Exploring Properties of Reorientation Surrounding Boundary Transfer and Shape Transformation Procedures.

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“We shape our buildings; thereafter they shape us.”

- ***Some guy, 1941***

Abstract.

Recent cue competition literature, such as Buckley, Smith & Haselgrove (2016a), and Herrera et al., (2022), have challenged the notion that learning about the geometric properties of an environment is processed in an encapsulated module. Here, the encoding of spatial features, such as arena boundaries, is thought to be prevented from interaction with non-spatial cues (e.g., landmarks), and therefore immune to standard overshadowing and blocking effects (Gallistel, 1990). Work presented in this thesis aims to further explore the malleability of this idea by exploring properties of reorientation – sometimes in the presence of landmarks.

Similarly, this thesis builds upon the work of Buckley et al., (2016b), which broadly suggests that reorientation behaviour is based upon allocentric or global spatial processing following an arena boundary transfer; however, as alluded to above, many results within the spatial cognition field may indeed be task or procedure specific. Here, we further test this idea by assessing navigational behaviour following boundary transfers under procedural conditions in which no reorientation methods are precluded (see also: Buckley et al., 2019).

Results reported within provide further evidence that under typical training-to-test paradigms, reorientation behaviour following a boundary transfer is indeed resiliently reliant on allocentric or global processing (experiments I:III). This effect can be broken thought the inclusion of landmarks (internal and external: see experiment IV), however, of crucial note, navigators within this experiment were able to accurately identify the global structure of their environment when faced with a post-test shape recognition task. Further results suggest this resilient effect may be specific to typical training-to-test paradigms; when faced with intermixed internal and external trials, navigators show no preference for reorientation based upon any spatial reference frame (see chapter IV).

In the final experimental chapter reported in this thesis, we explore a potential developmental trajectory of this resilient effect through the use of child participants (see chapter V). Here, navigators again typically navigate with regard to global shape structure when faced with training-to-test boundary transfer procedures. Unlike adult participants, however, children’s reorientation behaviour is less precise, potentially highlighting impaired or underdeveloped allocentric spatial processing abilities. Please see general discussion (chapter VI) for further discussion and potential directions for future research.

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I'll let you decide how you feel about that…

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Last and definitely not least: thank you to the furry goblins that get me out of bed every day;

Contents.

Chapter One: Literature Review.

1.1. Spatial Processing & Navigation.

Within academic literature there is no standardised definition for navigation; an act colloquially regarded as accurately ascertaining one's location and then following a route to another (Cambridge University Press, 2020). This ability is considered to be a particularly complex behaviour and is often thought to rely on a range of perceptual, mnemonic, and executive functions (Dudchenko, 2010). Successful navigation requires the integration of spatial cues (e.g. boundaries or landmarks), the selection of an appropriate strategy, and, if needed, an adaptation of that strategy mid-journey (Brodbeck & Tanninen, 2012).

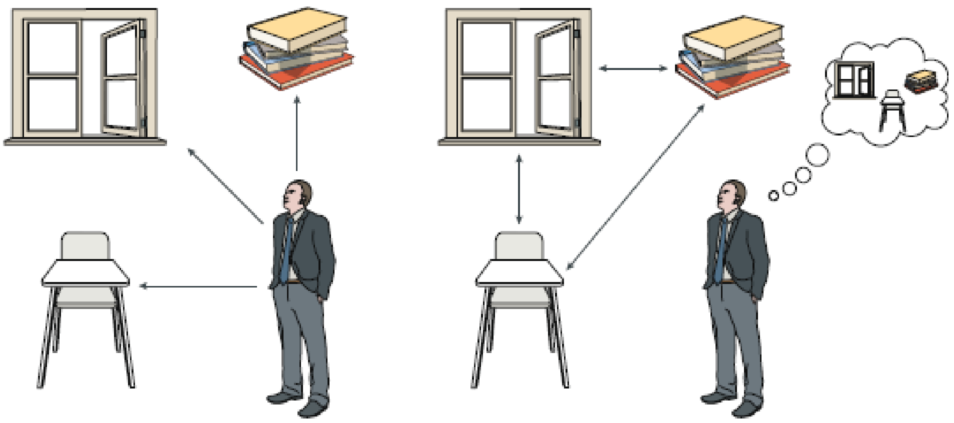
Humans, like many animals, can navigate effectively from one place to another within complex environments, and use this spatial knowledge to reorientate themselves when challenged with a spatial displacement. For example, after exiting a large shop, people can successfully reorientate themselves – the act of finding one's position in new or unfamiliar surroundings - and navigate back to the location of their parked car. This may be even though they are in a different location to that in which they originally entered the shop. The underlying cognitive mechanisms that permit this form of spatial reorientation are still under investigation, and recently the role of geometric information, such as the relationships between physical boundaries, has become a focus of attention (for reviews see: Cheng, Huttenlocher, & Newcombe, 2013; Lee, 2017). The experimentation reported in this thesis aims to build upon this growing field by exploring navigation with regards to environmental boundaries.

Given the complexity of this common behaviour, there is a plethora of research exploring the underlying cognitive and biological mechanisms which govern navigation. This includes substantial contribution from the cognitive, developmental, comparative, and neuroscientific fields, with literature ranging from the biomechanics of path integration (Andersen, Morris, Amaral, Bliss, & O' Keefe, 2009; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006), through to more general eye-tracking and decision making investigations (Franchak & Adolph, 2010; Kaplan, Schuck, & Doeller, 2017); for reviews see, Andersen et al., (2009); Dudchenko, (2010); Filimon, (2015); Golledge, (1999); Grieves & Jeffery, (2017); Jeffery, (2010); Spiers & Barry, (2015); Swanson, (2003); Thinus-Blanc, (1996).

Combined, the navigation literature suggests that, from an overarching cognitive perspective, typical navigating organisms are capable of two types of spatial processing – allocentric and egocentric (see figure 1). By wielding dual methods of spatial processing, it has been proposed that navigators develop multiple spatial representations - or internal reference frames - of their environments (Bodily, Eastman, & Sturz, 2011; Burgess, 2006; Kaplan et al., 2017). Subsequently, these reference frames can be utilised to inform active navigation.

Figure 1.

Egocentric (left) and allocentric (right) spatial processing.



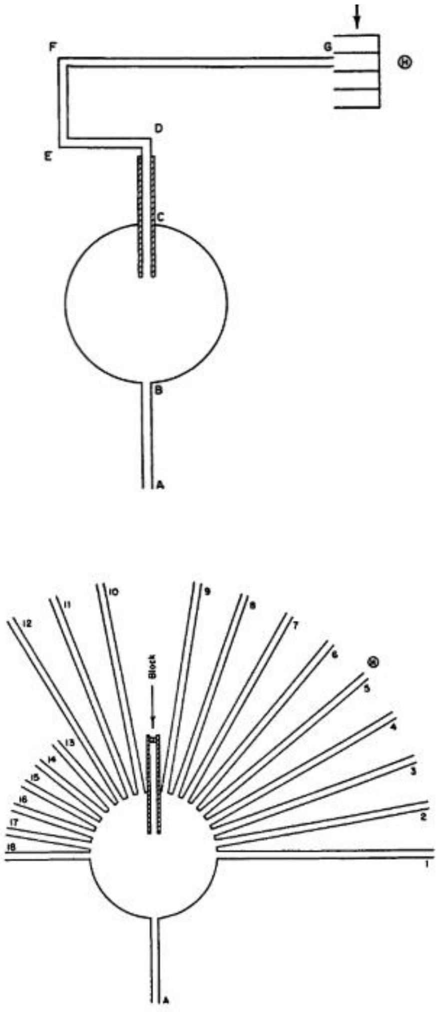
Note. Figure adapted from Coughlan et al., (2018). *. On the left, the positions of the window, the books and the chair are a function of the location of the viewer; on the right the positions of the objects are a function of each other's positions.*

An allocentric reference frame – often aligned with a "global" spatial representation or a "cognitive map" – is thought to be independent of the navigator and does not change as their position changes This concept was first alluded to in a series of nine papers by Edward Tolman (Tolman, Ritchie, & Kalish, 1946; Tolman, 1948). Tolman trained rats to follow a complex path towards a goal location having started in a central hub. When placed in a near identical maze where the previously trained path was no longer available, rats were found to prefer the path off the central hub that corresponded with the most direct route to the previously trained goal location (see figure 2). These "short-cut" results led Tolman to conclude that animals were able to understand locations and directions irrespective of the specific movements that were previously required to reach them. He named this phenomenon the "cognitive map" and began the notion that animals acquired an allocentric representation of space in which *the locations of objects and features are defined in terms of their positioning to each other and not the position of the navigator.*

The formation of an allocentric reference frame – or spatial/cognitive mapping - is not considered to be an absolute process, with navigators showing wide variability in performance. This variability has been linked to many factors, including age (Lester, Moffat, Wiener, Barnes, & Wolbers, 2017), emotional state (Chan et al., 2016; McEwen & Sapolsky, 1995), environmental familiarity (Hartley, Maguire, Spiers, & Burgess, 2003), environmental complexity (Golledge, 1999, 2003; Maguire, Burgess, & O'Keefe, 1999), and the onset of neurodegenerative disorders such as Alzheimer's disesase (Coughlan, Laczó, Hort, Minihane, & Hornberger, 2018).

Figure 2.

The "sun burst" maze used in Tolman and colleagues' experimentation (1948).



Note. Top represents the training path rodents originally used to locate the hidden goal ("H"). Bottom represents the subsequent test trial, in which the original route to goal location is no longer traversable; here, path "5" represents the most direct path to the previously trained goal.

Many learning theorists have aimed to further specify this allocentric spatial encoding, suggesting that animals specifically create and encode and/or retrieve a Euclidian cognitive map of their environment (Gallistel, 1990). Within this representation only the overall shape, distances and angles provided by environmental boundaries are thought to be encoded and then used for orientation and from there used to guide navigation (Cheng & Newcombe, 2005; Spelke & Lee, 2012; for a review, see Cheng, Huttennlocher & Newcombe, 2013). The motivation behind using such an impoverished encoding of allocentric information is that the environment changes substantially between the seasons. Features that may be used for navigation in summer may be entirely absent for some time after the first winter snow fall, for example. However, a more constant feature of the environment that transcends the seasons is the geometric relations between features. For example, three mountains may appear very different in the summer relative to the way in which they look in the winter. However, the geometric relations provided by the angles between their peaks remains the same, as do the boundaries created by valley rivers and cliff faces.

In contrast to the allocentric perspective of spatial encoding, space may also be represented in an egocentric manner, in which the location of objects and features are represented in terms of their relationship to the individual navigator (often aligned to "local encoding", see figure 1 (left)). For example, an individual's relative "left and right", in contrast to the more allocentric "west and east" of absolute space (Hu, Yang, Huang, & Shao, 2018). Again, processing space in such a manner is not considered to be an absolute process, with humans showing wide variability in navigation and spatial tasks thought to be more reliant on egocentric spatial processing (e.g. visual distance judgement and short distance straight-line traversing (see also: driving, skating, and using a wheelchair); for reviews see Golledge, (1999) and Hubbard, (2018)). This includes the use of local-geometric features and environmental landmarks to guide navigation (see immediate below).

It has been proposed that for navigation to be more effective, both egocentric and allocentric spatial reference frames are utilised

(Bodily et al., 2011; Dudchenko, 2010; Hartley et al., 2003; Lei, Mou, & Zhang, 2020; Marchette, Ryan, & Epstein, 2017). This is, in part, because a radical theory of sole egocentric *or* allocentric based navigation cannot account for all of the observable behavioural data. For example, as outlined above, the results from Tolman's original experimentation (1948) cannot be explained without the inclusion of allocentric spatial processing. That is to say, if the rats were to *only* encode spatial information relative to the previously trained egocentric body movements, there is no way for them to locate the goal at test as this route had been closed.

Similarly, the results from various shape transformation studies (where the overall shape of an environment is changed between training and test) cannot be explained without the inclusion of egocentric spatial processing (e.g. Buckley, Smith, & Haselgrove, (2016); Pearce, Good, Jones, & McGregor, (2004); see section 1.3 below).

Furthermore, various specific navigational strategies have been identified, each of which is thought to rely more heavily on either an allocentric or egocentric reference frame. Strategies thought to be more reliant on egocentric spatial processing include "view matching", in which the current visual input is compared with stored spatial memory and the navigator moves to reduce discrepancy (Cheng et al., 2013; Jain, Jakhalekar, & Deshmukh, 2017; Sturzl & Zeil, 2007); "beacon" strategies, where a navigator centrally lines up a goal location within their visual field before moving towards it (Bohbot et al., 2012); and "sequential" or "response" strategies (McGregor, Jones, Good, & Pearce, 2006; Pearce, Good, Jones, & McGregor, 2004), in which organisms habitually respond to environmental cues without reference to wider surroundings (e.g. "turn left at the junction" - see also: "piloting" and "route-following" (Gallistel, 1990; Hartley et al., 2003; Lei et al., 2020)). On the other hand, navigational strategies thought to be more reliant on allocentric spatial processing include "novel shortcut" taking (Tolman, 1948); "wayfinding", the act of getting from place to place in unfamiliar largescale environments where a start location and goal location are not visually linked (Hartley et al., 2003; Maguire et al., 2000; Maguire, Woollett, & Spiers, 2006); and "place" or "spatial" strategies, in which organisms encode spatial information with regard to the global structure of their environment (Bohbot et al., 2012; Morris, Garrud, Rawlins, & O'Keefe, 1982; Packard & McGaugh, 1996).

Some researchers have further suggested that better navigators are those who are able to swap from one spatial representation to another more freely (when compared to poorer navigators), choosing the more optimal behavioural strategy in any given navigational situation (Hartley et al., 2003; Restle, 1957). While egocentric-based spatial processing may be the default in for many organisms to engage with their surroundings, as bodily senses are egocentric in nature (e.g. vision), arguments have been made that stored allocentric representations are required to guide navigation over large scale or unfamiliar environments (Burgess, 2006; but see Filimon, 2015). Since both egocentric and allocentric spatial processing-based navigational strategies are employed by a variety of organisms across a variety of tasks, it has been proposed that the focus of future research should be to determine under what circumstances each reference frame is employed and what factors may influence this selection (Lee, 2017). This includes exploration into interpersonal navigator factors (i.e. the navigator), investigation into the use of environmental cues (i.e. the space) and any potential interaction.

1.2. Individual differences & Navigation.

A key factor thought to have influence over navigational performance is the age of the navigator (for reviews, see Bohbot et al., 2012; Konishi, Mckenzie, Etchamendy, Roy, & Bohbot, 2017; Lester et al., 2017; Wills & Cacucci, 2014; Newcombe, 2019; León, Tascón, & Cimadevilla, 2016). Broadly, this literature suggests that younger children and older adults have a bias towards navigational strategies thought to be more reliant on egocentric spatial processing (developmental research detailed further in section 1.3). Similarly, aspects such as emotional states, environmental familiarity and behavioural history are also thought to influence navigation strategy use. For example, individuals experiencing highted levels of stress, depression or anxiety are reported to engage in more egocentric-based navigation (Brown, Gagnon, & Wagner, 2020; Conrad, Galea, Kuroda, & McEwen, 1996; Kleen, Sitomer, Killeen, & Conrad, 2006; Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012; Sheline, Wang, Gado, Csernansky, & Vannier, 1996). In contrast, individuals who engage in more driving (without SATNAV), play more video games, or grew up in more rural areas are reported to be more proficient navigators and engage in greater levels of allocentric processing (Coutrot et al., 2022; Maguire et al., 2000; Murias, Kwok, Castillejo, Liu, & Iaria, 2016; Van Mier & Jiao, 2020).

Alongside these interpersonal factors, another aspect thought to influence navigational behaviour is how an individual is exposed to an environment over time. For example, it has been suggested that many navigational tasks may start in a rapidly learned, allocentric-based fashion using the global position of cues to orientate. With repetition and familiarity, however, this bias shifts to an egocentric based response strategy (Bast, Wilson, Witter, & Morris, 2009; Jeffery, 2010). Authors have described this as a navigational “autopilot” process, in which a predominantly action-based representation is formed, thus reducing the need for more intense perceptual spatial processing and freeing cognitive resources for other demands (Veronique D. Bohbot et al., 2012; Hartley et al., 2003). For these reasons it can be argued that navigating well-known routes or familiar environments may use automatic learned responses to the presence of known environmental landmarks (Lithfous, Dufour, & Després, 2013). However, the time required for this automation is ambiguous and task dependant, possibly taking seconds, minutes (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003), days (Barnes et al., 2005) or much longer.

A clear demonstration of this effect, was provided by Iaria et al., (2003). Here, researchers aimed to explore the use of different navigational strategies during the 4/8VM. This virtual maze task was intentionally designed to allow for two distinct place-learning strategies and is very commonly used in navigation research (e.g. O’keefe & Nadel, 1979). The virtual environment is composed of an eight-arm radial maze with a central starting location. Participants must systematically retrieve items from the end of each arm (not visible from the centre) without re-entering previous arms. Probe trials are used to assess navigational strategies used and included manipulations such as raising wall heights to conceal extra-maze landmarks (visual landmarks beyond the accessible boundaries of the arena). Iaria et al., categorised participants during debriefing; if a participant associated arms with self-coded numbers or letters to complete the task, they were defined as non-spatial (egocentric), and if a participant mentioned the use of *at least two* extra-maze landmarks they were categorised as spatial (allocentric). Upon categorisation a third group emerged – “Shift”. These were participants that started the task using an allocentric spatial strategy and over time shifted towards a non-spatial egocentric strategy. As early as the third block (≈20 minutes), many participants who had previously been using allocentric strategies to solve the task had begun shifting towards egocentric methods. Of note, participants in this shift group were able to complete the task faster than those who continuously used a single spatial strategy, supporting the notion that better navigators are those more flexible in their reference frame utilisation. Additionally, at the start of the experiment participants spontaneously chose either an egocentric or an allocentric strategy at an almost 50:50 rate.

Similarly, in a study by Hartley et al., (2003), participants were introduced to novel environments (two virtual towns) through two different exploration methods. One town was introduced via free exploration, whilst the second was introduced by following a fixed route (verbal instructions). At test, participants were assessed on their ability to find shortcuts in the first town (allocentric wayfinding) and asked to traverse the familiar route in the second (egocentric route following). Performance during these tasks was measured by comparing paths taken by participants against the "ideal path"; a path defined by calculating the most direct route possible taking the least amount of time. For comparison, a second group were simply asked to follow a visible trail in both environments (trail following) – an activity thought not to require spatial memory. Interestingly, participants who engaged in less allocentric processing (measured via fMRI inference) performed worse at the wayfinding task in the first environment. Further still, better navigators suggested higher levels of allocentric processing during the route following task, alongside displaying a higher level of egocentric processing (when compared to wayfinding and trail following). In complimentary fashion, poorer navigators suggested higher levels of egocentric spatial processing during the allocentric wayfinding task (see also; Doeller & Burgess, 2008).

As with most imaging research, however, additional caution must be made when interpreting brain imaging data with such reverse inference. Navigation is a complex behaviour, and is thus reliant on many neural pathways working in synchronicity (Swanson, 2003). For example, while hippocampus activity is quite famously aligned with allocentric spatial processes (O'keefe & Nadel, 1979), cognitive mapping is clearly not all the hippocampus does, with activation being associated with many other functions including inhibition and anxiety (Gray 1982; Davidson & Jarrard, 2004), sensorimotor function (Vanderwolf & Cain, 1994), and acting as a comparator to detect novelty (Gray, 2000). Many strategies considered more egocentric in nature may still employ hippocampal computations; for example, response strategies may rely on information regarding the temporal order in which landmarks have been encountered (Rondi-Reig et al., 2006). These systems are also open to experimental manipulation, such as imagined navigation (Horner, Bisby, Zotow, Bush, & Burgess, 2016). Combined, however, these findings further support the theory that effective navigation is dependent on the use of multiple types of spatial processing.

Alongside these interpersonal and environmental exposure variables, a final factor which may influence navigational performance or strategy choice is the spatial cues available within the environment itself. This includes the presence of landmarks and the overall geometry of any immediate boundaries (i.e. walls; for reviews see Cheng, Huttenlocher, & Newcombe, 2013; Lee, 2017). It is to this variable which we now turn our attention.

