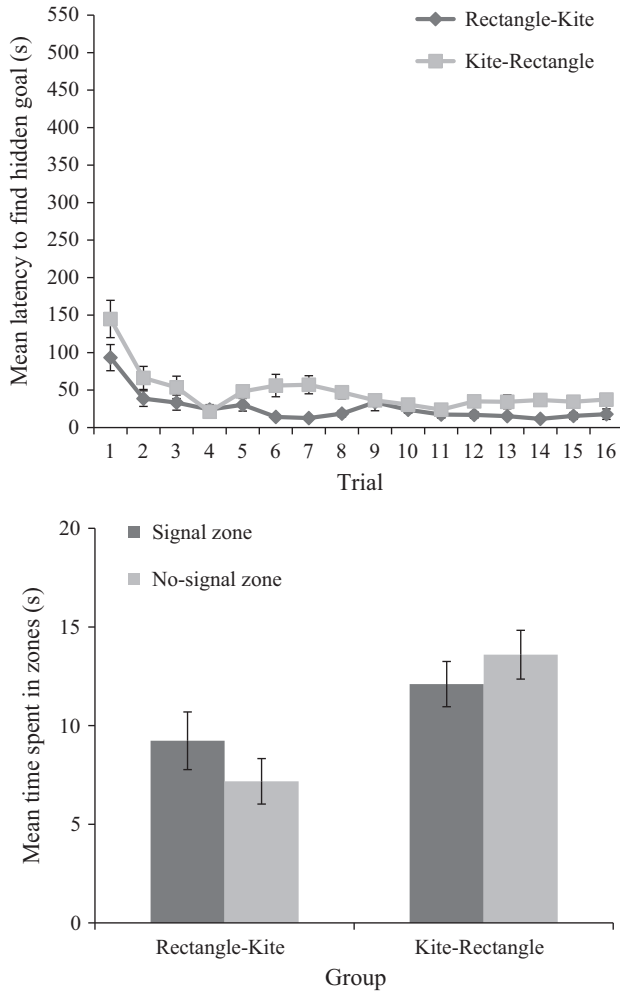
Fig. 13. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-kite and group kite-rectangle of Experiment 2b. Error bars show 1 ± standard error of the mean.

with a kite shaped arena (group kite-rectangle) throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within subjects factor of trial (1–16), revealed a significant main effect of trial, $F(15, 450) = 14.51$, $MSE = 1218.06$, $p < .001$, $\eta_p^2 = .33$ [.25–.36], confirming that participants became quicker to find the goal as trials progressed. There was also a main effect of group, $F(1, 30) = 12.06$, $MSE = 4955.94$, $p < .001$, $\eta_p^2 = .29$ [.08–.46], confirming that the rectangle-kite group took less time, overall, to find the hidden goal relative to the kite-rectangle group. The interaction between group and trial was not significant, $F(15, 450) = 1.48$, $MSE = 1218.06$, $p = .11$, $\eta_p^2 = .047$ [.00–.049].

3.2.4. Experiment 2b – test trial (inside)

During the test trial conducted on the inside of the rectangle-shaped arena, paired-samples t-tests revealed that there were no significant differences in the mean amount of time participants spent searching in the two signal zones, $t(15) = .019$, $p = .99$, $d = .004$ [−3.23–3.29], or the two no-signal

zones, $t(15) = 1.184$, $p = .26$, $d = .30$ [-1.55–5.45]. In the following analysis, therefore, we collapsed across both signal zones and also across both no-signal zones. The bottom panel of Fig. 13 displays the time spent, in seconds, searching within the signal or no-signal zones of the arena (see Fig. 14 for individual paths traversed). Again, participants in both the rectangle-kite and kite-rectangle groups spent an equivalent amount of time searching in both types of zone during the test trial. A two-way ANOVA, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within subjects factor of zone (signal or no-signal), again revealed only a significant main effect of group, $F(1, 30) = 10.44$, $MSE = 33.06$, $p = .003$, $\eta_p^2 = .26$ [.06–.44], showing that participants in the
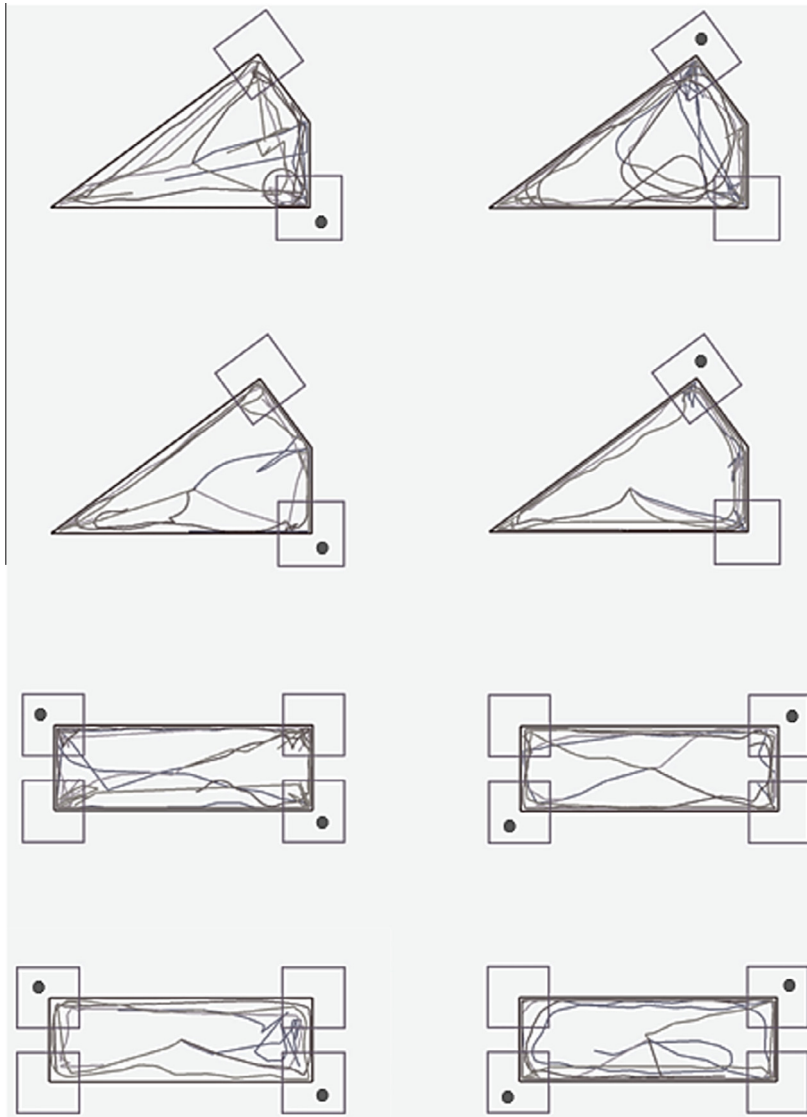
Fig. 14. Individual paths travelled during test trials of Experiment 2b. Each image displays the paths travelled by 4 participants during the test trial conducted on the inside of the arena. Black circles indicate the goal location (based on local-shape) during training on the outside of the arena, and the search zones used to measure behaviour are super-imposed on each image.