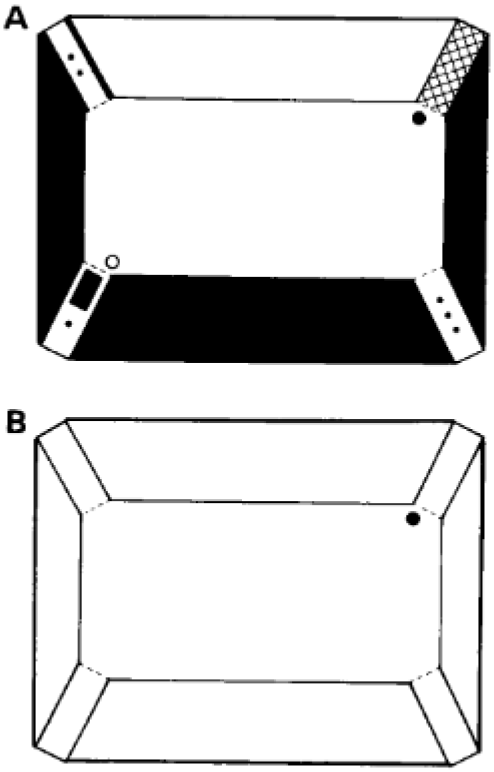
1.3. Boundary Use & Navigation.

Following Tolman's founding cognitive map experimentation, a prolific literature has established that a wide variety of animals can reorient with respect to the geometric information provided by the boundaries of an environment, including ants (Wystrach & Beugnon, 2009), fish (Sovrano, Bisazza, & Vallortigara, 2002), chicks (Vallortigara, Zanforlin, & Pasti, 1990), mountain chickadees (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005), pigeons (D. M. Kelly, Spetch, & Heth, 1998), rats (McGregor, Hayward, Pearce, & Good, 2004), rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001), as well as adult humans (Redhead & Hamilton, 2007, 2009) and children (e.g. Hermer & Spelke, 1996, 1994). However, despite the pervasive use of geometric information across species, there is considerable debate in the developmental (e.g. Newcombe, 2019; Piaget & Inhelder, 1997), cognitive (e.g. Cheng, Huttenlocher, & Newcombe, 2013; Lee, 2017), comparative (Pearce, 2009), and neuroscientific (e.g. Dudchenko, 2010; Jeffery, 2010) literature as to exactly how organisms encode information about boundary geometry during re-orientation.

A theory of shape-based reorientation that has influenced research in multiple disciplines suggests that organisms rely on the "global" shape of an environment to guide reorientation in an allocentric manner (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002). This notion can be traced back to seminal comparative studies conducted by Cheng (1986), who observed that rats encoded a goal location with respect to the ambiguous shape of their environment, even in the presence of internal (intra-maze) landmarks that unambiguously predicted the location of the goal (for a review see: Cheng, Huttenlocher, & Newcombe, 2013). In his Experiment 1, Cheng trained and tested rats within rectangles. During training, food was hidden adjacent to a uniquely panelled corner (see figure 3), with increasing levels of salience (see also: experiment 2, Cheng, 1986)

Figure 3.

The arenas used in Cheng's experimentation (1986).



Note. Figure adapted from Cheng, (1986). Top ("A") represents the initial training environment; this includes the location of the hidden food (black circle), unique corner landmarks (panels) and distinctively coloured walls (black & white). Bottom ("B") represents the final test arena.

During test, the rats were placed inside a new rectangle arena in the absence of landmarks and were found to search in both the correct corner (the corner the food was originally buried in) and the corner diagonally opposite. As both corners were geometrically identical (i.e. a concave corner with a short wall on the right of a long wall), Cheng concluded that the rats had encoded the entire shape of the arena and therefore used the global representation of their environment to locate their goal, as opposed to using the unique landmarks. He stated that searching in the diagonally opposite corner was simply a rotation error due to the overall shape of the arena being symmetrical on both the horizontal and vertical meridian.

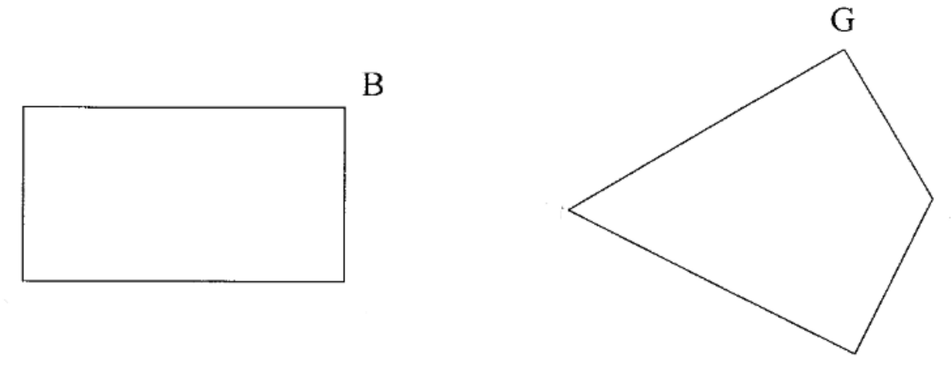
Further still, on the basis of these findings Cheng proposed a geometric module for reorientation, which: 1) encodes the global shape properties of an environment, and 2) is impervious to the influence of learning about non-shape cues, such as landmarks. In keeping with the ubiquitous use of shape information for guiding reorientation across species, Gallistel (1990) advocated the evolutionary benefit of relying on geometric cues within the environment, arguing, as was noted earlier, that whilst the appearance of an environment may change over time (e.g., the appearance of a mountain range will change with the weather across the seasons), the geometric layout of an environment will not (i.e. the broad shape of the mountain range will not change with seasonal weather). Consequently, it is advantageous for navigators to rely on the geometry of their environments to guide reorientation, as this remains constant.

Whilst some proponents of the geometric module have conceded that a strict interpretation of the hypothesis does not fully explain all empirically reported reorientation (Cheng et al., 2013), the notion that organisms navigate using global representations of boundary information has been championed in many studies of navigation (e.g. Cheng & Newcombe, 2005; Doeller & Burgess, 2008; Gouteux et al., 2001; Wall, Botly, Black, & Shettleworth, 2004; Wang & Spelke, 2002). For example, proposals similar to those of Cheng’s geometric module have been echoed in the developmental literature, in which a “boundary primacy” effect has been taken as evidence that children rely on the global-shape information provided by the boundary walls of an environment to reorientate – even if non-shape features are present (e.g. Lee & Spelke, 2010). For instance, in an experiment conducted by Hermer and Spelke (1996), children were required to find a toy that was hidden under one of four identical containers that were placed in the corners of a 4 x 6.25ft rectangular arena that comprised three white walls and one polarising blue wall. Here, children could unambiguously learn the location of the hidden toy with respect to the blue feature wall, but instead they were observed to rely on the ambiguous shape of the rectangular walls and, thus, searched equally often in the two geometrically equivalent corners of the environment, consistent with an allocentric strategy (in a similar fashion to Cheng's original rodents (1986; see also: Margules & Gallistel, 1988)).

The notion that animals encode global-shape representations has not gone unchallenged, however. According to local theories of shape-based reorientation, animals may encode, for example, the relative wall lengths that are provided by the conjunction of two walls in an egocentric manner. For a clear demonstration of this effect Pearce, Good, Jones, & McGregor, (2004). trained rats to find a hidden goal in one shape (e.g. a rectangle), before being tested in another (e.g. a kite; see figure 4)., individual local features of geometry can be matched across both of these arenas (i.e. you both have a concave corner wall with a short wall on the left and a long wall on the right). The results revealed that, rodents trained to locate a hidden goal at such a location in a rectangle will search at the corresponding identical location at test, even though the overall global shape of the environment was transformed (see also: Jeffery, 2010; McGregor et al., 2006; Pearce, 2009).

Figure 4.

The arenas used by Pearce, Good, Jones & McGregor (2004).



Note. Figure adapted from Pearce, Good, Jones & McGregor, (2004). Rodents trained to find food at corner "B" within the rectangular arena were found to search at corner "G" when placed inside the kite shaped enclosure.

This effect has been replicated in multiple species and across multiple human age ranges (Buckley, Smith, & Haselgrove, 2016a (experiment 1); Lew et al., 2014; Tommasi & Polli, 2004). For instance, Lew et al., (2014) trained adult humans to find a hidden goal that was located in a right-angled corner of a kite-shaped virtual environment, before transferring them to a rectangle-shaped virtual environment. Whilst the global shapes of these two environments differed, as above, both the kite- and rectangle-shaped environments contained at least one right angled corner where a short wall was to the left of a long wall, and at least one right angled corner where a short wall was to the right of a long wall. Upon being placed into the rectangle-shaped environment, Lew et al. (2014) observed that participants preferentially searched in the corner of the arena that shared the same local-shape properties that signalled the goal location in the kite shaped environment. Given that the global shape of the two environments in this experiment were different, this preference could only have been driven by local shape information.

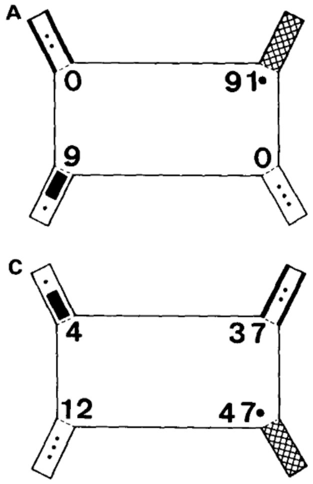
With these results in mind, it is possible to interpret the findings reported by Cheng (1986) by assuming that rats learned the location of the buried food on the basis of the local-shape information that was present only at the rewarded corner, and not on the basis of the global shape of the environment. According to this analysis, rats associated a goal with relative wall length information in an egocentric manner, such as the view of a short wall is to the left of long wall (Pearce et al., 2004), Crucially, in a rectangle, the baited corner and the corner diagonally opposite are identical in local shape geometric properties. Rats navigating on the basis of local shape information, then, would be expected to visit the diagonally opposite corner, as was observed in the experiments conducted by Cheng (1986: see also: Margules & Gallistel, 1988).

It is important to note, however, that evidence suggesting organisms encode local-geometric information provided by shape transformation experimentation does not constitute evidence against the encoding of global shape information. For instance, in the training stage of the experiment conducted by Lew et al. (2014), it is possible that participants encoded both the local- *and* global-shape properties of the kite shaped environment, consistent with a duel processing approach to spatial cognition (Bodily et al., 2011; Burgess, 2006; Lee & Spelke, 2010b) At test, however, the global representation of the kite shaped training environment would be incongruent to the now rectangle shaped test arena. Consequently, any global representation encoded by participants during training would be of little worth in guiding navigation during test; thus, biasing reorientation on the basis of the local-shape properties that were preserved between the training and testing environments.

This analysis may explain a number of results from experiments within the shape-transformation literature where both a global representation and a local egocentric feature (such as a landmark or isolated-wall section) are placed into competition, or simply no instruction is given, navigators have been shown to navigate to both an egocentric and allocentric representation at an equivalent rate. For example, in the final study reported by Cheng, (1986; experiment 3), rodents were again trained to locate a hidden goal (food) within a rectangular arena, with unique coloured panels present (see figure 5). For the rodents that received a test condition where the panels were rotated 90 degrees (thus, placing the boundary and landmark information into conflict), half of the rats searched at the corner which previously identified the goal location (and its diagonally opposite equivalent), and the other half continued to search at the unique landmark (see also: Iaria et al., (2003).

Figure 5.

The arenas and test data reported by Cheng, (1986; experiment 3).



Note. Figure adapted from Cheng, (1986). Rodents were trained to locate a hidden goal (black circle) within a rectangular arena (top ("A"; control)). For some rodents, at test ("C"), unique corner panels were rotated 90 degrees. Numbers represent the total percentage of time spent at each corner at test.

Similar results have been reported within the developmental literature, suggesting that reorientation strategy within some test scenarios may be task or parameter dependant. For instance, the "boundary primacy" effect as described above (Hermer & Spelke, 1996; Lee & Spelke, 2010). When the original Hermer and Spelke (1996) task was conducted in a larger rectangular arena (8 x 12 ft), children were able to use the polarising wall to reorient (Learmonth, Newcombe, and Huttenlocher, 2001; see also Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008). Children have also been shown to reorient using a polarising coloured wall in 7 x 7 ft rhombic space (Hupbach & Nadel, 2005), and in a large octagonal space (N. S. Newcombe, Ratliff, Shallcross, & Twyman, 2013). Finally, it has also been demonstrated that children are able to reorient using a local yellow polarising wall in a smaller rectangular arena (4 x 6 ft), providing they are first given pre-training in which they must find a hidden object in the centre of a yellow wall in an equilateral triangular arena (Twyman, Friedman, & Spetch, 2007).

It should also not go without mention that in each of the studies reported here, no attempt to assess if children encoded the global shape of their environment was made beyond providing them the opportunity to behaviourally respond to it at test; that is to say, experimenters made no effort to ask or infer from children if they can identify the global structure of their environment. It could be that children simply preferred to reorientate to the more salient polarising walls *while also* encoding the global shape of their test arenas – an idea we empirically test in chapter 5.

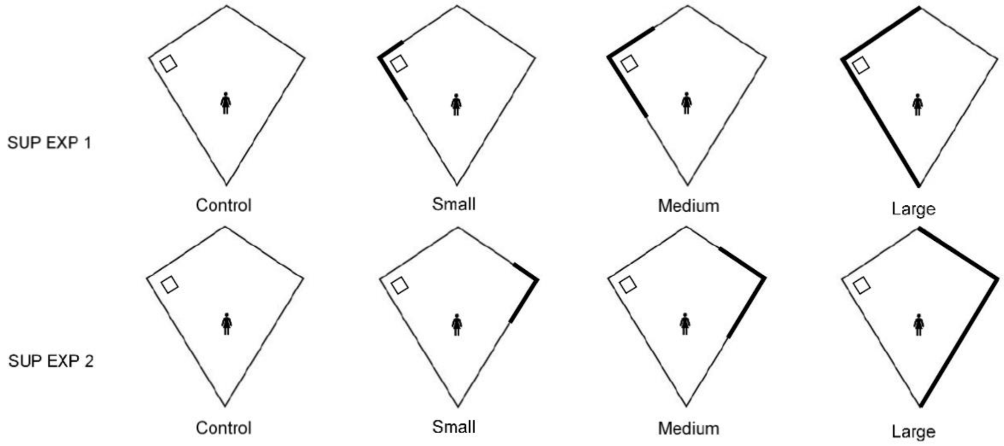
Theories similar to Cheng's geometric module have been echoed within the developmental literature, where children are reported to have a bias towards using intramaze cues to orientate, despite either extramaze cues or environmental boundaries providing valid goal-related spatial information (Buckley, Haselgrove, & Smith, 2015; Bullens, Iglói, Berthoz, Postma, & Rondi-Reig, 2010; Laurance, Learmonth, Nadel, & Jacobs, 2003). This preference for using intramaze cues to navigate has been suggested to be egocentric in nature, with some authors claiming that children find it difficult to link the geometric properties of isolated extra-maze landmarks; consequently, children may be using these proximal intramaze landmarks to navigate in a egocentric view-matching manner (Gouteux & Spelke, 2001; Lee & Spelke, 2010b). This cue-related orientation strategy, in which navigational behaviour is constrained or orientated around a second location or environmental feature, is thought to be evolutionally driven and developmentally beneficial as it encourages navigation with regards to a single focal point (such as a parent, tribe or dwelling: Bullens et al., 2010; Leplow et al., 2003; Cheng et al., 2013). It should be emphasised that data suggest children *may simply prefer* egocentric navigational strategies based around local features, and they are perfectly capable of demonstrating allocentric cognitive mapping in experimental situations as young as 36 months old (Nardini, Burgess, Breckenridge, & Atkinson, 2006; Nardini, Jones, Bedford, & Braddick, 2008). Of additional note, older children typically perform better in tasks of allocentric spatial processing, suggesting an observable developmental trajectory (Bostelmann, Lavenex, & Banta Lavenex, 2020; Wills & Cacucci, 2014).

Combined, the polarizing wall and shape transformation literature support a dual processing model of spatial cognition. As with adults and rodents, individual navigator circumstance and task specific design may influence behavioural strategy choice. Recent experimentation suggests that an important variable may be the placement of landmarks relative to any goal location and environmental boarders. For example, in a paper published by

Herrera et al, (2022; supplimentary experiments 1 & 2), adult human participants were trained within a kite (with landmarks), before being tested in a kite (no landmarks; see figure 6). During training, coloured panel landmarks were introduced, varying in size and proximity to the goal location.

Figure 6.

The arenas used by Herrera et al, (2022; supplementary experiments 1 & 2).



Note. Figure adapted from Herrera et al., (2022). Bold walls represent the landmark location and length (small, medium or large), whereas the square represents the goal location.

Results from the test stage of this experimentation display a clear overshadowing effect. Here, when placed inside the kite in the absence of any goal or landmarks, participants in supplementary experiment 1 spent significantly less time at the correct corner at test compared to their control group. This overshadowing effect seems to weaken gradually as the landmark's size decreases (see also: Chamizo, Manteiga, Rodrigo, & MacKintosh, 2006). No overshadowing effect was found amongst participants in supplementary experiment 2, suggesting that proximity between local features and goal locations may play a crucial role in test behaviour for experimentation of this type, alongside the encoding of global shape in general.

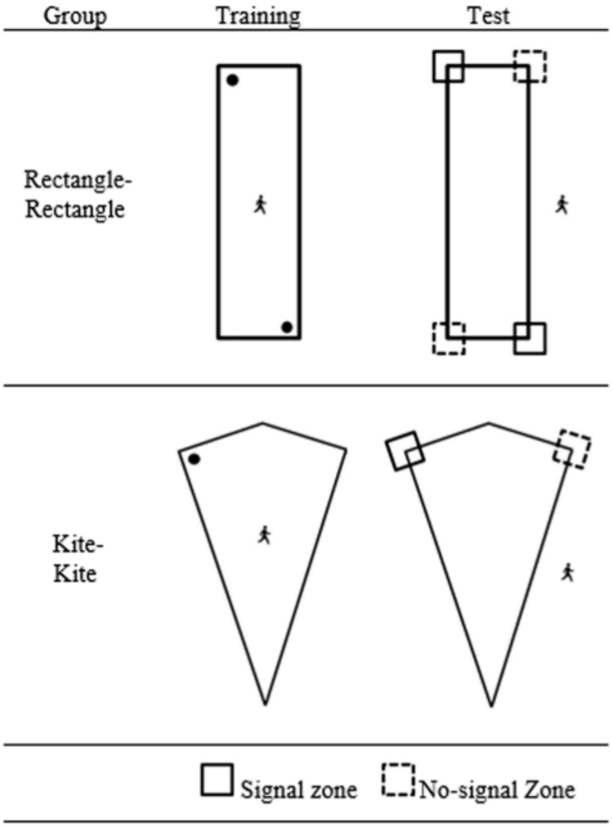
Part of the problem in exploring how the shape of an environment is encoded during navigation is that it is not entirely clear how to dissociate reorientation based on global information from local information *when using shape alone.* In most of the experimentation presented above (e.g. polarising wall studies), any local or egocentric elements are often aligned with *a landmark*, either isolated or integrated within a boundary itself (e.g. Herrera et al., 2022).

With regard to the use of boundaries alone, single-process accounts of global-shape encoding struggle to explain the results of many shape transformation studies, as shape transformation paradigms, by their nature, preclude the ability to navigate with respect to the entire Euclidian context of an environment, as this global context is changed between training and test (see also: Esber, McGregor, Good, Hayward, & Pearce, 2005; Pearce et al., 2004; Poulter, Kosaki, Easton, & McGregor, 2013; Buckley, Smith, & Haselgrove, 2016b). Similarly, theories of local-shape encoding cannot adequately account for data reported in various wayfinding and shortcut experimentation, such as those originally reported by Tolman (1948; See also Cheeseman et al., 2014; Menzel et al., 2005), or recent *boundary transfer studies* (Buckley et al., 2016b; Buckley et al., 2019).

In boundary transfer studies, participants are trained to find a hidden goal that is, once again, located *inside* a distinctively shaped environment, such as, at one of the right-angled corners of a kite-shaped environment. Participants are then tested on the *outside* of the same shaped environment, and their search behaviour examined (e.g. Buckley et al., 2016b, Experiments 1a & 1b; see figure 7). The results of these studies reveal that participants search at the external corner closest to the internal goal location, a result that is inconsistent with navigation based upon egocentric local spatial-processing, as the crucial local features present during training were no longer available at test (i.e., the concave-corner angles were replaced with convex corner angles, and the juxtaposition of the long and short walls was reversed). Consistent results were found in experiment 2 of Buckley et al, in which training was conducted *outside*, before a final *internal* test trial. Further still, in conditions where the global shape of the environment is transformed at the same time at which a boundary transfer is conducted (e.g., participants trained on the inside of a kite to find a hidden goal are tested on the outside of a rectangle), participants no longer show preference towards searching at any particular exterior corner, suggesting navigators are doing more than a simple "mental rotation" of a local representation of the rewarded corner and were sensitive to global structure changes (Buckley et al., 2016b, Experiment 3).

Figure 7.

The arenas used by Buckley et al, (2016b; experiments 1a & 1b).



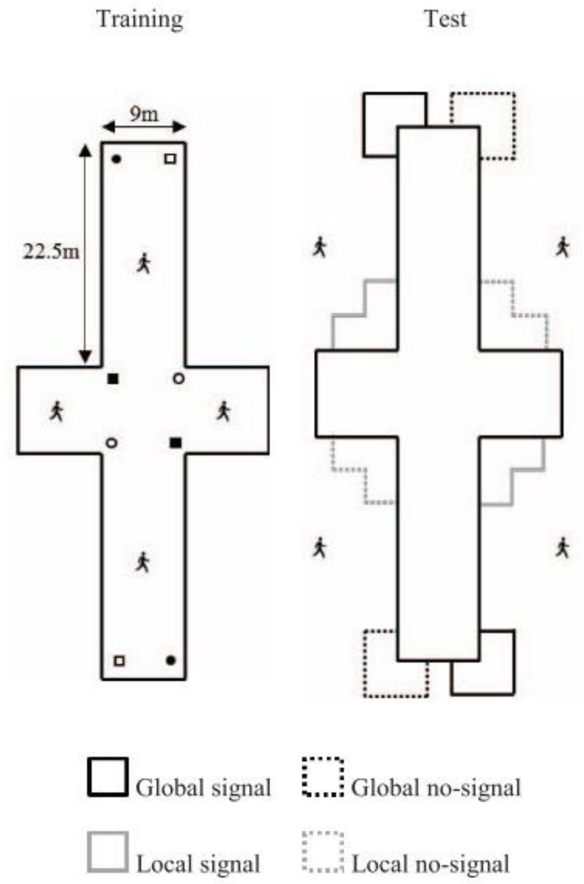
Note. Figure adapted from Buckley et al., (2016b). Top and bottom represent the training and test stages for experiment 1a and 1b, respectively.

Although these results are consistent with the idea that participants are using an allocentric representation of boundary geometry, it doesn't necessarily, rule out a more egocentric form of encoding during training, as this form of navigation, which is based upon local-shape representations, may be precluded by the boundary transfer, as all corner angles are reversed (i.e. concave corners become convex, and vice versa). This results in a mis-match of local geometric features between training and test environments; consequently, cues of global shape geometry may have been the only reorientation reference frame available.

In a recent paper, Buckley, Holden, Spicer & Haselgrove, (2019) investigated search behaviour following a boundary transfer, but under circumstances in which navigation based upon an egocentric spatial reference frame is not precluded. Adult human participants were again trained to locate a hidden goal, but now on the inside of a cross-shaped environment (see figure 8). The hidden goal was located adjacent to one of the right-angled corners on the inside of this environment (for example, at the concave corner where there was a long wall to the left of a short wall). Participants were then given a final test trial on the outside of the same-shaped environment. Interestingly, the structure of this environment comprises, on the outside, the same local-geometric features that signalled the goal location as during training on its inside. The results of this test showed that despite there being an opportunity to reorientate with regard to the geometry of the environment that matched the egocentrically-defined features from internal training, participants preferred searching in areas that were located closest to the goal location (the "global signal" zones). In contrast, they spent rather less time at areas that matched the egocentrically defined features of the local geometry from training (the "local signal" zones; see figure 8).

Figure 8.

The arenas used by Buckley et al, (2019; experiment 2).



Note. Figure adapted from Buckley et al., (2019). Open and closed squares and circles represent the four counterbalanced locations of the hidden goals employed during training. The person inside of the arena indicates the four starting locations used during training for all participants. Square search zones are superimposed on the diagram of the test environment and are labelled with reference to a counterbalancing group for whom the hidden goal was located by the closed circles. The person outside of the arena indicates one of four counterbalanced start locations for the test trial.

These results suggest the act of crossing an environmental boundary may be one of the task dependent factors that influence spatial reference frame utilization. Unfortunately no complimentary experimentation can be found within the developmental literature for additional inference. Here, To the best of our knowledge, studies exploring the sole use of environmental geometry is minimal, with only one shape-transformation experiment being reported in the developmental reorientation literature. In this experiment, children aged between 2 to 4 learned the location of a toy hidden in one of the corners of a rectangle-shaped environment, before receiving a test trial in a kite-shaped environment (Lew et al., 2014). Whilst responses to the correct and rotationally equivalent corner were above chance in the rectangle-shaped training arena, children displayed no preference for any corner of the kite-shaped test environment. Based on these findings, Lew et al. suggested that young children do not rely on local-shape representations to guide reorientation, but instead reorient using global-shape information. These findings also suggest that the ability to match local features of geometry in a new global context is a relatively later developing trait (Buckley et al., 2016b). It is, however, important to note that a demonstration of children failing to reorient on the basis of local geometry does not constitute evidence of children successfully reorienting on the basis of a global geometric representation. Again, then, it is rather difficult to interpret the results of shape-transformation experiments in terms of the question of whether a global representation of environmental shape is encoded because, like previous developmental studies of reorientation, the design of these experiments cannot reveal reorientation behaviour that relies on a representation of the global shape.

Consequently, as with adults, what cannot be determined from previous shape transformation experiments is the extent to which children rely on global- or local-shape representations when both types of representation can support reorientation. Studies employing procedures in which neither reference frame is precluded may provide additional data here, such as the boundary transfer paradigm reported by Buckley et al., (2019).

1.4. Structure of Thesis.

Empirically exploring the properties of reorientation following a boundary transfer will be the primary focus of experimentation reported in this thesis. This includes exploring a range of variables, including environmental familiarity (Bohbot et al., 2012; Lithfous, Dufour, & Després, 2013), exposure style (Maguire et al., 2006), and navigator age (Gazova et al., 2013; Lester et al., 2017; Rodgers, Sindone, & Moffat, 2012)

In Chapter 3, we both replicate and further investigate post-boundary transfer reorientation in a manner consistent with Buckley et al., (2019; experiment 2). Following this, we explore internal exploration strategy manipulations and the number of training trials participants receive. In the final experiment reported in chapter 3, we introduce salient local landmarks for both internal and external trials. These were integrated into the environment walls themselves, in a manner consistent with Herrera et al., (2022). The rationale behind this final manipulation is that a growing amount of literature suggests boundary-based learning appears to be "incidental" or obligatory (Bast et al., 2009; Cheng et al., 2013; Wall et al., 2004) – an idea supported by recent hippocampus-based research (boundary cells; Barry et al., 2006). Intra-maze landmarks of this kind may introduce an interesting confound, as they serve as *both boundary and landmark*.

In contrast, some authors have claimed that navigation based upon local landmarks is more consistent with an associative account of spatial learning, such as adhering to standard overshadowing and blocking paradigms (e.g. Chamizo, Aznar-Casanova, & Artigas, 2003; Chamizo, Manteiga, Rodrigo, & MacKintosh, 2006; Leising, Garlick, & Blaisdell, 2011; Miller & Shettleworth, 2007; Redhead & Hamilton, 2009; Stahlman & Blaisdell, 2009). Further still, some have suggested that this alone may support a basic distinction between associative and cognitive-map based spatial learning (Bast et al., 2009; Dudchenko, 2010; Hayward, Good, & Pearce, 2004; Wall et al., 2004). Of key note, however, results reported by Herrera et al., 2022 (supplementary experiment 1), and similar polarizing wall procedures directly refute this notion, alongside others akin to Cheng's geometric module hypothesis (Cheng, 1986; Gallistel, 1990). Here, a clear overshadowing effect occurred with exposure to the smallest landmark. Further still, the largest landmark, which captured 50% of the environmental boundary (see figure 6), still produced an overshadowing effect at test - albeit significantly smaller. This is despite the fact that both local- and global-*shape* boundary properties remaining consistent between training and test; that is to say, local geometric features surrounding the goal location remained the same (i.e. intercept angle, height and length etc.) – the only difference is was a change of colour for 2 walls.

Combined, these results further suggest that properties of shape-based encoding may be task or parameter dependent. To anticipate our results in this chapter, in all experiments participants still searched, at test, in regions of the arena more consistent with allocentric spatial processing, thus reproducing and extending the outcomes reported by Buckley et al. (2019).

In Chapter 4, we explore reorientation following a boundary transfer using the rectangle and kite-shaped arenas used elsewhere (e.g. Buckley et al., 2016b). Unlike previous shape transformation experiments, however, in which navigators are trained in one shape before being tested in a second, participants in Chapter 4 will alternate between two environments on a trial-to-trial basis for the entirety of their experiments. Participants are often split in to two conditions; for half of the participants have an egocentric-congruent goal location across both environments (i.e. *the goal is at the corner with a short wall on the left and a long wall on the right in both* *locations*.), or egocentric incongruent (i.e. *short on the left, long on the right in one shape, short wall on the right and long wall on the left in the other).* Performance between these two conditions will then then be explored.

Finally, the last experimental chapter reported in this thesis (chapter 5), we explore potential developmental effects surrounding this boundary transfer paradigm. Experimentation included in chapters 3 & 4, alongside published boundary transfer research such as Buckley et al., (2019), have primarily used a young-adult participant pool. As above, spatial mapping is not considered to be an absolute process, with individuals showing wide variability in navigation performance. Literature suggests that one of the largest contributors too this individual variability is an individuals age. Here, literature suggests young children may have impaired or underdeveloped allocentric spatial processing abilities, resulting in impaired cognitive mapping skills (Nardini et al., 2008; Nazareth, Weisberg, Margulis, & Newcombe, 2018; Wills & Cacucci, 2014). With this in mind, we do not know if young children will reorientate in a consistent manner, at test, to adults reported in Buckley et al., (2019). Alongside adapting this procedure for use with children, we mimic subsequent manipulations made in previous chapters (See Chapter 3, Experiment III). To again anticipate results, children generally display behaviour consistent with allocentric spatial processing following a boundary transfer, despite consistent local cues being present both internally and externally.

Chapter Two: General Methods & Experimental Notes.

An overview of the common materials and apparatus required for each experiment reported in this thesis can be found in the following chapter. Methods sections in subsequent chapters detail specific methodological and procedural manipulations used in individual experiments.

2.1. Apparatus.

2.1.1. IT Infrastructure.

2.1.1.1. Hardware.

All navigational environments were run on standard Apple Macintosh computers running Windows 10 with a screen size of 21.5” (2017 Apple iMac 21.5", Intel Core i5, 8GB RAM, 1TB HDD, Iris Plus Graphics 640, Silver).

2.1.1.2. Software.

MazeSuite and Blender software were used to construct the majority of structures used throughout this thesis (Ayaz, Allen, Platek, & Onaral, 2008; blender.org, 2015). Statistical analysis was carried out using RStudio and Jamovi (R Development Core Team, 2016; Rstudio Team, 2019; Şahin & Aybek, 2019). Mendeley was used for both literature review and reference management (Mendeley (Web), 2010).

2.2. Ethics & GDPR.

All participants across all experiments provided informed consent before commencing with any experimental procedure, and this research was authorised by the School of Psychology Research Ethics Committee (University of Nottingham). Participants were recruited via opportunity sampling around the Nottinghamshire area (UK; England) or as part of a university run public engagement event (Chapter 5: all experiments; see Chapter 5 introduction for further details). Each participant was provided with partial course credit or an inconvenience allowance (£2) for their time. Participants throughout Chapter 5 received a larger compensation for their participation in their respective wider events. Please see appendix A, B & C for standardised information sheet, consent form and debrief materials. All data were treated under the principles of General Data Protection Regulation (GDPR). All experiments were conducted in quiet, distraction-free environments, either as individual participants or in a small group (*N* < 5).

2.3. Virtual Structures & Maze Interaction.

In each of the experiments reported in this thesis, virtual environments were used to test navigational behaviour. Each environment was explored from a first-person perspective at a walking speed of 2m/s. Structures were simple in their geometry, created using wall lengths of 22.5 or 9m that had a height of 2.5m. These were either a rectangular cross shaped, with internal and external corners of 90 or 270 degrees. Similarly, a kite-shaped arena was also used for some experiments, configured such that it contained two 90 degree corners with the remaining two angles being 143.14 and 36.86 degrees. A consistent grassy texture was applied to the floor alongside a cream texture to all walls, and a black expanse was rendered as the sky. All navigation tasks were completed virtually from a first-person perspective and all structures were explored either internally or externally. Participants sat not more than 50 cm from the screen. Presses on the "up" and "down" cursor keys permitted the participant to move forward and backward within the arena, respectively. Presses on the "left" and "right" cursor keys permitted the participant to rotate counter-clockwise and clockwise within the arena, respectively. Start locations varied by experiment (please see individual methods sections for further detail).

2.4. Experimental Notes.

2.4.1. Notes on Behaviour as a Metric for Learning.

An important recurring theme found in many behavioural studies is the use of performance as a metric for learning, and thus it seems relevant to highlight the distinction between the two. During behaviour, performance is what we can define and measure via observation. Learning, on the other hand, is surprisingly hard to define satisfactorily (Pearce, 2013), with some authors suggesting there is no generally accepted definition (Haselgrove, 2012). Learning is generally thought to reflect a variety of underlying information processing processes that (we presume) are taking place in the brain. It is these covert processes that are responsible for the acquisition of knowledge, and, consequently, subsequent behavioural performance can be seen as the expression of this knowledge. In general terms, learning could be broadly interpreted as the acquisition of information by an organism – or when an experience results in a relatively permanent change in reaction to a situation (Domjan, 1998).

Of note, instances of latent learning have been reported in recent years (learning without behaviour; Horne, Gilroy, Cuell, & Pearce, 2012). Additionally, performance itself may also be learned, as is the case with sensorimotor skills; however, many authors argue performance is often a reflection of learning rather than being a participant in such a process. One can obstruct performance in some way (i.e. placing a barrier in a maze that an animal is familiar with) to block the expression of their learnt performance, but this won’t affect what the animal “knows” – it will generally try to find an alternative way to express this knowledge (Andersen et al., 2009; Edward C. Tolman, 1948).

Combined, literature suggests it is important to express caution when interpreting behaviour as a metric for learning; with this in mind, for experimentation reported within this thesis authors presume that measurable behavioural performance is a reliable measure of spatial knowledge acquisition.

2.4.2. Notes on Virtual Navigation.

All navigation tasks reported were conducted using virtual environments which may compromise both performance and behavioural validity. This procedural choice was primarily made for practicality, as virtual reality allows for tight control over experimental environments (alongside virtual buildings being cheaper to build). Additionally, methodologies using virtual tasks are more compatible with contemporary neuroimaging technology.

Exploring the full effects of transitioning real-world experimental tasks to virtual reality (VR) is beyond the scope of this thesis, with a large body of studies indicating that idiothetic cues, such as those provided by the vestibular system are important for the formation of spatial memories (Chrastil & Warren, 2013; Klatzky, Loomis, Beall, Chance, & Golledge, 1998). Similarly, recent literature suggests that changing between virtual reality and real-world environments adversely affects memory recall associated with either (Lamers & Lanen, 2021), suggesting VR methodologies may have impact on cognition in general. However, a large body of relevant navigational research has been recently published by the Human Machine Interaction and the Safety of Traffic in Europe project (HASTE; Carsten et al., 2005). Taken in broad scope, this extensive literature suggests that behavioural tendencies remain similar across both real and virtual environments. This persists across varying levels of simulator immersiveness (see Engström, Johansson, & Östlund, 2005 for review) and various cognitive tasks (e.g. Radvansky, Tamplin, & Krawietz, 2010), suggesting that virtual environments may be appropriate for the behavioural tasks reported within this thesis.

Per contra, VR based research has many disadvantages. First, VR does not have the same immersive quality of real life and can introduce additional confounds. For example, a distinct lack of vestibular feedback during virtual navigation can incite simulator sickness; a form of motion sickness is caused by an input mismatch between vestibular (inner-ear) and visual systems (Kennedy, Evans, Crawford, & Fettiplace, 2003). In severe cases this may present itself as feelings of nausea, blurred vision, difficulty concentrating, and in extreme conditions vomiting. Additionally, some literature suggests that cognitive workload is higher in VR when contrast to real world settings (Mehler, Reimer, Coughlin, & Dusek, 2009). Of note, increased cognitive workload has been suggested to effect both attention and perception (see Brookhuis, de Waard, & Janssen, 2001 for review).

Combined, research suggests that transitioning to VR methodologies from real-life settings is *unlikely* to have significant effects on *observable* behavioural tendencies. However the full effects of this shift are not currently understood, and neurological differences during these two experimental mediums are clearly inferred – for obvious reasons we are currently unable to test this, as contemporary technology is not capable of collecting navigational imaging data in a non-virtual setting.

2.4.3. Notes on Simulator Sickness.

As described in section 2.4, one of the most salient hurdles influencing the implementation of virtual navigation experiments is the occurrence of simulator sickness. Many authors suggest that this form of motion sickness can be influenced by a variety of individual-focused variables, including age (Carsten et al., 2005; Porter, 2011), ethnicity (Stern, Hu, LeBlanc, & Koch, 1993), body temperature (Bertin et al., 2005), self-reported gender identity (Biocca, 1992), and even a pre-warning of simulator sickness (S. D. Young, Adelstein, & Ellis, 2007).

However, it should be noted that across all 9 of the experiments reported in this thesis, only 1 instance of motion sickness has occurred, resulting in the immediate end of participation (*N* = 445).

2.4.4. Notes on Cultural Framing and Participant Pools.

These ideas and theories typically stem from, and will be treated within the context of typical western academic psychology. Additional spotlight must be cast on the fact that much of the core research being drawn upon for this thesis includes the use of non-human subjects – typically rodents. This includes all of the single cell work regarding the encoding of geometry. Additionally, many of the human participants used in this field of research are western, educated, industrialised, rich and democratic (W.E.I.R.D.; Henrich, Heine, & Norenzayan, 2010b). As this only represents 12% of the global population, appropriate caution must be taken when interpreting and generalising results (Dan, 2010; Henrich, Heine, & Norenzayan, 2010a). Later chapters also include the use of child participants, collected via a public engagement event held at the University of Nottingham (Psychology). Children were recruited at an annual event (Summer Scientist; for more details see SummerScientist.org). Here children complete several "research games" in exchange for tokens – these can then be exchanged for additional games and activity participation (they enjoy it, I promise!).

Chapter Three: Boundary Transfers.

When presented solely with environmental geometry, human participants have been found to navigate using both local features in an egocentric-type manner alongside the use of the entire global structure. For example, in recent shape-transformation experiments participants have been trained to locate a hidden goal on the inside of an environment that has one shape (e.g., a goal hidden adjacent to the right-angled corner of a kite-shaped environment) before being tested inside an environment that is another shape (e.g., a rectangle). At test, if the local features of the geometry previously associated with the goal are present (e.g., the right-angled corner in which a short wall is on the left of a long wall), then organisms should search in this location despite the overall shape change, which is precisely what adults humans and rats do (Buckley et al., 2016a, Experiment 1; Lew et al., 2014; Pearce et al., 2004).

However, shape transformation studies by their very nature preclude the ability to navigate with respect to the entire Euclidian context of the environment, as this global context is frequently changed between training and test. Consequently, boundary-transfer paradigms have been used to test theories of allocentric spatial-processing. Here, participants are trained to find a hidden goal that is, once again, located *on one side* of a distinctively-shaped environment, such as, at one of the right-angled internal corners of a kite. Participants are then tested on *the other side* of the same shaped environment, and their search behaviour examined (Buckley et al., 2016b, Experiments 1a & 1b; 2016a, Experiment 1; 2019; Holden, Whitt, & Haselgrove, 2021). The results of these studies reveal that participants searched at the external corner closest to the internal goal location - a result that is inconsistent with navigation based upon egocentric spatial-processing, as the crucial local features present during training were no longer available at test (i.e., the wall angles were reversed with concave corners present on the inside of the environment when viewed externally now being convex). Furthermore, in experiments where the global shape of the environment is transformed at the same time at which a boundary transfer is conducted (e.g., participants trained on the inside of a kite to find a hidden goal are tested on the outside of a rectangle), participants are generally lost at test (Buckley et al., 2016b, Experiment 3). These results are, however, compatible with navigation being based on an allocentric spatial reference frame.