kite-rectangle group spent more time in any of the measured zones compared to participants in the rectangle-kite group. The main effect of zone was not significant, $F < 1$, nor was the interaction between zone and group, $F(1, 30) = 2.89$, $MSE = 17.40$, $p = .10$, $\eta_p^2 = .09$ [.00–.26].

To assess performance at test to chance, we expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1), and compared to a chance value of .5. One sample t-tests conducted on individual mean proportions of time spent in the signal zone revealed that neither the rectangle-kite, $t(15) = 1.517$, $p = .15$, $d = .38$ [.47–.69] or kite-rectangle, $t(15) = 1.149$, $p = .27$, $d = .29$ [.41–.53] groups spent significantly more time in the signal zone than would be expected by chance.

3.3. Discussion

Following a change in the overall shape of the arenas between training and testing, participants in Experiments 2a and 2b displayed no preference for searching by either of the right-angled corners of the test environment when moved from one side of the arena to the other (e.g. from inside to outside). Participants did not spend significantly more time in the signal zone over the no-signal zone and, likewise, the mean proportion of time spent in the signal zone was not different to what would be expected by chance. These results are not consistent with the idea that organisms encoded an allocentric representation of the principal axis of the shapes of the environments they navigated in, and reoriented using this parameter (Cheng & Gallistel, 2005). If participants in Experiments 2a and 2b were reorienting on the basis of the principal axis, we should have obtained a preference for the signal zone, over the no-signal zone, as in Experiments 1a and 1b. The results of Experiments 2a and 2b are, however, consistent with the notion that participants reorient on the basis of a global representation of the shape of the environments. Changing the overall shape of an environment between training and test will result in the global-shape representations of these two shapes failing to match, resulting in a loss of the preference for searching in one test zone over another. Like Experiments 1a and 1b, the results of Experiments 2a and 2b also provide no support for the idea that participants reoriented on the basis of local-shape information at test. If participants learned to find the goal inside the corner of a rectangle where the short wall was the left of a long wall, then when transferred to the outside of a kite-shaped arena, participants should have explored the corner of the exterior of the arena that best matched this description.

Participants in Experiments 2a and 2b did not show a significant preference for searching in the corners that would be predicted by reorientation based on the principal axis or local-shape information of the test environment. It is important, however, to determine whether this non-significant result supports the null hypothesis (that there was no difference in time spent in each zone), or supports no conclusion at all (Dienes, 2011). To determine between these possibilities a Bayes factor was calculated, where values less than .33 indicate support for the null hypothesis, values above 3 indicate support for the alternative hypothesis, and values between .33 and 3 indicate no support for either hypothesis (Jeffreys, 1961; see Dienes, 2008 for a rationale). To calculate a Bayes factor, it is necessary to estimate a plausible effect size. In order to achieve this, we combined the data from Experiments 1a and 1b, and collapsed across groups. Using the data from all 64 participants recruited from Experiment 1, we observed a mean difference of 11.94 s between the duration of time spent in the signal and no-signal zones. Combining data from Experiments 2a and 2b and collapsing across groups, we observed a mean difference of 1.87 s ($SE = 1.45$). Following Dienes (2011: see also www.lifesci.sussex.ac.uk/home/Zoltan_Dienes/inference/Bayes.htm), Experiments 2a and 2b were modelled with a 2-tailed distribution with a mean of 0 (indicating no difference between the time spent in the signal and no-signal zone) and a SD set to 11.94. This yielded a Bayes factor of .27, indicating support for the null hypothesis.

An additional benefit to conducting Experiments 2a and 2b was that it allowed us to rule out the possibility that, in Experiments 1a and 1b, participants were using some form of mental rotational strategy to solve the task, such as a perspective transformation (Tversky, Kim, & Cohen, 1999; Zacks, Vettel, & Michelon, 2003). That is, during training, participants may have encoded the local-shape information that signalled the goal location and, during the test trial, imagined what that local-shape information would look like from a different perspective. For example, a participant

who learned that the goal is located in a right-angled corner where a short wall was to the left of a long wall, on the inside of the arena, could then transform this representation in order to search where a short wall to the right of a long wall creates a 270° join, on the outside of the environment. If participants were using such a strategy in Experiments 1a and 1b, then it stands to reason that participants in Experiments 2a and 2b should display the same search preference as participants in Experiments 1a and 1b, which they did not. That being said, Experiment 2 was not specifically designed with the purpose of assessing if participants were using mental transformations during navigation, and so it remains for future research to more comprehensively explore their role in search behaviour following a transfer from one side of a boundary to another. One manner in which the use of spatial transformations might be explored in future research is to measure latency to make a choice about where to search at the beginning of the test trial. If participants employ spatial transformations in order to determine where to search at test, it would presumably take longer to make a decision compared to strategies that do not require transformation of space (e.g. encoding the global-shape of the environment). Unfortunately, the timing of our task was controlled by participants and, thus, we are unable to address this question with our current data. Participants were presented with instructions prior to the test trial, and pressed enter when they were ready to begin. Consequently, in our current procedure, there is no way to determine whether participants are executing mental transformations prior to the beginning the test trial, or immediately after starting the test trial.

4. Experiment 3

A number of experiments have now shown that when training and testing both occur inside arenas, participants will display a bias in search behaviour, despite a change in the global shape of the environment (Buckley, Smith, & Haselgrove, 2016; Esber et al., 2005; Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004). For example, training organisms to find a goal hidden at the inside corner of a rectangle where a long wall is to the left of a short wall results in a preference for searching at the corner of a kite-shaped arena that has the same local features. In terms of the outcomes of Experiments 2a and 2b, these results are reassuring, as they point to the fact that behaviour can transfer between arenas that have different global shapes. Consequently, the disruption of behaviour that was observed in Experiments 2a and 2b may not have been a consequence of the change in the global shape of the arena alone but, instead, a consequence of a change of global shape in conjunction with a shift from the inside to the outside of the arena (or vice versa). All of the experiments that have tested the transfer of search behaviour between arenas of different global shapes have, however, been conducted with training and testing conducted on the inside of these arenas. It is, therefore, possible that the same transfer would not be evident if training and testing occurred on the outside of the arena. This being the case would hinder our interpretation of Experiments 2a and 2b, as a failure to observe transfer between one side of the arena to the other might solely be due to the fact that training (or testing) occurred on the outside of the arena and, for some reason, participants were not able to guide their behaviour on the basis of the local-shape information, or the principal axis of environments, when on the outside of the environments.

In order to rule out the possibility mentioned above, in Experiment 3, we sought to replicate the effects observed by Buckley et al. (2016) when administering training and testing outside of a shape, to ensure the suitability of our testing procedure. Participants in group rectangle-kite were trained to find a hidden goal on the outside of a rectangle-shaped arena before receiving a test trial administered on the outside of a kite-shaped environment. Similarly, participants in group kite-rectangle were trained on the outside of a kite-shaped arena and tested on the outside of a rectangle-shaped arena (see Fig. 15). Based on the results of past studies (Buckley et al., 2016; Esber et al., 2005; Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004) we expected participants would successfully transfer their search behaviour from the training stage to the test stage, despite the transformation of the testing arena to a different shape. For example, participants trained to find the hidden goal adjacent to the exterior corner of a rectangle-shaped arena where the long wall was to the left of a short wall, would search at the same-featured corner when tested on the outside of a kite-shaped arena.
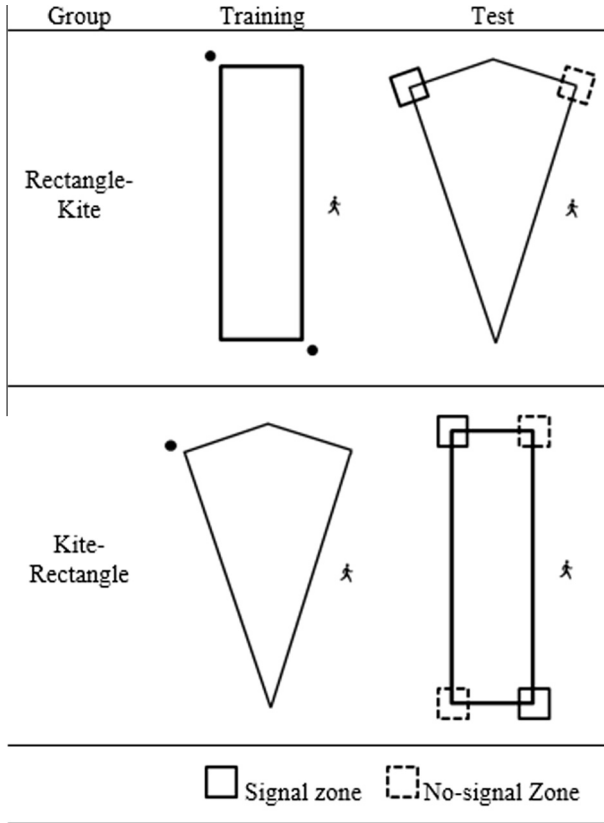
Fig. 15. Schematic views of the training and test environments of Experiments 3. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates that participants were navigating on the outside of all arenas.

4.1. Method

4.1.1. Participants

32 undergraduates were recruited from the University of Nottingham (23 female), aged between 18 and 37 years (mean = 21.66, SD = 5.19). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

4.1.2. Materials

All material details for training arenas were identical to those presented for Experiment 1b. All testing arenas were identical to those presented for Experiment 1a.

4.1.3. Procedure

Participants in group rectangle-kite were trained to find a hidden goal at a particular corner of a rectangle-shaped environment, before receiving a test trial on the outside of a kite-shaped arena. In contrast, participants in group kite-rectangle were trained to find a hidden goal at a particular corner of a kite-shaped environment, before receiving a test trial on the outside of a rectangle-shaped arena. For both groups, the training procedure was identical to Experiments 1b and 2b, and the testing procedure was identical to Experiments 1a and 2a. The signal and no-signal zones used to recorded behaviour during the test trial were defined in same manner as described for Experiment 2.