In a recent study, we have investigated search behaviour following a boundary transfer, but under circumstances in which navigation based upon an egocentric spatial reference frame is not precluded (Buckley et al., 2019). Participants were again trained to locate a hidden goal, but now on the inside of a cross-shaped environment (see previous figure 8 (or 9, below)). The hidden goal was located adjacent to one of the right-angled corners on the inside of this environment (for example, at the concave corner where there was a short wall to the left of a long wall). Participants were then given a final test trial on the outside of the same-shaped environment. Interestingly, the structure of this environment comprises, on the outside, the same local-geometric features that signalled the goal location as during training on its inside – a feature unique to the boundary transfer literature. The results of the test showed, however, that despite there being an opportunity to navigate with regard to the local features of the environment of local geometry, participants were found to significantly prefer searching in areas that were located closest to the goal location, rather than at areas that matched the egocentrically defined features of the local geometry from training. A result that is consisted with participants having encoded an allocentric representation of their environment.

The experiments reported in this chapter aim to build on this line of research, further exploring this boundary-transfer effect and the circumstances which might favour or encourage the use of an allocentric or egocentric spatial reference frame during navigation and re-orientation.

As results reported by Buckley et al., (2019) have a strong theoretical influence on this this line of research, The opening experiment of this thesis is a replication of their Experiment 2. Participants were again trained to locate a hidden internal goal within a cross-shaped environment before a final surprise external test trial. The only procedural change was that unlike in previous procedures, participants only received 8 internal training trials. Otherwise, the experiment was identical to that described by Buckley et al (2019)

During the training stages of the experiments described in Experiment I and by Buckley et al. (2019, 2016b), participants were required to navigate, on multiple occasions, from multiple starting points in order to find the hidden goal. It is possible that this manner of training, in which multiple, relatively novel, routes are traced on several trials favoured a more allocentric “wayfinding” strategy. Hartley et al., (2003), for example, required participants to learn about a town in a virtual-reality environment either by free exploration, or by repeatedly following a fixed route. They found that hippocampal activity was associated with actively and accurately navigating via new routes, whereas a broader network of regions was engaged when a fixed route was followed (including caudate regions). They suggested that repeated rehearsal of a route encourages a more egocentric action-based representation of that route, rather than a more perceptual-spatial representation. This idea is explored in Experiment II again using the cross maze. Participants had to find a hidden goal that was located adjacent to one of the right-angled corners on the inside of a cross maze, before being required to search for the same goal on the outside of the arena. However, unlike in previous research in which participants began each trial from multiple different starting locations, participants began each trial from the same central starting point. On the basis that this manipulation favours an action-based representation of the arena (e.g., walk towards the corner where there is a short wall to the left of a long wall), rather than a perceptual-spatial one, we might then expect participants to no longer show a bias towards exploring the allocentric-signal regions at test, and instead respond to the local features of geometry in an egocentric manner.

In Experiment III, the impact of manipulating the amount of training given to participants prior to a boundary transfer is investigated. Previous research suggests that cognitive mapping can be a particularly rapid process (Bast et al., 2009), with many authors suggesting that with repeated exposure to an environment comes a shift from allocentric-spatial learning methods to more egocentric-response learning (Cook & Kesner, 1988; R. G. M. Morris et al., 1982; Packard & McGaugh, 1996). This has been described as a navigational "autopilot" process, in which a predominantly egocentric action-based representation is formed, thus reducing the need for more intense perceptual spatial processing and freeing cognitive resources for other demands (Veronique D. Bohbot et al., 2012; Hartley et al., 2003). Despite this, Buckley et al., (2019) found that with a training procedure that resulted in asymptotic level of performance, participants did not show any preference towards exploring egocentric zones following a boundary transfer. It might, therefore, also be possible that providing extensive opportunities to navigate to a hidden goal also favours the establishment of a more allocentric representation of the shape of the arena, as additional egocentrically-encoded visual scenes on each trial may come to be combined to produce a salient cognitive map. Thus, in Experiment

III, participants received either two, four or sixteen training trials within a cross-shaped environment before receiving a test trial was on its outside.

Finally, In Experiment IV we aim to explore the effects of providing coloured-panel landmarks on the inside of the training arena before testing in the presence or the absence of these panels In this experiment, all participants were presented with coloured corners during internal training trials before a surprise final external test trial. During this final trial participants were equally split into two groups; half were put outside the regular cross maze as used before – with a crème texture applied throughout. For the remaining participants, the coloured panels were located on the external local correct and local incorrect corners of the arena. Previous research has suggested that the introduction of local landmarks may inhibit navigation by, and recognition of the global shape of an environment (Buckley, Smith, & Haselgrove, 2014, 2015), however results in this area are inconsistent (but see: Hayward, Good, & Pearce, 2004). Recent publications suggest that task-specific factors such as the spatial and temporal contiguity of these elements may play a crucial role in behavioural outputs when exposed to landmarks during training (Herrera et al., 2022 (supplimentary meterials)).

To anticipate our results, in all experiments reported in this chapter, participants still searched, at test, in regions of the arena more consistent with allocentric spatial processing, thus reproducing the outcomes reported by Buckley et al. (2019; for exception, see Experiment IV). These results further imply that this spatial representation is relatively resilient to the manipulation of training parameters that might otherwise be expected to undermine it.

3.1. Experiment I.

During Experiment I, participants were required to locate a hidden goal at one of the right-angled corners on the inside of a cross-shaped arena. Following training, participants were given a single (surprise) test-trial in which they were located on the outside of the same arena and in which, unbeknownst to them, there was no goal to find. During this final trial, their search behaviour was measured in four external regions (figure 9).

3.1.1. Participants.

32 individuals were recruited from in and around The University of Nottingham. Participants were aged between 18 and 33 (*M*ean = 21.15, *SD* = 3.27, *f*emale = 13).

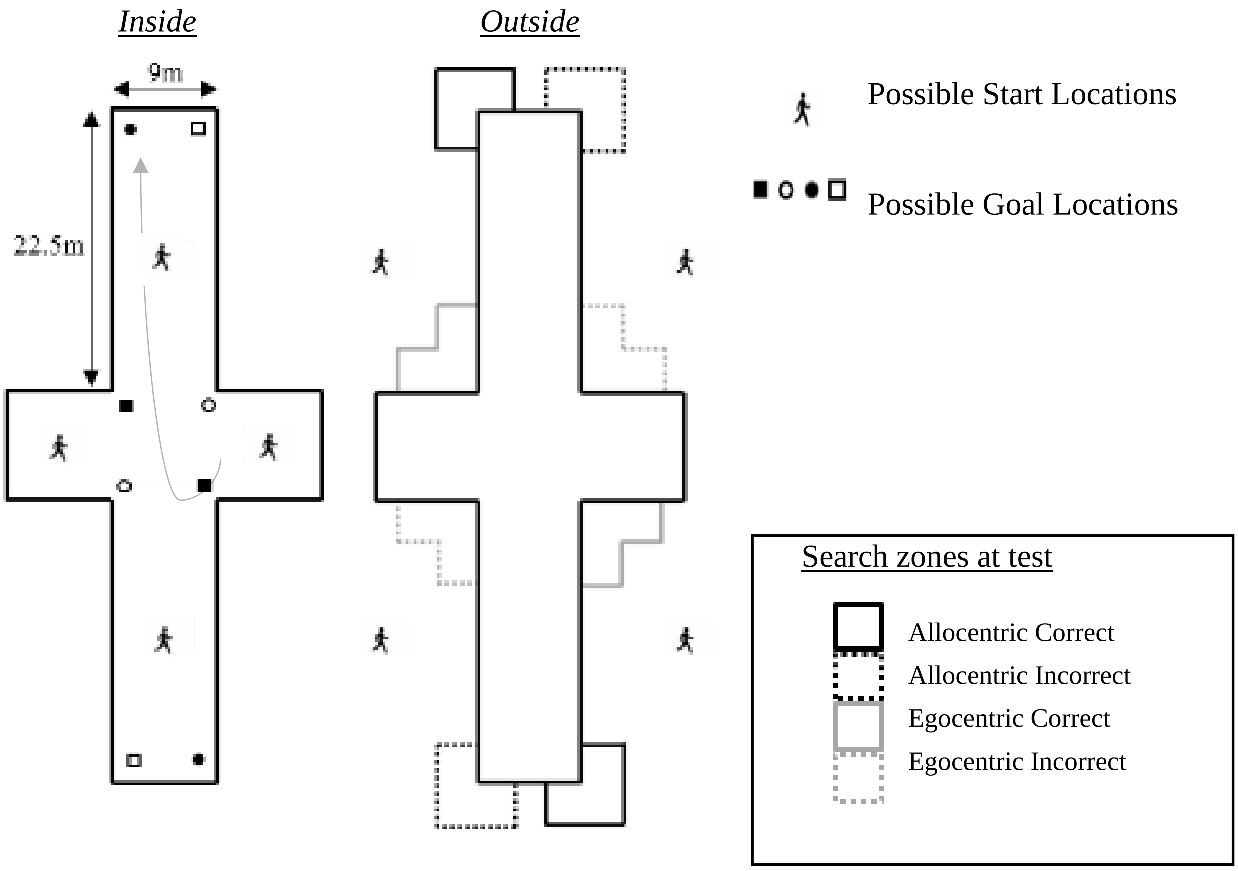
3.1.2. Materials.

As detailed in the general discussion, MazeSuite software was used to create the cross-shaped virtual environment used for this experiment. Participants were tasked with locating a "hidden connection zone" to progress from trial to trial. These invisible goal locations are always 1.08m^2 zones placed 2.48m away from the walls. Consequently, participants cannot simply traverse a path flush to an area wall to find a hidden goal. To allow for rotational errors in the plus-maze (as the shapes are symmetrical on two meridians) two goal locations were placed within the environment during these trials. Additionally, for trials including the plus-maze a total of four goal locations were available – see figure 9.

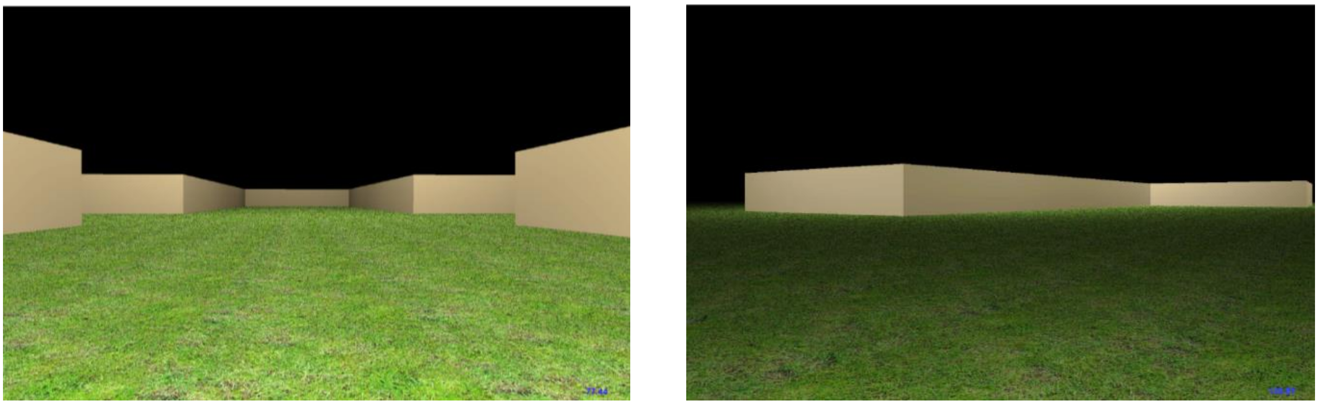
Figure 9.

Plan view of the cross maze. The arena is a simplified cruciform architecture.

A.



B.



Note. A: The schematic view of the cross maze arena This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. External search zones are consistent with this training, as are all four goal locations (counterbalanced within studies). B: Sample screen captures taken from inside (left) and outside (right) of the structure.

Following trials in which a participant is required to find a hidden goal, we measure test-trial performance or navigational behaviour in extinction – i.e. where no hidden goal is present. To do this, we analyse time spent in L-shaped search zones placed outside the environment (long sides 6.48m, short sides 3.24). These were created and positioned around the convex and within the concave right-angled corners see figure 9.

Assessing spatial behaviour during extinction tests in such a manner is common in experiments conducted with both non-human animals (e.g. McGregor, Horne, Esber, & Pearce, 2009), human adults (Buckley et al., 2019; Holden et al., 2021; Redhead & Hamilton, 2009), and we have successfully used test trials without the presence of a hidden goal in navigational experiments with children previously (Buckley et al., 2015).

3.1.3. Procedure.

After being briefed on the procedure and signing a standardised consent form, participants were presented with the following instructions:

> *This study is assessing navigation using a computer generated virtual environment. During this experiment, you will complete 8 trials. In each trial, you will be placed into a room that contains a connection area. You will not be able to see the connection area, however once you walk near it, an automatic message will pop up saying "Connected!". Your aim is to end the trials as quickly as possible by walking to the connection area.*
>
> *To start with, you may find that the connection area is difficult to find. <u>The connection area does not move though</u>, so it is possible to learn its specific location as the experiment*

> *progresses. It is a good idea to fully explore the environment during the first trial to become aware of your surroundings. This should help you in learning where the connection area is. If you have difficulty finding the area, a white flag will appear indicating its location.*

No time limits were imposed during internal training trials, and each trial only ended once the hidden goal had been located. The exception to this was if two minutes elapsed during one of these acquisition trials, at which point a small white flag would appear at the goal location. Once the goal had been found, participants would no longer be able to move and a message reading "*Connected!*" would appear in a dialog box in the centre of the screen – after pressing *"OK"* the next trial would begin.

Participants started each trial at one of two start locations within the arena: (a) at a point between the centre of the arena and the end of one of the long arms and (b) at a point between the centre of the arena and the end of one of the short arms (mirrored – see Figure 9). Figure 9 includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. External search zones are consistent with this training, as are all four goal locations (counterbalanced). The direction that participants faced was chosen at random at the start of each trial. During training, participants began training equally frequently at each of the start locations. Once training was completed, the following instructions were presented on screen:

> *In the next trial, you will again have to locate the connection area. The location of the connection area hasn't changed, so it will be in the same location as before.*

> *However, you will be navigating around the outside of the building. You may find the connection area a bit weaker, so it may be harder to locate. You cannot get inside the building – please do not just circle the building. Please go to where you think the connection area is.*

Upon pressing enter, a single 2-minute final test trial began in which, unknown to subjects, there was no hidden goal to find. Participants were counterbalanced to start at one of four start locations facing the centre of one of the four long walls (see figure 9).

Training performance was measured by recording the time taken for participants to locate the hidden goal in each trial. Performance during the final test trial was measured by recording the duration of time spent within eight external search zones (see figure 9) Search zones can be grouped by spatial reference frame; The allocentric-correct zone is defined as the region on the opposite side of the intersection of the walls in which the goal lay during training. The allocentric-incorrect zone is defined as the region that contains a corner that is a mirror image of the corner in the allocentric-correct zone (e.g. if the allocentric-correct zone is a convex corner created by a short wall being to the left of a long wall, the allocentric-incorrect zone is a convex corner created by a long wall being to the left of a short wall). The egocentric-correct zone is defined as the region containing a corner on the outside of the arena that, from a first-person perspective, is identical to the corner on the inside of the arena that contained the hidden goal. The allocentric-incorrect zone is defined as the region that contains a corner that is the mirror image of the corner in the egocentric-correct zone.

3.1.4. Results.

In all experiments reported in this thesis we treat data with an analysis of variance (ANOVA) alongside appropriate post-hoc t-tests. An alpha level of .05 was adopted for assessing statistical significance, alongside the use of both generalised and partial eta squared, in addition to appropriate confidence intervals (η^2_G; η^2_P Olejnik & Algina, 2003; Lakens, 2013). Figures represent estimated marginal means associated with each respective model, *not descriptive statistics* (Amrhein et al., 2019; Frost, 2019; Wasserstein & Lazar, 2016). For these, please contact the author ((if this were an actual publication, the open-source data hosting link would go around here)). Similarly, any post-hoc analysis is also conducted on respective estimated marginal means.

3.1.4.1. Acquisition.

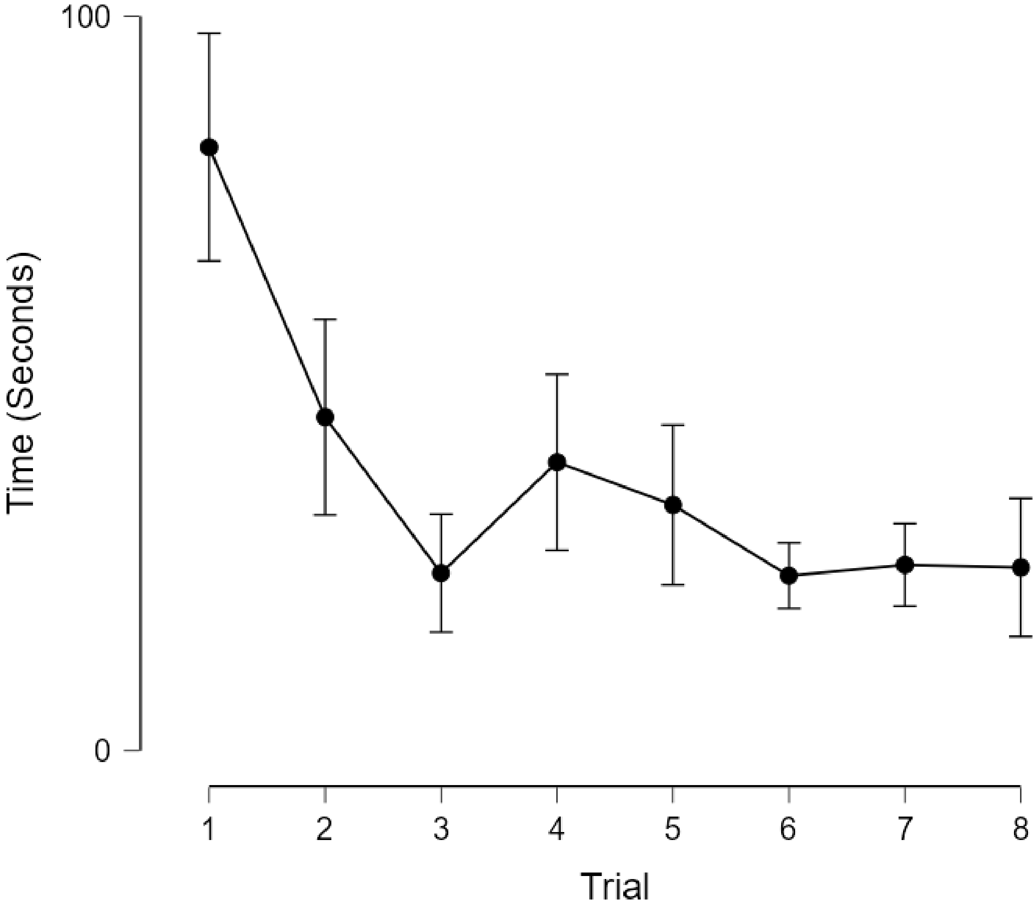
Figure 10 displays the estimated mean latency, in seconds, for participants to find the hidden goal across all 8 trials from the training stage. The mean latency to find the hidden goal decreased as training progressed with the mean latency reaching asymptote at around 30s after 2 trials.

A one-way repeated measures ANOVA with a within-subjects factor of trial (1-8) revealed a significant main effect, $F(4.16, 31) = 14.78$, $p < .001$, $\eta^2_G = .248$, 95% CI [.22,.38]. Of note, Mauchly's test for sphericity suggests a violation of this assumption, $W = .04$, $P < .001$; consequently, a Greenhouse-Geisser correction has been applied to these statistics.

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) suggest a clear one-trial learning effect (Rock, 1957; but see Roediger & Arnold, 2012), with latencies on the first trial being significantly longer in comparison to all other trials, $t(31) = 10.16$, $p < .001$. No other comparisons were found to be significant. (Of n*ote*, the Welch-Satterthwaite method for computing degrees of freedom utilises both observed observations (“*N*”) and observed variance; consequently, here, *df* is not reliably “*N*-1”).

Figure 10.

Experiment I: The mean latency to locate the hidden goal during the eight internal training trials.



Note. Error bars represent +/-1 standard error of the mean.