4.2. Results

4.2.1. Acquisition (outside)

The top panel of Fig. 16 shows that the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal decreased across trials for both the rectangle-kite and kite-rectangle groups. Participants learning on the outside of a rectangle-shaped arena (group rectangle-kite) found the goal quicker than participants learning on the outside a kite shaped arena (group kite-rectangle) throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within subjects factor of trial (1–16), revealed a significant main effect of trial, $F(15,450) = 22.01$, $MSE = 958.02$, $p < .001$, $\eta_p^2 = .42$ [.35–.45], confirming that participants became quicker to find the goal as trials progressed. There was also a main effect of group, $F(1,30) = 19.24$, $MSE = 1867.34$, $p < .001$, $\eta_p^2 = .39$ [.16–.55], confirming that the rectangle-kite group took less time to find the hidden goal
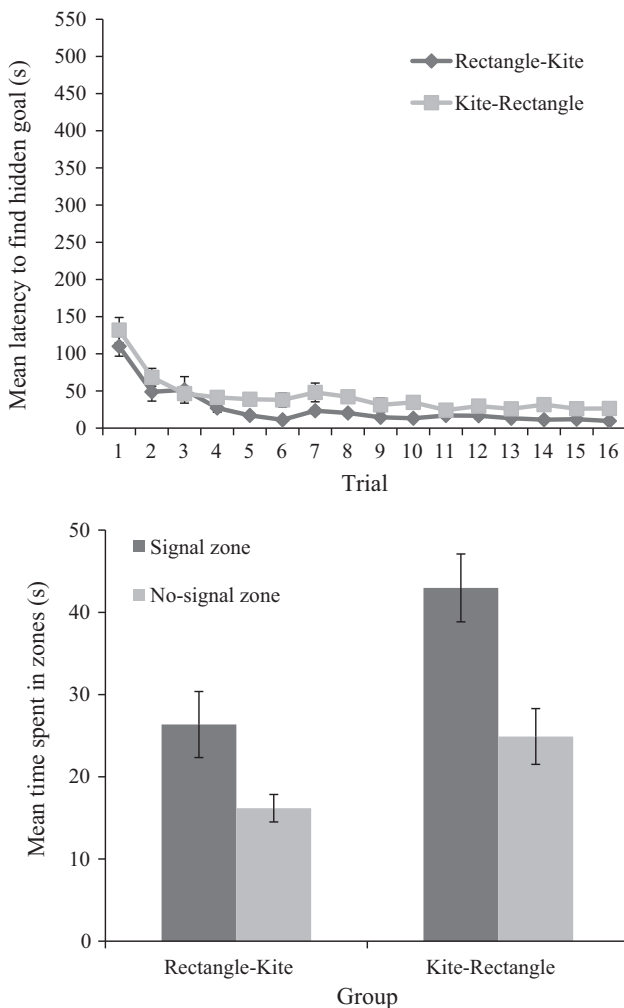

Fig. 16. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-kite and group kite-rectangle of Experiment 3. Error bars show 1 ± standard error of the mean.

relative to the kite-rectangle group during the course of training. The interaction between group and trial was not significant, $F < 1$.

4.2.2. Test trial (outside)

During the test trial conducted on the outside of the rectangle-shaped arena, paired-samples t-tests revealed that there were no significant differences in the mean amount of time participants spent searching in the two signal zones, $t(15) = .106$, $p = .92$, $d = .03$ [−10.36–9.38], or the two no-signal zones, $t(15) = 1.719$, $p = .11$, $d = .43$ [−.87–8.14]. In the following analysis, therefore, we collapsed
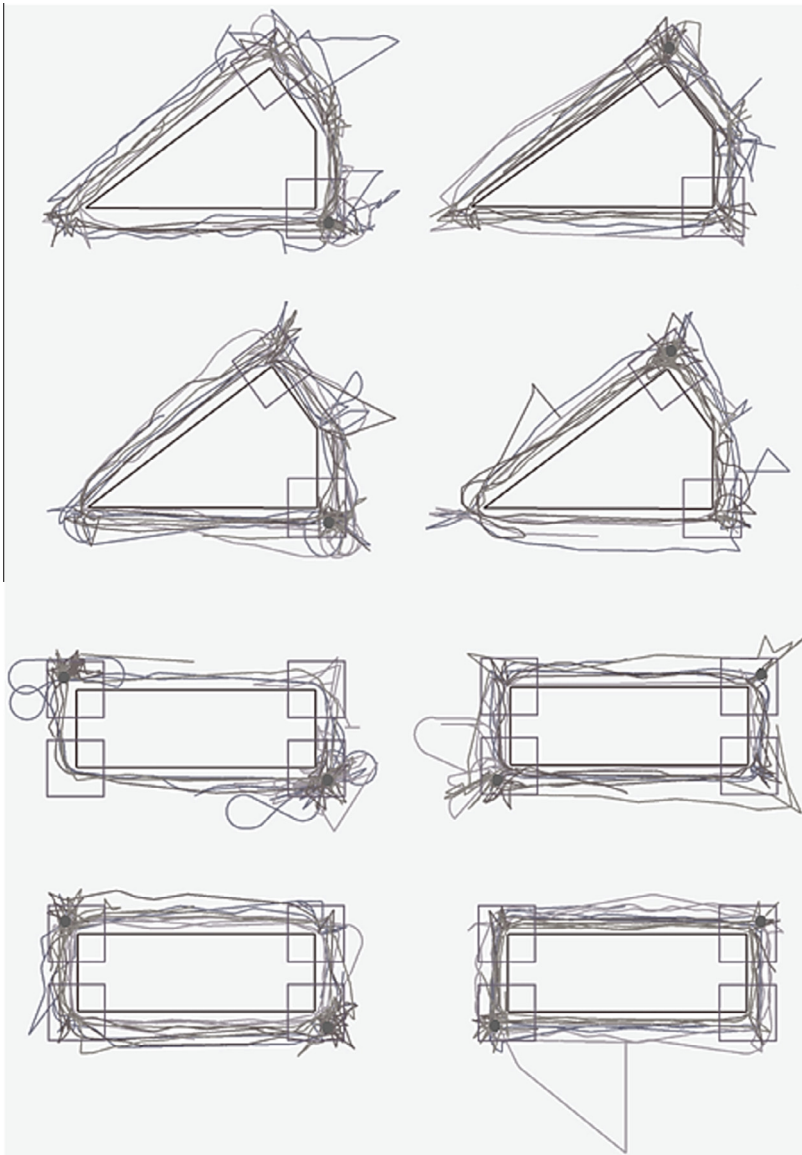
Fig. 17. Individual paths travelled during test trials of Experiment 3. Each image displays the paths travelled by 4 participants during the test trial conducted on the outside of the arena. Black circles indicate the goal location during training, and the search zones used to measure behaviour are super-imposed on each image.

across both signal zones and also across both no-signal zones. The bottom panel of Fig. 16 shows the time spent, in seconds, searching within the signal and no-signal zones of the arena (see Fig. 17 for individual paths traversed). Participants in both the rectangle-kite and kite-rectangle groups searched for more time in the signal zone of the arena, compared to the no-signal zone. A two-way ANOVA, with a between subjects factor of group (rectangle-kite or kite-rectangle) and a within subjects factor of zone (signal or no-signal), revealed a main effect of zone, $F(1,30) = 12.54$, $MSE = 254.60$, $p < .001$, $\eta_p^2 = .29$ [.08–.47], confirming that participants spent more time in the signal zone than the no-signal zone. A significant main effect of group also revealed that participants in the kite-rectangle group spent more time in both zones compared to participants in the rectangle-kite group, $F(1,30) = 20.52$, $MSE = 125.22$, $p = .001$, $\eta_p^2 = .41$ [.17–.56]. There was, however, no significant interaction between group and zone, $F < 1$.

To assess performance at test to chance, we expressed the time spent searching in the signal zone as a proportion of the time spent searching in signal and no-signal zones (see Table 1), and compared this to a chance value of .5. One sample t-tests conducted on individual mean proportions of time spent in the signal zone revealed that both the rectangle-kite group, $t(15) = 3.156$, $p = .007$, $d = .79$ [.53–.67] and kite-rectangle group, $t(15) = 3.086$, $p = .008$, $d = .77$ [.54–.73], spent significantly more time in the signal zone than would be expected by chance.

4.3. Discussion

Participants trained to find a hidden goal at a corner on the outside of an arena that had a distinctive shape preferentially searched at the same exterior corners of a different-shaped environment that shared the same local-shape cues. This was evidenced by the fact the participants spent significantly more time searching in the signal zone than the no-signal zone, and also by the mean proportion of time spent in the signal zone being greater than would be expected by chance. These data replicate, and extend the generality of, the results of a number of previous studies in which training and testing has occurred on the inside of an environment (Buckley et al., 2016; Esber et al., 2005; Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004). More importantly, for the current discussion, they demonstrate that it seems not to matter whether the shape of the arena changes from a rectangle to a kite between training and test when both of these stages of the experiment are conducted on the same side (inside *or* outside; see also Buckley et al., 2016). Experiment 3, along with Experiments 1a and 1b, therefore, serves as a positive control for Experiments 2a and 2b. In the general discussion, these results will permit more substantive discussion about the mechanisms that might underpin the transfer of search behaviour between the inside and the outside of an arena, when its overall shape remains the same, or changes.

5. General discussion

In Experiments 1a and 1b, participants were trained to find a hidden goal in the right-angled corner of one side of an arena (e.g. an inside corner of a kite). At test, participants were placed on the alternate side of the same shape (e.g. the outside of the kite) and in both Experiments participants spent more time exploring the right-angled corner that would have been closest to the goal signal during training, compared to the other right-angled corner. In Experiments 2a and 2b, participants were again trained to find a hidden goal on one side of an arena, before receiving a test on the alternate side of the arena. For Experiments 2a and 2b, however, the global shape of the training arena was changed from a kite to a rectangle (or vice versa) between training and test. Under these circumstances, participants displayed no preference for searching by either of the right-angled corners at test. Finally, following only a change in the shape of the arena between training and testing, participants in Experiment 3 preferentially searched at the exterior corners of a test environment that shared the same local-shape information that signalled the goal location in a training environment.

Prior to discussing the theoretically interesting implications of our data, it is important to address two findings that have been observed in all three experiments reported here. First, participants trained with a rectangle-shaped arena found the goal quicker than participants trained with a kite-shaped

arena. Second, participants tested in rectangle-shaped arenas spent more time in any of the measured zones compared to participants tested in kite-shaped arenas. Both of these effects can be explained by the fact the rectangle-shaped arenas in our experiments contained twice as many hidden goals, or twice as many measured zones, compared to the kite shaped arenas. Consequently, during training, participants trained in a rectangle-shaped arena had a 50% chance of travelling to a corner that contained a hidden goal, whereas, participants trained in a kite-shaped arena only had a 25% chance of selecting the corner that contained the goal. Similarly, the total time spent in any of the measured zones during a test trial conducted with a rectangle-shaped environment was the sum of four zones, whereas, for a test trial conducted with a kite-shaped environment it was only the sum of two zones.

Turning now to the results of our test trials, it is difficult to explain the results from all three of our experiments by assuming that organisms encode only one representation of the space in which they navigate, as the results of at least one experiment presented here are inconsistent with theories based on local-shape information, a global representation of the shape of the environment, or reorientation based on the principal axis of an environment. First, if animals encoded only local-shape information (e.g. as proposed by Pearce et al., 2004) then it would be possible to account for the results of Experiment 3 by suggesting that participants reoriented on the basis of the local geometric-cues that signalled the location of the hidden goal during training, and transferred this behaviour to the novel test environment. It is, however, difficult to then explain why participants displayed no preference for searching in the corner consistent with reorientation based on local geometric cues during Experiments 2a and 2b. Moreover, participants in Experiments 1a and 1b failed to search by the corner that best matched the local properties of the corner from training (no-signal zone) and, instead, searched more at the alternative corner (signal zone).