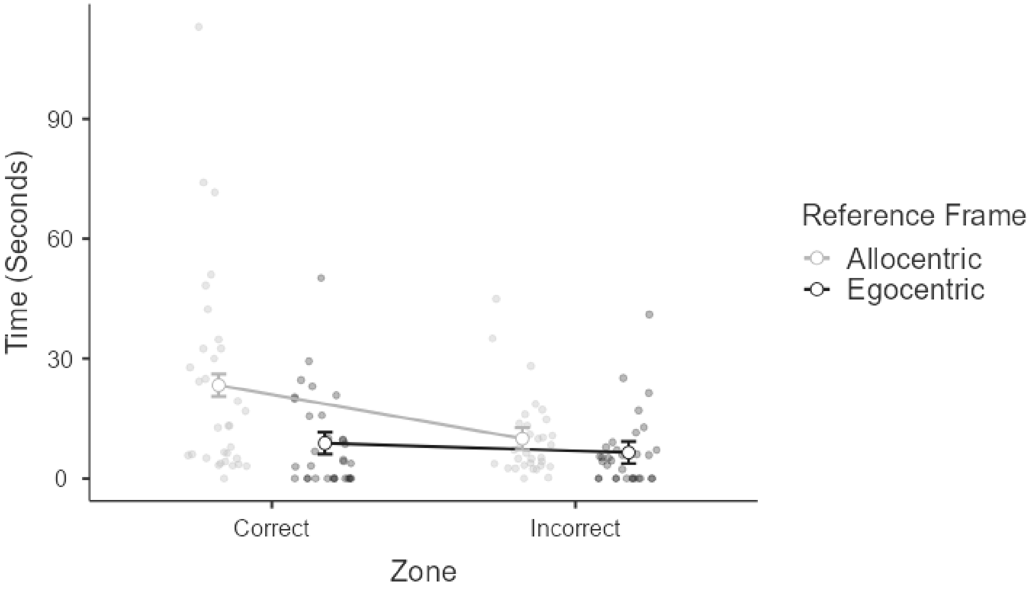
3.1.4.2. *Test.*

Please see figure 11 for estimated marginal means for total time spent in each external search zone. Brief visual inspection of said figure suggests participants spent much more time in the allocentric correct zone when compared to all other zones. A 2 (reference frame: allocentric or egocentric) x 2 (zone: correct or incorrect) two-way ANOVA of individual search times revealed significant main effects of both reference frame, *F*(1,3) = 10.55, $p < .001$, η^2_P = .384, 95% CI [.01,.17], and zone, *F*(1,3) = 8.05, $p = .005$, η^2_P = .061, 95% CI [.01,.15], alongside a significant interaction, *F*(1,3) = 3.95, $p = .039$, η^2_P = .154, 95% CI [.01,.11].

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) revealed that participants spent significantly more time in the allocentric-correct zone over all other zones; the allocentric-incorrect zone, *t*(124) = 3.412, $p = .005$, egocentric-correct zone, *t*(124) = 3.703, $p = .002$, and egocentric-incorrect zone, *t*(124) = 4.303, $p < .001$. There was no significant difference in search times between the egocentric-correct zone over the egocentric-incorrect, t(124) = .601, $p = .999$, or any additional significant comparisons, *t*(124) = .891, $p = .999$.

Figure 11.

Experiment I: Estimated mean time spent within each of the external search zones during the final test trial.



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean (i.e., an accurate representation of the ANOVA model).

3.1.5. Discussion.

During each training trial, participants in Experiment I were required to find a hidden goal located adjacent to one of the right-angled corners within a cross shaped arena. Following this, participants were given a final test trial on the outside of the same arena, during which there was no goal to find. Navigational behaviour on this final test trial was measured by their time spent in 4 external search zones.

Replicating the effect first reported in Buckley et al., (2019), participants spent significantly more time in the two allocentric search zones than the two egocentric zones; furthermore, participants spent significantly longer in the allocentric correct than the allocentric incorrect zone, implying that this search was driven by a relatively precise representation of the goal location within this frame of reference. No preference was shown for time spent in the egocentric-correct search zone over the egocentric-incorrect zone. The environmental structure used during Experiment I contained identical features of local geometry on both the inside and outside, alongside an identical visual theme (e.g. arena walls, floors, sky). Consequently, these results are consistent with the suggestion that the act of crossing an environmental boundary incites reorientation based upon an allocentric reference frame.

However, during the training stage of Experiment I and in the boundary transfer study reported by Buckley et al. (2019, 2016b), participants were required to navigate from multiple starting points in order to find the hidden goal. It is possible that this manner of training, in which multiple, relatively novel, routes are traced on several trials favoured a more allocentric “wayfinding” strategy following boundary transfer.

Contrary to this, it has been suggested that repeated rehearsal of a static route encourages a more egocentric action-based representation of that route, rather than a more perceptual-spatial representation (Hartley et al., 2003). This is explored in Experiment II, in which participants began each trial from a single central starting location.

3.2. Experiment II.

Participants in Experiment II were again trained to locate a hidden goal at one of the right-angled corners of the inside of the cross-shaped arena that was used in Experiment I. Following this training, participants faced a single final test trial on the outside of the same structure in which, unbeknownst to them, there was no hidden goal to find. During this final trial their search behaviour was measured the same four external regions used in Experiment 1.

In Experiment I and previous boundary-transfer research (e.g. Buckley et al., 2019), participants started each of their training trials from one of several locations within the training arena. It is possible that this manner of training, in which multiple, relatively novel, routes are traced on several trials favoured a more allocentric "wayfinding" strategy. Hartley et al., (2003), for example, required participants to learn about a town in a virtual-reality environment either by free exploration, or by repeatedly following a fixed route. Results from this study suggested that repeated rehearsal of a route encourages a more egocentric action-based representation of that route, rather than a more perceptual-spatial representation.

The question of interest is whether for Experiment II is if the route taken by participants between the starting location and the goal location is restricted on each trial, then, in keeping with the proposals of Hartley et al, participants may employ an egocentric strategy during training. Consequently, at test, participants bias towards search at the allocentric correct and incorrect zones may be undermined. In order to realise this, in Experiment II, participants began each training trial at the same location, at the centre of the cross-shaped arena, before receiving the same test on the outside of the arena that was employed in Experiment 1.

3.2.1. *Participants.*

16 individuals were recruited from in and around The University of Nottingham – aged between 21 and 36 (*M* = 26.06, *SD* = 4.29, *f* = 8).

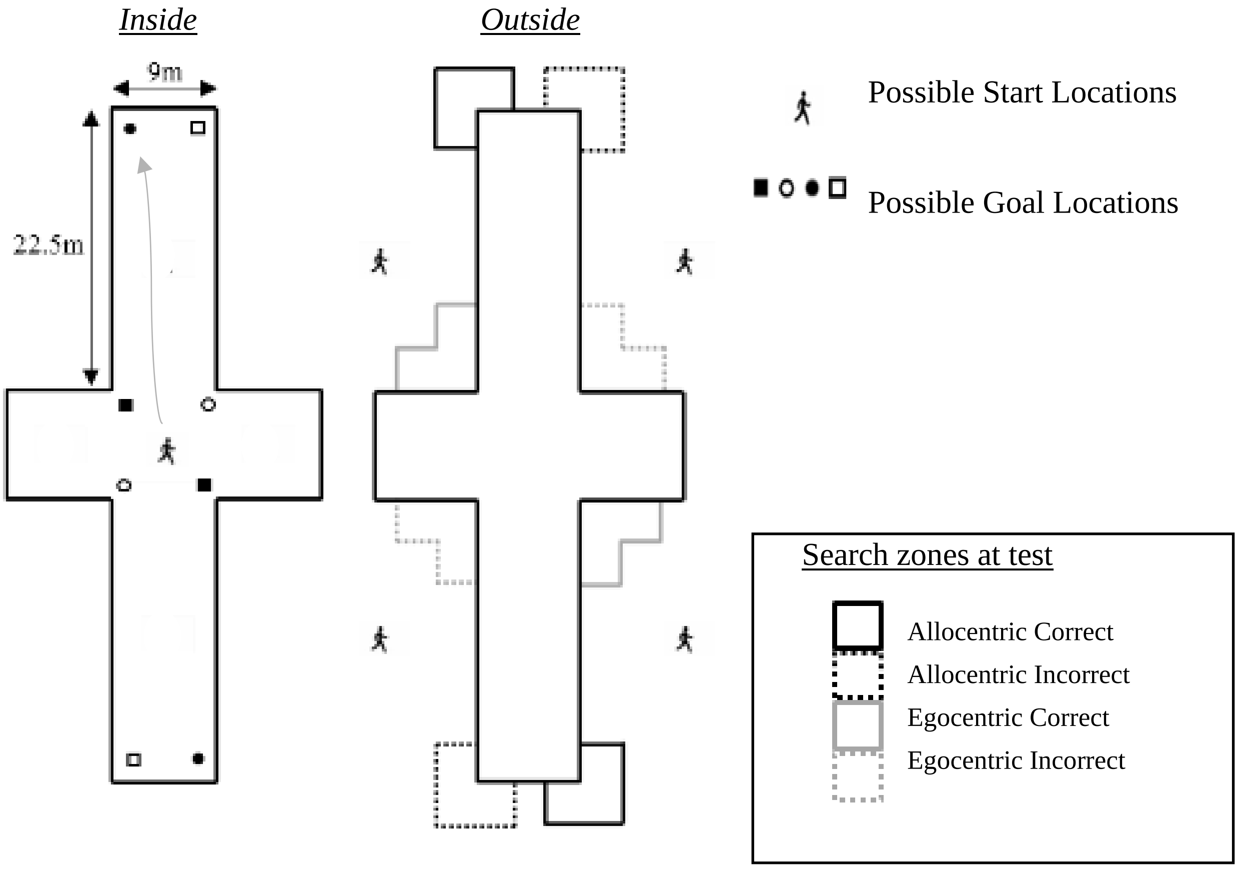
3.2.2. *Procedure.*

The materials and procedure used for this experiment were identical to Experiment I with the following exception:

Participants started each internal training trial facing a random direction between 0 and 369 degrees in the centre of the arena. The centre of the arena was defined as a point that intersected the halfway point along the long axis of the arena with the halfway along the short axis of the arena (see figure 12).

Figure 12.

Plan view of the cross maze used in Experiment II. The arena is a simplified cruciform architecture.
***A*.**



Note. The schematic view of the cross maze arena This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. External search zones are consistent with this training, as are all four goal locations (counterbalanced within studies).

3.2.3. Results.

3.2.3.1. Acquisition.

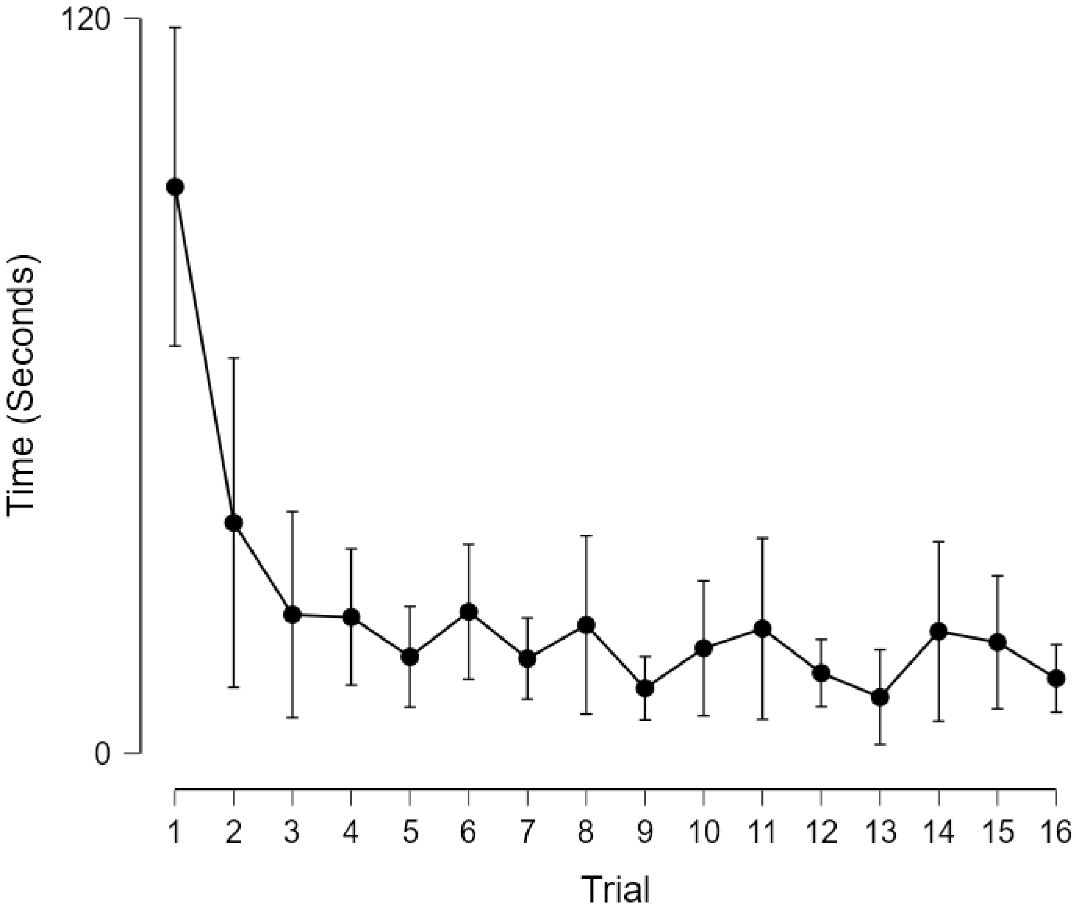
Figure 13 shows the mean latency, in seconds, for participants to find the hidden goal across all 16 trials from the training stage. Participants quickly improved as trials progressed, with mean latency reaching an asymptote of performance of around 25s to find the hidden goal from trial three onwards. Pre-analysis checks suggest a violation of the sphericity assumption for trial, $W < .01$, p

< .001; consequently, a Greenhouse-Geisser correction is applied to subsequent statistics.

A one-way repeated measures ANOVA of individual escape latencies with a within-subjects factor of trial (1-16) revealed a significant main effect, $F(3.57,15) = 9.14$, $p < .001$, $\eta^2_G = .31$, 95% CI [.23,.41]. Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) suggest, again, one-trial learning (Rock, 1957), with latencies on the first trial being significantly longer than all other trials, $t(15) = 5.285$, $p < .001$. No other comparisons were found to be significant, $t(15) = -1.9$, $p = .55$.

Figure 13.

Experiment II: Mean time taken to locate the hidden goal during each internal training trial.



Note. Error bars represent +/-1 standard error of the mean.

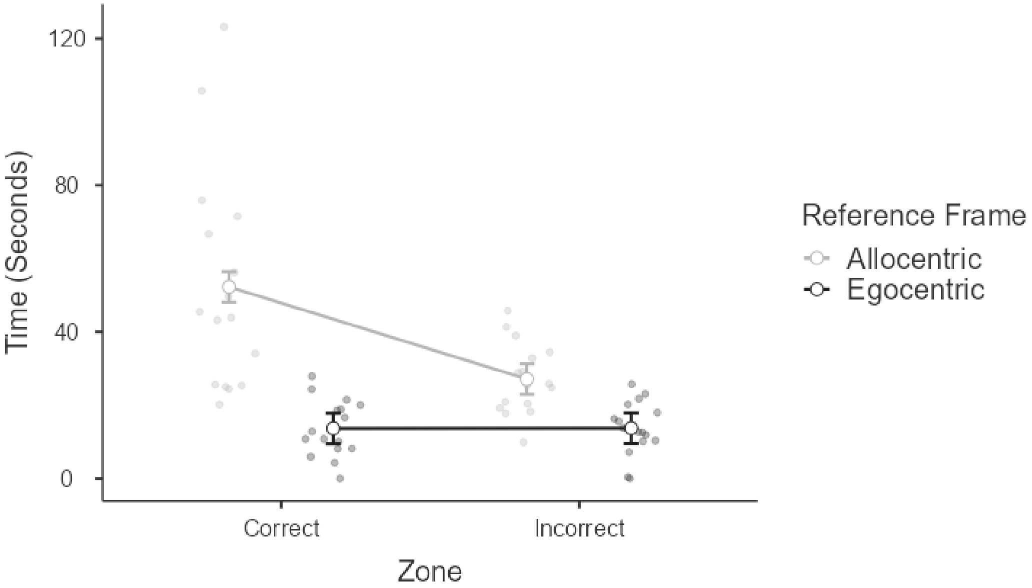
3.2.3.2. <u>Test.</u>

Figure 14 displays estimated marginal means for time spent in each external search zone during the final test trials conducted on the outside of the arena. In keeping with the results of Experiment 1, and the results of Buckley et al., (2016b; 2019) participants spent more time in the allocentric-correct zone relative to all other zones. A 2 (encoding: allocentric or egocentric) x 2 (zone: correct or incorrect) two-way ANOVA of individual search times revealed significant main effects of both encoding, $F(1,3) = 38.89$, $p < .001$, $\eta^2_P = .39$, 95% CI [.01,.59] and zone, $F(1,3) = 9.05$, $p = .004$, $\eta^2_P = .131$, 95% CI [.06,.65], alongside a significant interaction $F(1,3) = 9.14$, $p = .004$, $\eta^2_P = .13$, 95% CI [.23,.77].

Post-hoc Bonferroni adjusted comparisons (Welch's) revealed that participants spent more time in the allocentric-correct zone over the allocentric-incorrect zone, $t(60) = 4.265$, $p < .001$. There was no significant difference in search times between the egocentric-correct zone relative to the egocentric-incorrect zone, $t(60) = -.011$, $p > .999$.

Figure 14.

Experiment II: Estimated mean time spent within each of the external search zones during the final test trial.



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean.

3.2.4. Discussion.

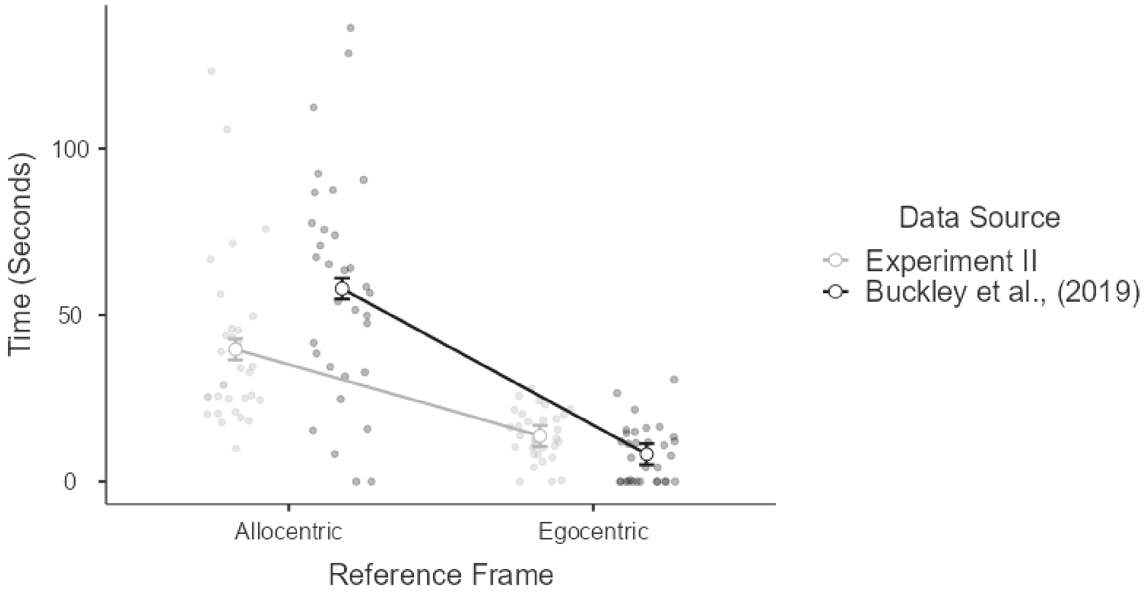
On each training trial, participants in Experiment II were required to navigate from the centre point of the inside of a cross-shaped arena to a goal that was hidden adjacent to a corner. Following this stage of the experiment, participants were given a test trial on the outside of the same arena and tasked with locating the goal location, in extinction. An analysis of participants' search behaviour revealed that the search zone participants explored the most was located at a corner that was closest to the location of the hidden goal on the inside of the arena, and very little time in a region that shared the visual properties of the corner that contained the hidden goal during training.