Second, the notion that animals encode a representation of the global geometry of the environment (Cheng, 1986; Gallistel, 1990) is consistent with the observation that participants preferentially searched in the signal zone during the test trials of Experiments 1a and 1b. Reorienting only on the basis of a representation of the global environmental shape is also consistent with the fact that participants displayed no preference for any corner at test during the test trials of Experiments 2a and 2b, as the global geometry of training and testing environments differed. Reorientation based on the global geometry of the environment is not, however, consistent with the results of Experiment 3. As with Experiments 2a and 2b, the overall shape of the training and test environments differed in Experiment 3, and so participants should have displayed no preference for any corner. Instead, participants preferentially searched in the corner predicted by theories based on local geometric cues and the principal axes of shapes (see also: Buckley et al., 2016; Esber et al., 2005; Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004).

Third, reorientation based on the principal axis of the geometry of the environment (Cheng & Gallistel, 2005), can account for the results Experiment 3. At test in this experiment, participants searched on the same side of the principal axis to which they were trained to find the goal. Furthermore, if it is assumed that the principal axis is encoded in an allocentric reference frame, then it is possible for reorientation based on the principal axis to explain the results of Experiment 1a and 1b in the same manner. Again, participants searched on the same side of the principal axis to which they were trained to find the goal. If, however, participants in Experiments 1a, 1b, and 3 transferred behaviour between kite- and rectangle-shaped environments (and vice versa) on the basis of an allocentric representation of the principal axis, then it is not clear why there was no preference for the signal zone in Experiments 2a and 2b, as was observed in Experiment 3.

Given the above discussion, it seems necessary to invoke multiple representations of environmental shape in order to successfully explain our data. One way to explain the observations reported here is to assume that participants encoded the location of the goal with respect to an allocentric representation (view-independent) of the global shape of the arena, as well as with respect to an egocentric representation (view dependent) of the local-shape information at the goal corner. Between the training and test trials of Experiments 1 and 2, participants experienced an unexpected change in reference point (i.e. a move from inside to outside, or vice versa). It has been argued that behaviour based on egocentric representations is disrupted following a change in reference point (e.g. Burgess, 2006,

2008), thus, search behaviour at test in these experiments would have been determined only by the allocentric representation of the global shape of the arena. This would permit a search bias to emerge in Experiments 1a and 1b, but not in Experiments 2a and 2b, as the overall shape of the training and test environments were only congruent in Experiments 1a and 1b. The overall shape of the training and test environments were not congruent in Experiment 3, however, in this experiment there was not an unexpected change in reference point between training and test. Consequently, transferring local-shape information from the training to the test environment would permit a search bias to occur. The results of Experiment 3, then, would be considered formally equivalent to those presented by Lew et al. (2014: see also: Buckley et al., 2016; Pearce et al., 2004).

Whilst it is possible to explain our data by assuming participants reorient on the basis of an allo-centric representation of the global shape of the environment and an egocentric representation of local-shape information, we cannot rule out the suggestion that participants also encoded allocentric information about the principal axes of the shapes they navigated. It is possible to account for the results of our three experiments by assuming that search behaviour at test is a function of the integration of different search biases established from different representations. Participants in Experiment 1, therefore, preferentially searched at the signal corner because this was consistent with reorientation on the basis of a representation of the global shape of the environment, and with the principal axis of the shape, whereas searching at the non-signal corner was only consistent with reorientation based on local-shape information. In Experiment 2, participants did not display a search bias because searching at the signal corner was consistent with reorienting on the basis of the principal axis of the shape, and searching at the no-signal corner was consistent with reorientation based on local-shape information. Finally, participants preferentially searched in the signal corner in Experiment 3 because this was consistent with reorientation based on the principal axis and local-shape information, and searching at the no-signal corner was not consistent with any spatial representation. One manner in which search biases established from different representations of environmental shape may be integrated is by a weighting system that determines which representations are used to guide behaviour on the basis on the current task (Ratliff & Newcombe, 2008; see also Cheng & Newcombe, 2005; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008; Twyman & Newcombe, 2010), and the argument above is predicated on the assumption that each representation is given equal weighting. As noted in a review by Cheng et al. (2013), it is necessary to precisely specify how search biases that are established from such radically different spatial representations would combine to determine behaviour under this weighting approach.

It worth highlighting from the above discussion that, in order to provide any explanation for the data collected in Experiments 1–3, it appears necessary to assume that humans encode a global representation of the shape of the environment in which they navigate. This finding is consistent with previous experiments conducted in our laboratory, in which human participants have been able to recognise the shape of the environments in which they had previously navigated, even when the shape of the environment was not task relevant (Buckley, Smith, & Haselgrove, 2014). In addition, the data presented here lend some support to the geometric module hypothesis (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), in which it is proposed that: (1) organisms encode a global representation of the shape of an environment, and (2) this process is encapsulated, such that is not prone to interference from non-geometric cues, such as landmarks. The experiments presented here provide core evidence for the encoding of a global representation of the shape of an environment; however, it must be noted that our experiments do not address the issue of encapsulation. Experiments in which landmarks have interfered with learning about environmental geometry (e.g. Buckley et al., 2014, 2015; Cole, Gibson, Pollack, & Yates, 2011; Horne, Iordanova, & Pearce, 2010; Horne & Pearce, 2009, 2011; Pearce, Graham, Good, Jones, & McGregor, 2006; Wilson & Alexander, 2008) have led to many authors to doubt the existence of the geometric module (Cheng, 2008; Pearce, 2009; Twyman & Newcombe, 2010). As we noted in the introduction, though, previous shape-transformation experiments have failed to dissociate reorienting responses made on the basis of a representation of the global-shape of an environment from responses based on local-shape information, or the principal axis. Consequently, it remains unclear whether encoding a representation of the global shape of an environment is subject to interference from non-shape cues (for reviews see:

Cheng, 2008; Cheng & Newcombe, 2005; Lew, 2011). We are currently addressing this issue in our laboratory, using a modification of the inside-to-outside transfer tests presented here.