These results reproduce the effect reported in both Experiment I and by Buckley et al., (2019; Expeirment 2). In discussing their results, Buckley et al. emphasised that it remained unclear how any viewpoint dependent theory of navigation and re-orientation could account for the biases observed in participants search behaviour at test (Cheng et al., 2013; Mcgregor et al., 2006; Pearce et al., 2004). Instead, they conclude that re-orientation, following a boundary transfer was more compatible with a more allocentric, cognitive map, like representation of space (Gallistel, 1990; Spelke & Lee, 2012; Tolman, 1948).

Experiment II expands upon the results of Buckley et al., by demonstrating geometry-based allocentric re-orientation following navigational training in which participants began each training trial from the same start point. Thus despite having acquired a relatively impoverished number of routes from the start location to the goal, participants still seem to have acquired something akin to a cognitive map (Hartley et al., 2003). The real-world analogy here is that the bus driver, who traverses the same route every day, may still acquire a more sophisticated spatial representation of the geometry of their navigated world than may at first be expected. However, does this sophistication match that of the proverbial taxi driver who may traverse different routes every day (Maguire et al., 2000)? One way in which to address this question is to combine the test data from the current experiment with those reported in Experiment 2 by Buckley et al. (2019). If impoverishing the number of routes from the starting location to the hidden goal has a deleterious effect on allocentric navigation then we would expect to see participants spend longer exploring, specifically, the allocentric search zones during the test in the Buckley et al. data set relative to the current data set. This is precisely what we observed. Figure 15 shows the amount of time (in seconds) that participants explored the allocentric and egocentric search zones (estimated marginal means; averaged) in the current test and the test reported by Buckley et al., (experiment 2); We chose not to compare experiments I & II presented in this thesis due to the mismatch number of internal training trials. Here, we see that participants across both experiments display a similar pattern of results.

Figure 15.

Comparison Data: Estimated mean time spent within external search zones (averaged)



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean.

A 2(data source: Experiment II or Buckley et al., 2019) x 2 (reference frame: allocentric or egocentric) x 2 (zone: correct or incorrect) ANOVA was conducted on the test data for these experiments. Common main effects across both studies were again significant (Reference frame: $F(1,120) = 143.42$, $p < .001$, $\eta^2_P = .544$, 95% CI [.42,.63]. Zone: $F(1,120) = 32.70$, $p < .001$, $\eta^2_P = .214$, 95% CI [.09,.33]), alongside a significant main effect of data source, $F(1,120) = 4.08$, $p = .046$, $\eta^2_P = .03$, 95% CI [.01,.11], and data source by encoding interaction, $F(1,120) = 14.09$, $p < .001$, $\eta^2_P = .10$, 95% CI [.02,.21]. No other interactions were found to be significant. Further post-hoc analysis revealed that participants in the above reported Experiment II spent significantly less time in the allocentric zones in contrast to participants reported by Buckley et al., 2019, $t(120) = -4.08$, $p < .001$.

It is possible that the difference we observe between the current data and that reported by Buckley et al. is a consequence of some unanticipated cross-experiment confound (e.g., participant motivation or experimenter effects). Whilst it is difficult to rule out such matters with complete confidence, we do note that the difference observed between the two studies was restricted to the duration of time spent exploring the allocentric regions of the test environment, as no difference was observed in the egocentric zones, $t(120) = 1.23$, $p > .999$. Furthermore, an additional repeated measures ANOVA of the training data with a between subjects effect of experiment (Experiment II or Buckley et al., 2019) revealed only a main effect of trial, $F(15,450) = 21.57$, $p < .001$, $\eta^2_G = .36$, 95% CI [.33,.45], in the two studies; the between subjects effect of data source, $F(1,30) = 0.215$, $p = .646$, $\eta^2_G = .01$, 95% CI [.01,.03], and the Trial x Data source interaction were both non-significant, $F(15,450) = 0.439$, $p = .967$, $\eta^2_G = .01$, 95% CI [.01,.02]. Thus, there is some merit to the idea that whilst restricting the number of paths from a starting point to a goal location may impoverish allocentric navigation, it still remains by far the dominant spatial reference frame employed following a boundary transfer.

An examination of Figure 13 reveals that, similar to Experiment 2 reported by Buckley et al. (2019), participants learned the location of the hidden goal during the training stage remarkably quickly. Indeed, post-hoc analysis of these data suggest that, after the first training trial, no further gains in performance were observed, indicating a one-trial learning effect, and the prospect that participants may have formed an allocentric representation of their environment remarkably quickly. However, it is still entirely possible that more egocentric strategies guided navigation during early training trials, and it was not until later in training before performance came under the control of allocentric strategies. As repetition and repeat exposure have been suggested to effect both navigation style (Hartley et al., 2003) and learning strategy (i.e., place and response learning; Morris, Garrud, Rawlins, & O'Keefe, 1982; O'Keefe & Nadel, 1979; Packard & McGaugh, 1996), the aim of Experiment 3 was to explore the impact of varying the amount of training given to participants in a cross-shaped arena during stage 1, before testing was conducted on the outside of the same arena.

3.3. Experiment III.

During Experiment III, participants were again required to locate a hidden goal at one of the right-angled corners on the inside of a cross-shaped virtual arena Following training, participants were given a single test trial on the outside of the same arena in which, unbeknownst to them, there was no goal to find. During this final trial their search behaviour was measured in the same four external search regions as used previously in Experiments 1 and 2. In previous boundary transfer experiments, participants have received a large number of training trials on one side of an arena before being transferred to the other side of the arena. (Buckley et al., 2019, 2016a, 2016b; Lourenco, Huttenlocher and Vasilyeva, 2005). Interestingly, it has been suggested that lengthy and repetitive training encourages a shift towards more egocentric navigational strategies (Morris et al., 1982; O'Keefe & Nadel, 1979; Packard & McGaugh, 1996), yet results from these boundary transfer studies suggest a bias towards allocentric-based search behaviour even after performance had remained at a stable asymptote for a number of trials. Thus, it remains possible that the procedures used in Experiments I & II encouraged a more egocentric strategy to guide navigation during early training trials, which was replaced with a more allocentric reference frame later in training. The purpose of Experiment III was to explore this possibility by training different groups to find the hidden goal for either two, four or sixteen trials on the inside of the cross-shaped arena, before testing all groups with a single trial, in the absence of the hidden goal, on the outside of the arena.

3.3.1. Participants.

48 individuals were recruited from in and around The University of Nottingham – aged between 18 and 23 (*M* = 20.33, *SD* = 1.09, *f* = 25). Participants were split equally into three experimental groups: 2 training trials (*M* = 20, *SD* = 1.14, *f* = 8), 4 training trials (*M* = 20.43, *SD* = .96, *f* = 7) and 16 training trials (*M* = 20.56, *SD* = .99, *f* = 10).

3.3.2. Procedure.

The materials and procedure used for this experiment were identical to Experiment I with the following acceptation:

Participants were equally split into three experimental groups, each of which received a different number of training trials on the inside of the arena during stage 1: 2 trials, 4 trials or 16 trials.

3.3.3. Results.

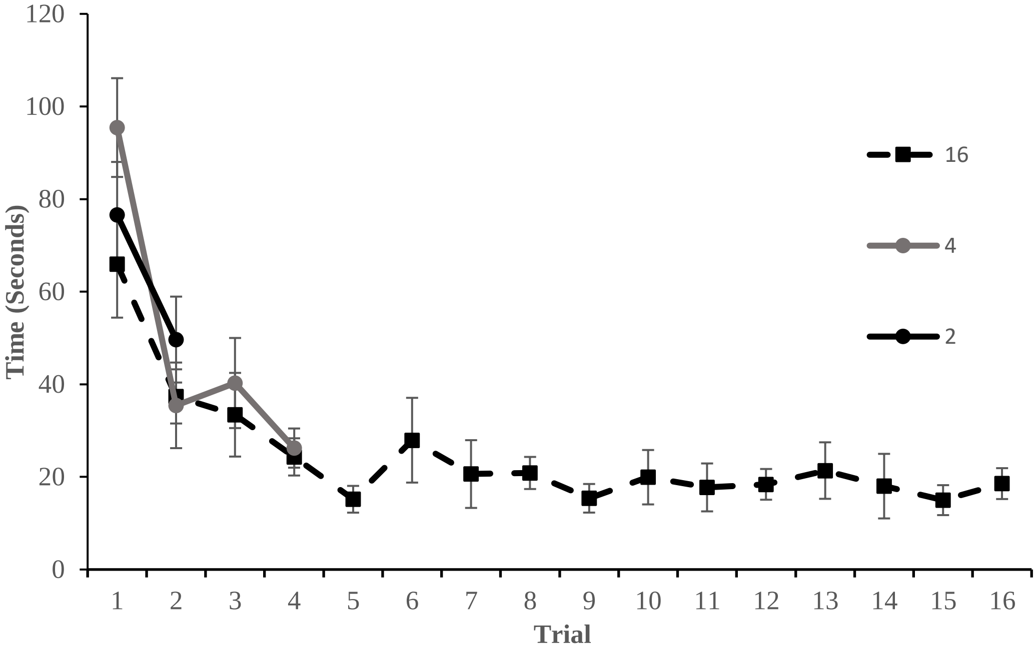
3.3.3.1. Acquisition.

Figure 16 displays the mean time taken and standard deviation for participants in all conditions to locate the hidden goal on each trial. Participants quickly improved as trials progressed, regardless of condition, and participants in the 16-trial condition display a pattern of results similar to those reported in Experiments I & II. As the different groups received different numbers of trials during training, the first and final training trial were compared. A 3(Condition: training trials; 2,4 or 16) x 2 (trial: first and last) repeated measures

ANOVA of individual escape latencies revealed a significant main effect of trial, $F(2,45) = 36.48$, $p < .001$, $\eta^2_G = .30$, 95% CI [.22, .59], no main effect of group, $F(1,45) = 3.23$, $p = .055$, $\eta^2_G = .06$, 95% CI [.17, .21], and no significant interaction, $F(2,45) = 2.37$, $p = .11$, $\eta^2_G = .05$, 95% CI [00, .28]; see figure 17. Bonferroni adjusted post-hoc pairwise comparisons reveal that participants completed the final trial significantly faster that the first, $t(45) = 6.04$, $p < .001$.

Figure 16.

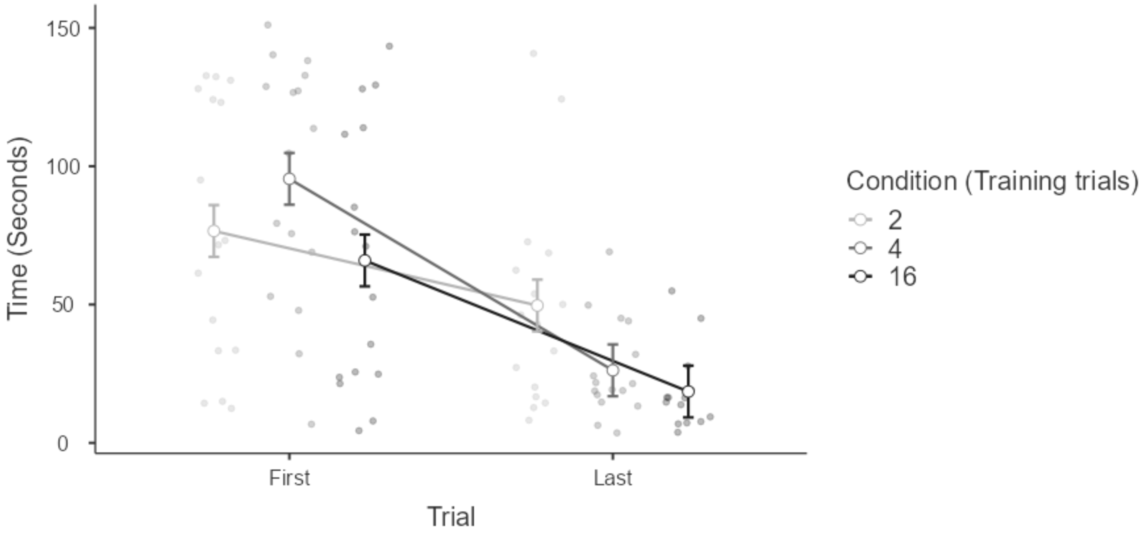
Experiment III: Mean time taken to locate the hidden goal during each internal training trial, split by condition (training trials; 2, 4 or 16).



Note. Error bars represent +/-1 standard error of the mean.

Figure 17.

Experiment III: Estimated mean latency to find the hidden goal for both the first and final trials of each condition (internal training trials: 2, 4 or 16).



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean.

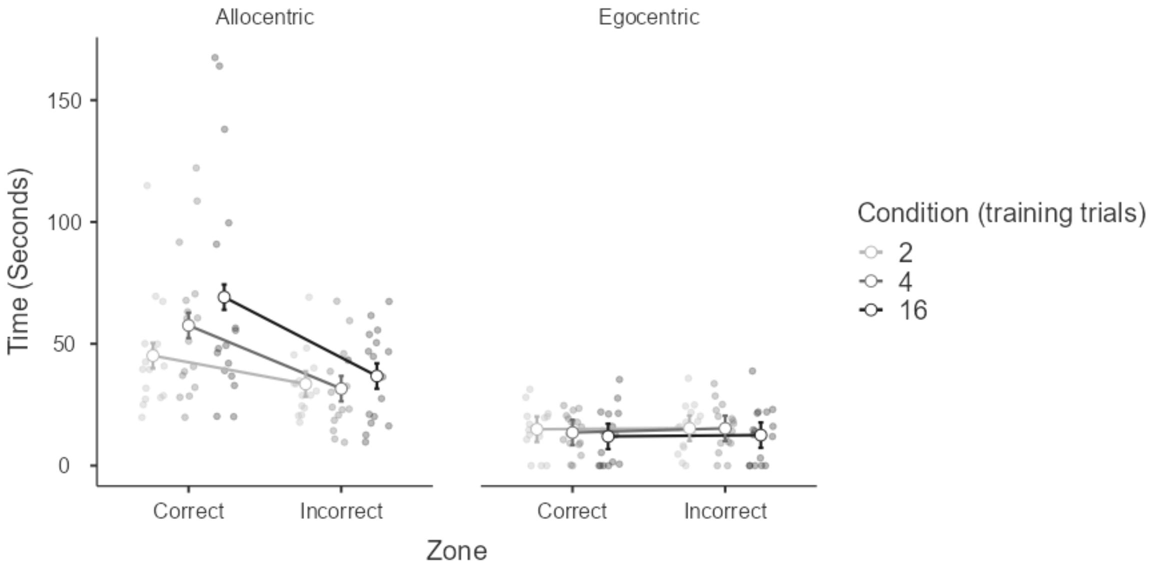
3.3.3.2. <u>Test.</u>

Figure 18 displays estimated means for time, in seconds, spent by each group in each external search zone. In keeping with the results of Experiment 1, participants spent more time in the allocentric correct zone than in the allocentric incorrect zone, and that, furthermore, there was no difference in the amount of time spent exploring the two egocentric zones. Most importantly, this pattern of results was observed in all three groups. A 3 (condition: 2, 4 & 16 internal training trials) x 2 (reference frame: allocentric or egocentric) x 2 (zone: correct or incorrect) ANOVA of individual search times revealed main effects of both reference frame, $F(1,11) = 111.54$, $p < .001$, $\eta^2_P = .38$, 95% CI [.42, .72] and zone, $F(1,11) = 14.03$, $p = .001$, $\eta^2_P = .072$, 95% CI [.05, .41], alongside a significant interaction between these variables, $F(1,11) = 16.27$, $p < .001$, $\eta^2_P = .083$, 95% CI [.07, .45]. No main effect of condition was found, $F(2,11) = 1.08$, $p = .341$, $\eta^2_P = .012$, 95% CI [00, .23], nor any other significant interactions involving this variable (largest $F(2,11) = 1.08$, $p = .341$, $\eta^2_G < .01$).

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) revealed that while participants preferred the allocentric-correct zone over the allocentric-incorrect zone, $t(180) = 5.51$, $p < .001$, no significant preference was found for the egocentric-correct zone over the egocentric-incorrect $t(180) = -.21$, $p > .999$. Finally, participants searched significantly longer within the allocentric-correct zone over the egocentric-correct zone, $t(180) = 10.32$, $p < .001$

Figure 18.

Experiment III: Estimated mean time spent within each of the external search zones during the final test trial.



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean.

3.3.4. Discussion.

Participants in Experiment III were required to locate a hidden goal, from multiple start locations over 2, 4 or 16 training trials, using the same cross-shaped arena as described in Experiments 1 and 2In a subsequent test trial conducted on the outside of the same arena participants were tasked with finding the goal, now in extinction. Participants across all conditions were found to significantly prefer searching within the allocentric-correct zones over any other external search zones, regardless of the number of training trials conducted on the inside of the arena. Experiment III, thus, successfully reproduced the effect observed in Experiments I & II and the results reported by Buckley et al. (2019). That is to say, following a boundary transfer, participants' navigational behaviour at test was consistent with the use of an allocentric representation of the geometry of the previously explored arena. These results further suggest that an allocentric representation can be acquired relatively quickly (within two trials). These results are therefore consistent with the idea that a cognitive map is constructed rapidly (Bast et al., 2009; Burgess, 2006; Lee, 2017).

To sum up, in three experiments participants have been trained to locate a hidden goal on the inside of a cross-shaped arena, before receiving a final test trial on the outside of the same arena (Experiments I, II & III; Buckley et al., 2019 (experiment 2)). This arena matched both the surface textural features, and the individual features of local geometry on the outside to those seen on its inside. Across all experiments and in all conditions, participants re-orientated and navigated to the location of the hidden goal with respect to an allocentric spatial reference frame following the boundary transfer, despite measures taken to potentially undermine the impact of this frame of reference. These results build upon those reported by Buckley et al., (2016b) and suggest that allocentric reorientation following a transfer from the inside to the outside of an arena is surprisingly resilient.

In the last experiment reported in this chapter, we aim to further determine the resilience of this effect by introducing landmarks during internal training. The introduction of landmarks has been used to disrupt navigation in intradimensional-extadimensional shift (ID-ED), blocking and overshadowing paradigms. Specifically, the introduction of landmarks has been suggested to inhibit navigation by, and recognition of the global shape of an environment (Buckley et al., 2014; Buckley, Smith, et al., 2015), however results in this area are inconsistent (But see: Hayward et al., 2004; Herrera et al., 2022). Resent work suggest that task-specific factors such as the spatial and temporal contiguity of these elements may play a crucial role in behavioural outputs when exposed to landmarks during training (Herrera et al., 2022 (supplimentary meterials)).With this in mind, the introduction of (spatially congruent) landmarks both before and after a boundary shift may have measurable influence on behaviour at test.

3.1. Experiment IV.

In experiment IV, participants were again required to locate a hidden goal at one of the right-angled corners on the inside of the cross-shaped virtual arena. Following training, participants were given a single test trial on the outside of the same arena in which, unbeknownst to them, there was no goal to find. During this final trial their search behaviour was measured in the same four external search regions as used previously.

In previous experiments, during this final trial, participants spend more time in the zone that is consistent with them having encoded an allocentric representation of their environment. This boundary transfer effect seems resistant to manipulations in training length and internal navigation style (experiments II & III). The purpose of experiment IV was to further test the resilience of this effect by introducing landmarks to the procedure. The landmarks were defined as coloured panels situated upon 90 degree corners within the arena , in a manner consistent with Buckley et al., 2014; Herrera et al., 2022. These were present for all participants during internal training trials, with goal locations again 2m away from the corner at relevant landmarks. During the final test trial participants were split into two experimental groups. For half of the participants, landmarks were again present during this final trial at locations congruent with the internal features of local geometry. That is to say, if -during training - the hidden goal was located at a blue coloured corner where a long wall was on the left of a short wall, then the blue panel was located on an identical corner on the outside (group: landmarks). For these participants, allocentric and egocentric spatial reference frames are potentially placed into conflict upon this final trial, depending on how they had encoded the internal goal location. The remaining participants faced a test trial identical to previous versions – i.e. no external panels with a crème texture applied throughout (group: no landmarks).

Some authors have suggested that boundaries and geometric environmental information has a special status, in that encoding them does not follow general associative principles and are not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). However some research has suggested that the introduction of landmarks can interfere with navigation by, and recognition of global shape in a standard intradimensional-extradimensional shift (ID-ED; Buckley et al., 2014) and OS/blocking paradigms (Buckley, Smith, et al., 2015). However, these results may be task specific, with recent publications suggesting that the temporal and spatial contiguity between goal locations and landmarks may influence test-behaviour (Herrera et al., 2022). Here, larger and closer landmarks produced a blocking effect at test. This effect was not replicated with smaller or less spatially congruent landmarks (see Herrera et al., 2022).

With this in mind, it is unknown how participants in our landmarks condition will behave at test; will they respond to the overall allocentric structure or beacon towards the now-landmarked features of local geometry? Similarly, will the inclusion of landmarks during training interfere with encoding of the global structure for our no landmarks condition?

Finally, following the single test trial, participants were presented with a shape recognition task (see methods section below). In this, subjects were asked if they could identify the global structure of the experimental arena from a selection of similar buildings. This final manipulation was introduced as a rudimentary test of allocentric processing. That is to say; participants, at test, may *only* choose to behaviourally respond in a manner consistent with either allocentric or egocentric strategies. For example, participants navigating with regard to an egocentric reference frame may still be undertaking allocentric spatial encoding processes and are simply not behaviourally expressing these at test due to the specific task demands. By introducing a post-test shape recognition task we aim to further understand mechanisms to shape-encoding using procedure uniquely suited to humans.

3.1.1. Participants.

64 individuals were recruited from in and around The University of Nottingham – aged between 18 and 32 (*M* = 19.5, *SD* = 3.31, *f* = 32). Participants were split equally into two experimental groups: landmarks (*M* = 18.9, *SD* = 1.53, *f* = 20) and no landmarks (*M* = 20.1, *SD* = 4.38, *f* = 12).

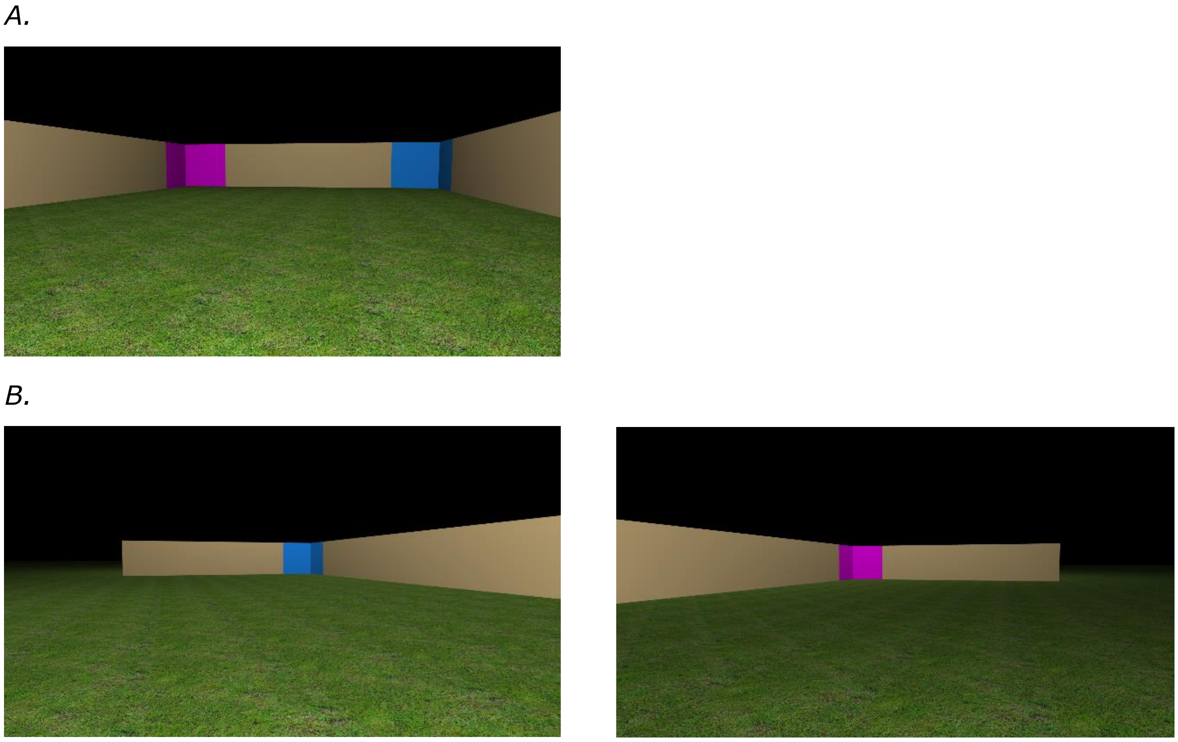
3.1.2. Procedure.

For half of participants (group: no landmarks) The materials and procedure used for the maze task within this experiment were near identical to Experiment I – with coloured landmarks being introduced to internal training trials. For the second half of participants, procedure was identical to that presented in Experiment I with the following key manipulations:

During all internal training trials, uniquely coloured panel landmarks were placed over the corners (matched upon lines of symmetry to allow for rotational errors in the cross-maze). Colours used were always blue and magenta, and landmarks were placed over both concave and convex corners (see figure 19). Landmarks were again present during the final external test trial at locations locally-consistent with their internal orientation. For example, if a concave corner with a short wall on the left and a long wall on the right was blue internally, it was blue externally (see figure 19).

Figure 19.

Landmarks introduced for Experiment IV; Condition: Landmarks.

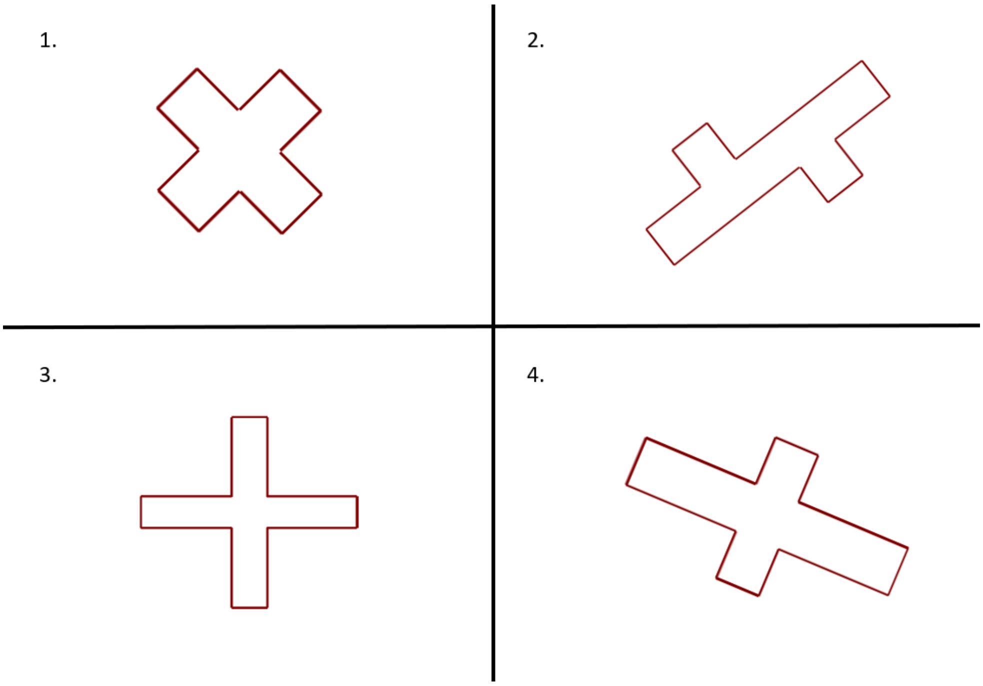


Note. A. & B. represents landmarks used both internally (top) and externally (bottom). In this example, landmarks are considered locally-congruent across the boundary transfer; for example, the blue landmark is at the concave corner at which a short wall is on the left of a long wall both internally and externally.

Following this maze task, participants were presented with the shape recognition task, in which they are asked to identify the shape of the arena that they had just been traversing from multiple similar options (see figure 20). Presentation order of these options was counterbalanced within this study.

Figure 20.

The post-test shape recognition task options presented to participants navigating the cross shaped arena.



Note. Here, the correct answer is option 4 (see Figure 9 for cross-reference).

3.1.3. Results.

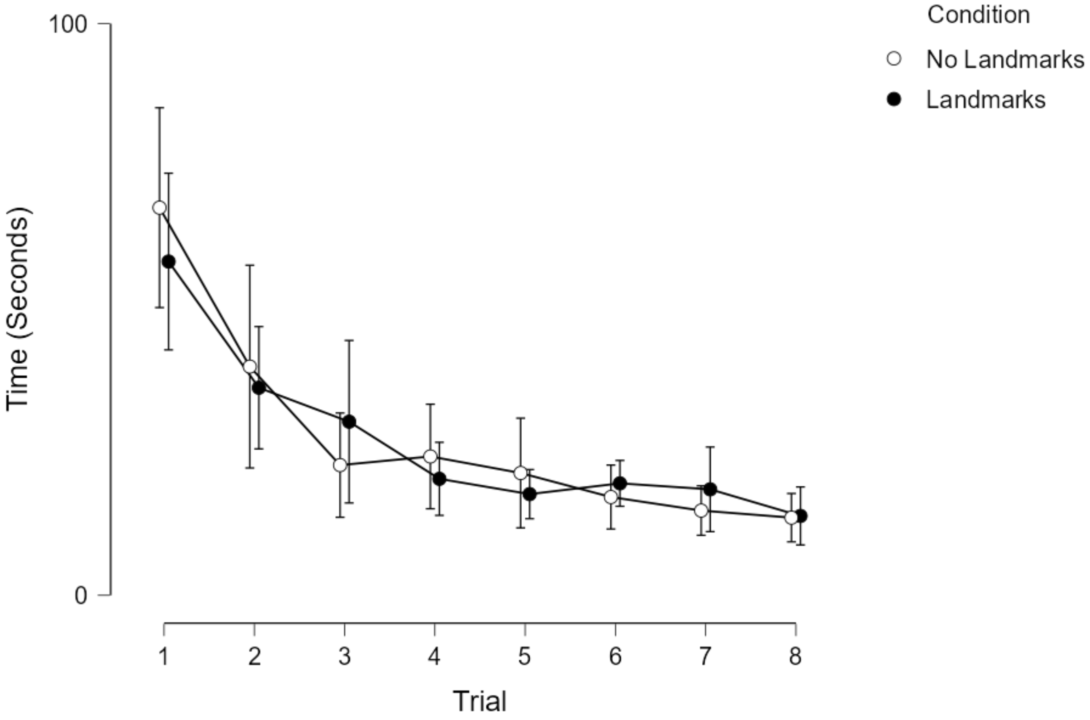
3.1.3.1. Acquisition.

Figure 21 displays the mean latency, in seconds, for all participants to find the hidden goal across all 8 trials from the training stage. The latency to find the hidden goal reduced as training progressed with the mean latency to find the goal reaching an asymptote of around 30s after 3 trials for both conditions. A repeated measures ANOVA with a within-subjects factor of trial (1-8) and between subjects factor of condition (landmarks or no landmarks) revealed a significant main effect of trial, $F(3.65, 226) = 21.349$, $p < .001$, $\eta^2_G = .23$, 95% CI [.17,.31], a non-significant main effect of condition, $F(1,62) = 0.097$, $p = .756$, $\eta^2_G < .01$, 95% CI [.00,.06], and no significant interaction, $F(3.65, 226) = 0.583$, $p = .660$, $\eta^2_G < .01$, 95% CI [.00,.01]. Again, pre-analysis checks suggest a violation of the sphericity assumption (*W* = .01, *p* <.001), and a Greenhouse-Geisser correction has been applied throughout.

In keeping with Experiments I to III, post-hoc Bonferroni adjusted pairwise comparisons suggest one-trial learning, with latencies on the first trial being significantly longer to all other trials, *t*(62) = 9.989, *p* < .001. No other comparisons were found to be significant, *t*(62) = -.8, *p* > .999 (Rock, 1957).

Figure 21.

Experiment IV: Mean time taken to locate the hidden goal for each condition during each internal training trial.



Note. Error bars represent +/-1 standard error of the mean

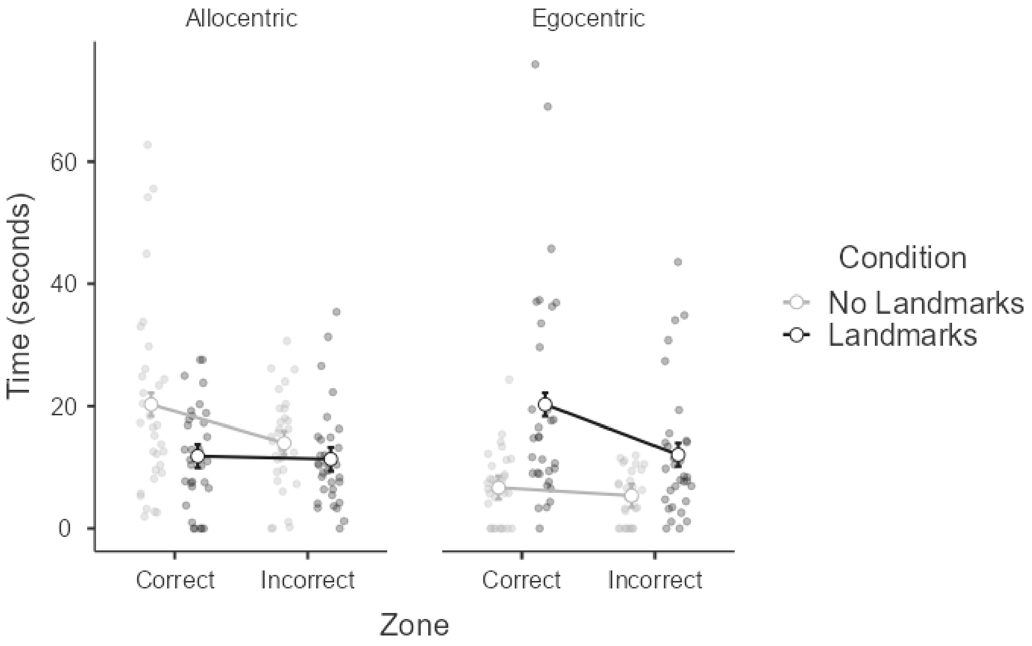
3.1.3.2. <u>*Test.*</u>

Figure 22 displays estimated marginal means for time, in seconds, spent by each group in each external search zone. Participants in the no landmarks condition display a pattern of search behaviour consistent with experiments I through III. Specifically, participants spent more time in the allocentric search zones when compared to the egocentric. Further still, they spent more time in the allocentric correct zone, when compared to the allocentric incorrect (indeed, to *all* other) zones. No difference is apparent between the egocentric search zones. However, of crucial note, participants in the landmarks condition do not replicate this pattern of results. Instead, here, participants show clear preference for the egocentric correct zone above all else. Differences in time spent in each of the other three zones appears quite minimal.

A 2(condition: landmarks or no landmarks) x 2(reference frame: allocentric or egocentric) x 2(zone: correct or incorrect) ANOVA revealed a non-significant main effect of condition, $F(1,7) = 2.827$, $p = .098$, $\eta^2_P = .011$, 95% CI [.01, .05], a significant effect of reference frame, $F(1,7) = 5.706$, $p = .018$, $\eta^2_P = .11$, 95% CI [.01, .07], and zone, $F(1,7) = 9.082$, $p = .003$, $\eta^2_P = .015$, 95% CI [.01, .09]. Additionally, a significant interaction between condition and reference frame was found, $F(1,7) = 33.309$, $p < .001$, $\eta^2_P = .118$, 95% CI [.05, .19], crucially, the three-way interaction between condition, reference frame and zone was significant, $F(1,7) = 5.50$, $p = .020$, $\eta^2_P = .021$, 95% CI [.01, .06]. No other interactions were found to be significant $F(1,7) = 0.25$, $p = .65$, $\eta^2_G = .001$, 95% CI [.01, .02].

Figure 22.

Experiment IV: Estimated mean time spent within each of the external search zones during the final test trial, split by condition.



Note. Error bars represent +/-1 standard error of the mean.

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) revealed that participants in the no landmarks condition spent more time in the allocentric correct zone than the egocentric correct, *t*(248) = 5.01, *p* < .001, and egocentric incorrect, *t*(248) = 5.48, *p* < .001. No further comparisons with this zone were found to be significantly different, <u>including time spent by the no landmarks condition in the allocentric incorrect zone</u>, *t*(248) = 2.33, *p* = .581, and landmarks egocentric correct zone, *t*(248) = .002, *p* = .999. To compliment, time spent by participants in the landmarks condition in the egocentric correct zone was significantly higher to all other zones (within condition, *t*(248) =, *p* = .031).Further still, time spent in this zone was significantly higher than time spent in this zone by the no landmarks condition, *t*(248) = -4.99, *p* < .001, alongside time spent by the no landmarks condition in their egocentric incorrect zone, *t*(248) = -5.48, *p* < .001. No other comparisons were found to be significant, *t*(248) = 3.11, *p* = .057.

3.1.3.3. Shape Recognition Task.

Table 1 displays the number of participants who chose each option for the post-navigation shape recognition task. Here, clear preference is shown for the correct shape choice, with more participants choosing this than the other 3 shapes (combined). Chi squared analysis confirms visual inspection, suggesting all participants showed preference for the correct shape (equal variance assumed; X^2 (3, *N* = 64) = 75.5, *p* < .001.), regardless of condition (X^2 (3, *N* = 64) = 5.75, *p* = .124).

Table 1.

Shape choices made by participants during the post-test shape recognition task in experiment IV.

	Condition		
Shape Choice	**Landmarks**	**No Landmarks**	**Total**
1	6	2	8
2	1	3	4
3	1	5	6
4 (correct)	24	22	46
Total	32	32	64

Note. Option 4 denotes the correct choice. Shape choice order is consistent with the order presented in Figure 19, however the presentation order was counterbalanced within this individual study.

3.1.4. Discussion.

During each training trial, participants in Experiment IV were required to a hidden goal location inside a cross shaped arena. Following this, participants faced a surprise final test trial on the outside of said arena in which there was no goal to find. Navigational behaviour on this final test trial was measured by their time spent in 4 external search zones.

Landmarks were present for all participants during internal training trials. However, during the final test trial participants were split into two experimental groups. For half of the participants, the landmarks were again present during this final trial at locations congruent with the internal features of geometry. For example, if the corner at which a long wall was on the left of a short wall was blue inside; it was blue outside (group landmarks). For these participants, allocentric and egocentric spatial reference frames may potentially be placed into conflict upon this final trial. The remaining participants faced a test trial identical to previous versions – i.e. no external panels, with a crème texture applied throughout (group: no landmarks).

An analysis of acquisition data suggests that during internal training, no differences were found with regards to latency to find the hidden goal. Consistent with experiments I, II and III, post-hoc pairwise comparisons suggest a strong single trial learning effect in both conditions.

At test, a significant three-way interaction was found. Participants in the no landmarks conditions were found to spend more time in the allocentric search zones, in keeping with results shown in Experiments I to III, and in Buckley et al (2016b, 2019). However, unlike previous experimentation using this cross maze, participants in the current in the no-landmarks condition showed no difference in the time spent in the allocentric correct zone in comparison with the allocentric incorrect zone. These findings suggest that the inclusion of landmarks may interfere with or influence reorientation with reference to a *precise* allocentric reference frame (Buckley et al., 2014), alongside the notion that navigation with reference to an allocentric reference frame is relatively resilient following boundary transfer (see experiments I, II & III).

Additionally, the inclusion of local landmarks during *both* internal acquisition and the final test trial further modified behaviour. Unlike all other previous boundary transfer experiments, participants in this group spent more time in the egocentric correct zone when compared to all other zones. Additionally, this amount of time was comparable to the amount of time spent in the allocentric correct zone by the no landmarks condition. This result suggests that the inclusion of salient landmarks during both internal training and external test trial can significantly modify behaviour following boundary transfer. Participants in this condition expressed behaviour consistent with egocentric spatial processing, by, it is assumed, associating the goal location with the salient local feature.

With this in mind, it is interesting to note that when faced with the shape recognition task, participants in both the local landmarks and no landmarks condition were still able to correctly identify the global structure of the arena. This suggests that although participants in the local landmarks condition re-oriented in a manner that was consistent with egocentric spatial processing at test, elements of allocentric spatial processing were still encoded (Bast et al., 2009).

More generally, the results from other spatial navigation studies suggest the inclusion of landmarks at or near a hidden goal may block or overshadow spatial learning based upon the geometry of the arena, a result which could be explained under a traditional cue-competition paradigm (e.g. Rescorla & Wagner, 1972). Typically, such cue competition effects are expected to occur when stimuli are in competition with each other as signals for a specific outcome (e.g. an invisible connection area). However, it is possible that local features within the global environment serve as additional signposts *alongside the global geometry*, rather than as separate cues competing for association with an outcome (the connection area). Under these conditions, there is no theoretical reason to expect the shape of an arena to compete with landmarks for control over behaviour (but see Herrera et al., 2022).