5.1. Conclusion

The notion that organisms encode a global representation of the shape of their environment was suggested some 30 years ago (Cheng, 1986; Gallistel, 1990) and, despite a lack of evidence to support this claim, it has continued to be influential in the spatial learning literature. Our knowledge about the manner in which organisms learn about boundaries, however, has been largely based on studies that have examined reorientation within environments, which has limited our theories of shape-based reorientation (e.g. Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990; Miller & Shettleworth; 2007, 2008, 2013; Pearce, 2009). By studying reorientation on the outside of a bounded space, the current results provide, to the best of our knowledge, the first evidence that adult humans reorient using an allocentric representation of the global geometry of the environments. An important challenge for future research will be to determine the precise conditions under which this representation of the global geometry combines with other spatial representations to control behaviour, and to determine whether it is subject to interference.

Acknowledgments

Appendix A. Participant instructions when training was conducted inside of an arena, and the test trial was conducted on the outside

Instructions prior to acquisition trials:
This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 16 trials. In each trial, you will be placed into a room that contains a Wi-Fi hot spot. Your aim is to end the trials as quickly as possible by walking into the hot spot.

You will view the environment from a first person perspective, and be able to walk into the hot spot from any direction using the cursor keys on the keyboard. Once you've found the hot spot a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the hot spot is difficult to find. <u>The hot spot does not move though</u>, so it is possible to learn its specific location as the experiment goes along. It's a good idea to fully explore the environment on the first few trials to become aware of your surroundings. This should help you in learning where the hidden hot spot is.

This session should take around 20 min. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

Instructions prior to test trial:
In the next trial, you will again have to locate a Wi-Fi signal. The location of the Wi-Fi signal hasn't changed, so it will be in the same location as before.

However, you will be navigating around the *outside* of the building. As the Wi-Fi signal will be travelling through the walls of the building, it will be a bit weaker, and so it may be harder to locate.

Press enter to start.

Appendix B. Participant instructions when training was conducted outside of an arena, and the test trial was conducted on the inside

Instructions prior to acquisition trials:

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 16 trials. In each trial, you will be placed outside a building. Somewhere near the building there will be a mobile signal hot spot. Your aim is to end the trials as quickly as possible by walking into the hot spot.

You will view the environment from a first person perspective, and be able to walk into the hot spot from any direction using the cursor keys on the keyboard. Once you've found the hot spot a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of a wall when the trial begins, but the wall in which you start at will change in each trial.

To start with, you may find the hot spot is difficult to find. The hot spot does not move though, so it is possible to learn its specific location as the experiment goes along. It's a good idea to fully explore the outside of the building on the first few trials to become aware of your surroundings. This should help you in learning where the hidden hot spot is.

This session should take around 20 min. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

Instructions prior to test trial:

In the next trial, you will again have to locate a mobile signal. The location of the mobile signal hasn't changed, so it will be in the same location as before.

However, you will be navigating around the *inside* of the building. As the mobile signal will be travelling through the walls of the building, it will be a bit weaker, and so it may be harder to locate.

Press enter to start.

References

Ayaz, H., Allen, S. L., Platek, S. M., & Onaral, B. (2008). Maze Suite 1.0: A complete set of tools to prepare, present, and analyze navigational and spatial cognitive neuroscience experiments. *Behavior Research Methods, 40*(1), 353–359.

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*(5), 665–674.

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2014). Shape shifting: Local landmarks interfere with navigation by, and recognition of, global shape. *Journal of Experimental Psychology: Learning Memory and Cognition, 40*(2), 492–510.

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2015). Learned predictiveness training modulates biases towards using boundary or landmark cues during navigation. *Quarterly Journal of Experimental Psychology, 68*(6), 1183–1202.

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016). Blocking spatial navigation across environments that have a different shape. *Journal of Experimental Psychology: Animal Learning and Cognition, 42*(1), 51–66.

Burgess, N. (2006). Spatial memory: How egocentric and allocentric combine. *Trends in Cognitive Sciences, 10*(12), 551–557.

Burgess, N. (2008). Spatial cognition and the brain. *Annals of the New York Academy of Sciences, 1124*(1), 77–97.

Cheng, K. (1986). A purely geometric module in the rats spatial representation. *Cognition, 23*(2), 149–178.

Cheng, K. (2005). Reflections on geometry and navigation. *Connection Science, 17*(1–2), 5–21.

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences, 12*(9), 355–361.

Cheng, K., & Gallistel, C. R. (2005). Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi & Polli (2004). *Journal of Experimental Psychology: Animal Behavior Processes, 31*(2), 254–259.

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), 1–23.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin, 133*(4), 625.

Cheng, K., & Spetch, M. L. (1998). *Mechanisms of landmark use in mammals and birds: Spatial representation in animals* (pp. 1–17). New York, NY, US: Oxford University Press.

Cole, M. R., Gibson, L., Pollack, A., & Yates, L. (2011). Potentiation and overshadowing of shape by wall color in a kite-shaped maze using rats in a foraging task. *Learning and Motivation, 42*(2), 99–112.

Dienes, Z. (2008). *Understanding psychology as a science: An introduction to scientific and statistical inference.* Basingstoke: Palgrave Macmillan.

Dienes, Z. (2011). Bayesian versus orthodox statistics: Which side are you on? *Perspectives on Psychological Science, 6*(3), 274–290.

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. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 58*(1), 69–91.

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

Gallistel, C. R., & Matzel, L. D. (2013). The neuroscience of learning: Beyond the Hebbian synapse. *Annual Review of Psychology, 64*, 169–200.

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General, 130*(3), 505.

Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters, 1*(3), 314–317.

Hayward, A., Good, M. A., & Pearce, J. M. (2004). Failure of a landmark to restrict spatial learning based on the shape of the environment. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 57*(4), 289–314.

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370*(6484), 57–59.

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61*(3), 195–232.

Horne, M. R., Iordanova, M. D., & Pearce, J. M. (2010). Spatial learning based on boundaries in rats is hippocampus-dependent and prone to overshadowing. *Behavioral Neuroscience, 124*(5), 623–632.

Horne, M. R., & Pearce, J. M. (2009). A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pretraining. *Learning & Behavior, 37*(2), 167–178.

Horne, M. R., & Pearce, J. M. (2011). Potentiation and overshadowing between landmarks and environmental geometric cues. *Learning & Behavior, 39*(4), 371–382.

Jeffery, K. J. (2010). Theoretical accounts of spatial learning: A neurobiological view (commentary on Pearce, 2009). *Quarterly Journal of Experimental Psychology, 63*(9), 1683–1699.

Jeffreys, H. (1961). *Theory of probability.* Oxford, UK: Oxford University Press.

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2010). Re-orienting in space: Do animals use global or local geometry strategies? *Biology Letters, 7*(3), 372–375.

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*(3), 259–269.

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for *t*-tests and ANOVAs. *Frontiers in Psychology, 4*(863), 1–12.

Lew, A. R. (2011). Looking beyond the boundaries: Time to put landmarks back on the cognitive map? *Psychological Bulletin, 137*(3), 484–507.

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 human adults and young children (*Homo sapiens*): Implications for representation of local geometry by spatial systems. *Developmental Psychobiology, 56*(3), 421–434.

Lourenco, S. F., & Huttenlocher, J. (2007). Using geometry to specify location: Implications for spatial coding in children and nonhuman animals. *Psychological Research Psychologische Forschung, 71*(3), 252–264.

Lourenco, S. F., Huttenlocher, J., & Vasilyeva, M. (2005). Toddlers' representations of space: The role of viewer perspective. *Psychological Science, 16*(4), 255–259.

Lubyk, D. M., Dupuis, B., Gutierrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: Angles weigh in. *Psychological Bulletin and Review, 19*, 436–442.

Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning & Behavior, 16*(4), 404–410.

McGregor, A., Horne, M. R., Esber, G. R., & Pearce, J. M. (2009). Absence of overshadowing between a landmark and geometric cues in a distinctively shaped environment: A test of Miller and Shettleworth (2007). *Journal of Experimental Psychology: Animal Behavior Processes, 35*(3), 357–370.

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*(3), 314–321.

Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes, 33*(3), 191–212.

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*(3), 419–422.

Miller, N. Y., & Shettleworth, S. J. (2013). Associative models of instrumental learning: A response to Dupuis and Dawson. *Journal of Experimental Psychology: Animal Behavior Processes, 39*(3), 287–293.

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology, 18*(9), 689–693.

Pearce, J. M. (2009). The 36th Sir Frederick Bartlett Lecture: An associative analysis of spatial learning. *Quarterly Journal of Experimental Psychology, 62*(9), 1665–1684.

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 for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30*(2), 135–147.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on-the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 201–214.

Poulter, S. L., Kosaki, Y., Easton, A., & McGregor, A. (2013). Spontaneous object recognition memory is maintained following transformation of global geometric properties. *Journal of Experimental Psychology: Animal Behavior Processes, 39*(1), 93–98.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science, 19*(12), 1301–1307.

Redhead, E. S., & Hamilton, D. A. (2007). Interaction between locale and taxon strategies in human spatial learning. *Learning and Motivation, 38*(3), 262–283.

Redhead, E. S., & Hamilton, D. A. (2009). Evidence of blocking with geometric cues in a virtual watermaze. *Learning and Motivation, 40*(1), 15–34.

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition, 85*(2), B51–B59.

Spelke, E. S., & Lee, S. A. (2012). Core systems of geometry in animal minds. *Royal Society Philosophical Transactions Biological Sciences, 367*(1603), 2784–2793.

Steiger, J. H. (2004). Beyond the *F* test: Effect size confidence intervals and tests of close fit in the analysis of variance and contrast analysis. *Psychological Methods, 9*(2), 164.

Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin & Review, 18*(5), 848–854.

Sturz, B. R., Forloines, M. R., & Bodily, K. D. (2012). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin & Review, 19*(2), 270–276.

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*(2), 246–253.

Sturz, B. R., Kilday, Z. A., & Bodily, K. D. (2013). Does constraining field of view prevent extraction of geometric cues for humans during virtual-environment reorientation? *Journal of Experimental Psychology: Animal Behavior Processes, 39*(4), 390.

Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews, 36*(2), 799–824.

Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition, 7*(1), 53–59.

Tversky, B., Kim, J., & Cohen, A. (1999). Mental models of spatial relations and transformations from language. *Advances in Psychology, 128*, 239–258.

Twyman, A. D., & Newcombe, N. S. (2010). Five reasons to doubt the existence of a geometric module. *Cognitive Science, 34*(7), 1315–1356.

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representations: A test with chicks (*Gallus gallus domesticus*). *Journal of Comparative Psychology, 104*(3), 248.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6*(9), 376–382.

Wang, R. F., & Spelke, E. S. (2003). Comparative approaches to human navigation. In K. Jeffery (Ed.), *The neurobiology of spatial behavior* (pp. 119–143). Oxford, UK: Oxford University Press.

Wilson, P. N., & Alexander, T. (2008). Blocking of spatial learning between enclosure geometry and a local landmark. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*(6), 1369–1376.

Wystrach, A., & Beugnon, G. (2009). Ants learn geometry and features. *Current Biology, 19*(1), 61–66.

Zacks, J. M., Vettel, J. M., & Michelon, P. (2003). Imagined viewer and object rotations dissociated with event-related fMRI. *Journal of Cognitive Neuroscience, 15*(7), 1002–1018.