3.2. Chapter Discussion.

In Experiments I, II, III & IV, human participants were required to locate a hidden goal that was always located adjacent to a right-angled corner within a cross-shaped virtual arena. Following this training, participants were faced with a surprise test trial on the outside of this arena and tasked with finding the area on the outside that best corresponded to the location of the internal goal location. This cross-shaped arena was used as it provides identical features of geometry, from a first-person perspective both internally and externally. Consequently, at test, participants may re-orient themselves and search for the goal with regard to either an allocentric reference frame, or individual egocentric features.

Experiment I replicated the boundary transfer experiment reported by Buckley et al., (2019) but with a minor modification to 8, rather than 16 training trials. Following a boundary transfer, participants again spent significantly more time in external search zones that suggest the use of an allocentric spatial reference frame for navigation. Subsequent studies in this chapter explored this effect by making procedural adaptations to increase the probability of using either a local, or egocentric frame of reference.

Experiment II tested the idea that restricting the number of routes taken by participants on each training trial would bias them into a more egocentric frame of reference – a bias that would be revealed at test by influencing how much time was spent at the allocentric and egocentric search zones. Unlike previous research (Experiment I, Buckley et al., 2019), participants during each training trial started at a single central start location – resulting in a navigation strategy that may be more akin to egocentric-route following as opposed to allocentric-wayfinding (Hartley et al., 2003). Despite this manipulation, participants were found to spend significantly more time in the zone consistent with them having encoded an allocentric representation of their environment. Moreover, participants spent significantly more time in the correct allocentric zone, suggesting this representation is relative precise. No preference was shown for time spent in the egocentric-correct search zone over the incorrect, replicating the pattern of results reported by Buckley et al., (2019) and in Experiment I.

In Experiment III, we explored whether restricting the amount of training to either two, four or sixteen trials inside the arena would result in differences in the amount of exploration, at test, in the allocentric and egocentric search zones. In all conditions, participants rapidly learned to find the hidden goal. More importantly, at test, participants across all conditions preferred to search in the allocentric-correct zones over any other external search zones. This pattern of results is consistent with those reported by Buckley et al., (2019, 2016b) and suggests that participants had encoded an allocentric representation of their environment and subsequently used this as the basis of reorientation following a boundary transfer. More importantly, this allocentric frame of representation is, apparently, relatively resilient to variations in training that might be anticipated to undermine it;

neither restricting the path from start location to goal (Experiment II) or restricting the amount of training (Experiment III) during initial training primed egocentric-based orientation following boundary transfer.

During the final experiment reported in this chapter, multiple salient landmarks were introduced during internal trials for all participants at locations spatially congruent and incongruent with the invisible goal locations (i.e. directly next to them, and at adjacent corners; coloured panels). For half of the participants, these landmarks were again present during this final trial at locations that were congruent with the local geometry of the inside of the arena. Thus, for example, if a landmark was located at the convex corner which had a long wall to the left of a short wall then the landmark was located at an identical corner on the outside (group: landmarks). The remaining participants faced a test trial identical to Experiments I, II and III. It has been suggested that boundaries and geometric environmental information has a special status, in that its encoding does not follow general associative principles and is not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). Results from our Experiment IV conflict with these proposals. Participants in the "no landmarks" group were found to orientate with regards to the global structure in a manner consistent with previous experiments reported in this chapter (I, II & III). Participants in group "local landmarks", however, were found to significantly prefer searching at the external areas congruent with their internal landmark location. Of note, when faced with a shape recognition task, all participants across both groups were able to correctly identify the global structure of the environment they had just been exposed to. This suggests that the inclusion of salient landmarks during internal training trials did not disrupt allocentric spatial information acquisition. Rather, it influenced the expression of behaviour specific to this task (see also: (Hayward et al., 2004; Herrera et al., 2022).

Combined, these results again support the idea of a dual-processing model of spatial acquisition. The results further support the notion that both an allocentric and egocentric reference frame are encoded for active navigation, and participants may choose to behave with regards to either, depending on the task at hand (Bodily et al., 2011; Dudchenko, 2010; Han & Becker, 2014; Hartley et al., 2003; Iaria et al., 2003; Kelly & McNamara, 2010; Restle, 1957). With this in mind, these findings suggest that the act of crossing an environmental boundary encourages the use of an allocentric reference frame for orientation, and that its use is particular resistance to manipulations that may be expected to undermine it (see: Experiments II & III).

Additionally, participants in all experiments displayed particularly rapid learning, suggesting that the formation of these spatial representations is relatively immediate – indeed just under 40% of participants in the 2-trial group in Experiment III spent less than 90s within the arena, and yet still this condition revealed a pattern of reorientation consistent with the acquisition of a cognitive map. When the data from the from the test trial of Experiment II were compared to the test data of Experiment 2 reported by Buckley et al., (2019), then there was some evidence that restricting the number of start locations attenuated the amount of time spent in the allocentric search zones. Interestingly, in this comparison, there was no specific effect on the allocentric-correct zone. That is to say, participants in the current Experiment II reduced the amount of time they spent in both the allocentric correct and incorrect zones. This raises the possibility that if there is an impoverishment in the representation of the allocentric shape of the environment then it is an impoverishment of a relatively imprecise representation – a “fuzzy” spatial map (Kosko, 1986), a possibility that is noted in our discussion of the test results of the No Landmarks group in Experiment IV, who showed no difference in the time spent in the allocentric correct zone relative to the allocentric incorrect zone.

To explore these ideas further, we conduct additional research in the final experimental chapter reported in this thesis, with focus upon the developmental trajectory of this boundary-transfer effect (see chapter five). However, in the following chapter, we further explore the effects of local-geometry encoding with both shape-transformation and boundary-transfer paradigms. Previous experimental procedures within this field typically adopt a two-stage approach: training and test (i.e., training in one shape, before being tested in another). Below, to further explore the acquisition of shape-based information, we adopt an intermixed methodology in which participants switch between environments on a trial-by-trial basis.

Chapter Four: Intermixed Trial Procedures.

The Experiments reported in the previous chapter suggests that the act of crossing an environmental boundary is a resilient primer for allocentric-based spatial reorientation. That is to say, 1) crossing an environmental boundary encourages re-orientation rooted in allocentric spatial processes, and 2), this is quite resistant to experimental manipulations that might undermine this (e.g. manipulating the internal navigational strategies used (see experiment II), or number of training trials (see experiment III).

However, this observation does not alone preclude the possibility for re-orientation or navigation based upon egocentric representations following a boundary transfer. Indeed, as seen in Experiment IV. Here, landmarks were introduced during both internal training and external test environments (matched for local features of environmental geometry; condition: landmarks). At test, participants in this landmarks condition showed a clear preference for the external egocentric correct zone (i.e., preference for searching at the landmark which had signalled the goal location during internal training trials. In the following chapter, the aim is to explore spatial reorientation further in both shape transformation and boundary transfer paradigms.

As discussed in the general introduction, many authors have found that both human participants and non-human subjects are able to match local features of geometry within a new global context. For example, when trained to find a hidden goal in a corner with a *short wall on the left of a long wall* in a kite, navigators will orient to the location which *exactly* matches this description in a rectangle (and vice versa; see Buckley et al., 2016b; Lew et al., 2014; Pearce et al., 2004). All of these experiments have adopted a procedure in which a goal is hidden in a consistent location in the same shaped environment over a series of trials, before a final test trial is given to participants in which the conditions of training are changed by placing participants into a new context. For example, at test participants may be placed in a novel-shaped environment, or instead onto the outside of the training arena for a single test trial - and the transfer of spatial behaviour is examined. However, an alternative method of assessing the transfer of spatial behaviour is possible, which removes the need for a final (and single) test trial and instead examines the rate at which the location of a goal is learned over successive trials. Experiment V adapted the shape transformation procedure so that navigators are alternated between two different-shaped environments on a trial-to-trial basis for the entirety of the experiment. Half of the participants have a local-congruent goal location across both environments. For these participants *the goal will always be at, for example, a corner where a short wall is to the left of a long wall*. For the remainder of the participants this training will be local incongruent. For example, for these participants, the goal will be located adjacent to a corner where the *short wall is to the left of a long wall in one shape, but located adjacent to a corner where the short wall is to the right of a long wall in the other condition).* Performance between these two conditions will then be explored. Here, we may expect that participants in the local congruent condition transfer learning more successfully from one global context to another (i.e., from the rectangle to the kite), when compared to those in the incongruent condition, resulting in a shorter latency to complete the procedure. As previous experimentation exploring shape transformations has typically examined performance in a single test trial, it remains to be determined if the egocentric representation of the goal location influences performance beyond a single instance of re-orientation.

In Experiment VI, we again explore the potential of an egocentric bias following prolonged training (Veronique D. Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; R. G. M. Morris et al., 1982; Packard & McGaugh, 1996). Here, participants are first overtrained in a consistent shape (32 trials), before the introduction of a second environment, again using intermixed trials in a manner consistent with Experiment V. Previous experimentation exploring overtraining suggests that lengthy and repetitive training encourages a shift towards more egocentric navigational strategies (Morris et al., 1982; O'Keefe & Nadel, 1979; Packard & McGaugh, 1996). With this in mind, it is unclear how behaviour in the current experiment will differ between those in the egocentric congruent and incongruent conditions.

In the final experiment reported in this chapter, Experiment VII, we again adopt an intermixed-trial procedure. Here, participants alternate between the inside and outside of the cross maze on a trial-by-trial basis. Participants were separated into four experimental groups. For one group, the external goal was at the allocentric-correct corner, relative to the internal goal location. For the second group, the external goal location was located at the egocentric-correct corner. Remaining participants were split into two additional groups – see methods section. Such boundary transfer procedures, in the absence of landmarks, are typically thought to resiliently encourage reorientation with regards to an allocentric reference frame (Buckley et al., 2019, Holden et al., 2021, see also: Experiments I, II, III). Consequently, we may expect that participants in the global congruent condition transfer learning more successfully from one global context to another (i.e., inside to outside), when compared to those in the local congruent or incongruent conditions, resulting in a shorter latency to complete the procedure.

4.1. Experiment V.

Shape-transformation paradigms have revealed that rodents (Pearce et al., 2004), chicks (Tommasi & Polli, 2004), and adult humans (Buckley et al., 2016b) can reorient on the basis of local-shape cues. For instance, following training to find a hidden goal in a rectangle-shaped arena where a short wall is to the left of a long wall, a test trial conducted in a kite-shaped arena will reveal a bias towards searching in the right-angled corner of the kite that shares the same local-shape cues that that were associated with the goal location in the rectangle (e.g., Pearce et al., 2004). Given that the global geometry of the training and test environments differs in a shape-transformation paradigm, it has been argued that any preferential search behaviour in the test environment must be based upon local-geometry representations (Pearce et al., 2004). This type of reorientation is widely considered to be egocentric in nature, with participants being able to complete the task using a single beacon (Veronique D. Bohbot et al., 2012), sequential or response strategy in either context (Bohbot et al., 2012; McGregor et al., 2006; Pearce et al., 2004). Importantly, explanations relating to spatial representations derived from global-shape parameters (e.g., the principal axis – Cheng & Gallistel, 2005) have been empirically dismissed (McGregor et al., 2006).

Unlike previous shape transformation experiments, in which navigators are trained in one shape before being tested in a second, participants in Experiment V will alternate between kite and rectangle-shaped environments on a trial-to-trial basis for the entirety of the experiment. Half of the participants had a local congruent goal location across both environments (i.e., *the goal is at the corner with a short wall on the left and a long wall on the right in both shaped environments*.), while the other half had an incongruent goal location (i.e. *short on the left, long on the right in* *one shape; short wall on the right and long wall on the left in the other).* By manipulating the location of the goal on each trial between different shaped environments in this manner, we aim to further explore the acquisition and integration of egocentric-representation based orientation using a relatively novel method. As previous experimentation exploring shape transformations has typically examined performance in a single test trial (e.g., Pearce et al., 2004), it remains to be determined if the egocentric representation of the goal location influences performance beyond a single instance of re-orientation. On the basis of the shape transformation studies reported by, for example, Buckley et al., 2016b) we may expect that participants in the local congruent condition will transfer their learning about the location of the goals with respect to the local features of the environment between the kite and rectangle shapes. Given that the goal location and local features are congruent (i.e., the same) between trials for this condition it then follows that transfer should result in more rapid learning of the goal location than in the incongruent condition, possibly resulting in a shorter latency to complete the overall procedure.

4.1.1. Participants.

32 individuals were recruited from in and around The University of Nottingham – aged between 18 and 34 (*M* = 19.87, *SD* =3.33, *f* = 23). Participants were split equally into two experimental groups: local congruent (*M* = 19.43, *SD* =2.73, *f* = 11) and incongruent (*M* = 20.31, *SD* = 3.82, *f* = 12).

4.1.2. Procedure & Materials.

After being briefed on the procedure and signing a standardised consent form, participants were presented with the following instructions:

> *This study is assessing navigation using a computer-generated virtual environment. During this experiment, you will complete 32 trials. In each trial, you will be placed into a room that contains a connection area. You will not be able to see the connection area, however once you walk near it, an automatic message will pop up saying "Connected!". Your aim is to end the trials as quickly as possible by walking to the connection area.*
>
> *To start with, you may find that a connection area is difficult to find. However, it is possible to learn its specific location as the experiment progresses. It is a good idea to fully explore the environment during the first trial to become aware of your surroundings. This should help you in learning where the connection area is. If you have difficulty finding the area, a white flag will appear indicating its location.*

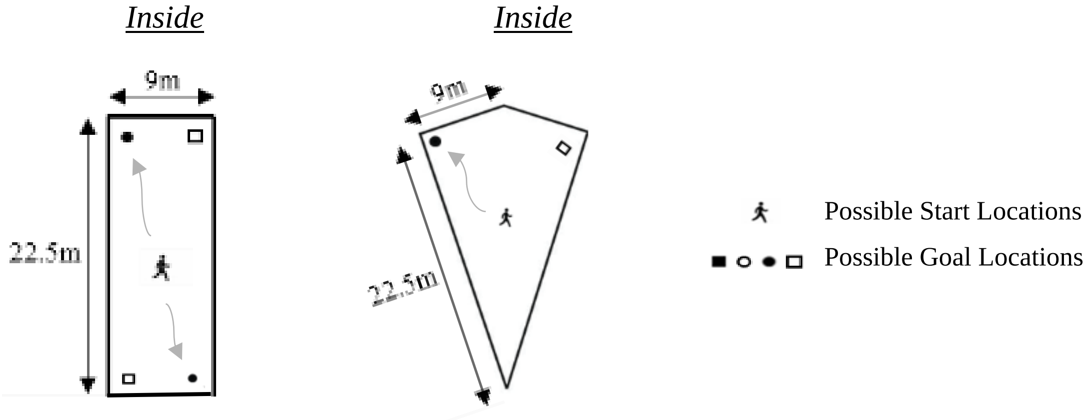
From here, participants alternated between the kite and rectangle-shaped environments on a trial-by-trial basis for the remainder of the experiment (see figure 23). No time limits were imposed during these 32 training trials (16 in each shape), and each trial only ended once the hidden goal had been located. The exception to this was when two minutes elapsed during one of these acquisition trials, at which point a small white flag would appear at the goal location. Once the goal had been found, participants would no longer be able to move and a message reading "*Connected!*" would appear in a dialog box in the centre of the screen – after pressing *"OK"* the next trial would begin.

On each trial, participants always began at a point halfway between the acute and obtuse corners of the kite-shaped arena, or the centre of the rectangle arena; the direction in which participants faced was randomized (around 0 and 259°) on each trial. The entire experiment ended upon completion of the final trial.

For participants in the Local Congruent group, the goal location in both kite and rectangle was at an corner where the local features of the corner were identical between the two shapes (e.g. *the goal was located at the corner with a short wall to the left and a long wall in both arenas*), while participants in the incongruent group the goal location was at a corner where the local features were not identical between the two shapes (i.e. in a rectangle the goal was located where there was a *short wall on the left and a long on the right in one shape, whereas in the kite it was located where there was short wall on the right and a long wall on the left).*Participants were counterbalanced to start their first trial in either kite or rectangle (within conditions). The location of the goal was counterbalanced within conditions; for half of participants in the rectangle (in either condition), the goal location was located where there is a *short wall on the left and a long on the right. For the other half, this was reversed (i.e.* a *short wall on the right and a long on the left)*. Performance was measured by recording individual participants time to complete the entirety of the experiment, alongside measuring the time taken to complete each individual trial in both shapes.

Figure 23.

Plan view of the rectangular and kite-shaped arenas.



Note. The schematic view of both the kite and rectangular shaped arenas. This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. This is consistent across both available shapes, resulting in a local congruent condition representation. The geometry of these structures is identical to those used in Buckley et al., 2016a, 2016b.

4.1.3. Results.

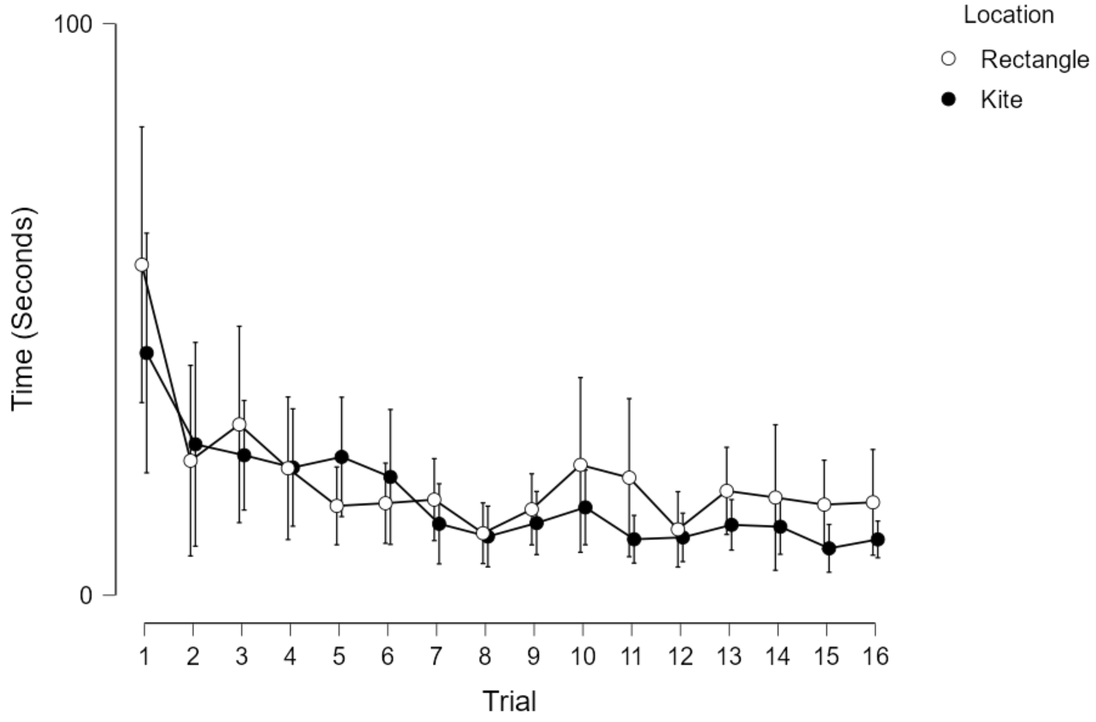
Figure 24 displays the mean latency, in seconds, for participants to find the hidden goal across all 32 training trials. The mean latency to find the hidden goal decreased as training progressed, regardless of condition.

A repeated measures ANOVA with a within-subjects factor of. trial (16) and between subjects factors of location (kite or rectangle), and condition (local congruent or incongruent) reveals a significant main effect of trial, $F(5.44,186.16) = 713.94$, $p < .001$, $\eta^2_G = .163$, 95% CI [.12,.20], and non-significant main effects of location, $F(1,450) = .041$, $p = .906$, $\eta^2_G < .001$, 95% CI [.00,.01], and condition, $F(1,30) = 0.034$, $p = .855$, $\eta^2_G < .01$, 95% CI [.00,.01], and no significant interactions, $F(15,450) = 0.877$, $p = .661$, $\eta^2_G = .02$, 95% CI [.00,.02]. Pre-analysis checks suggest a violation of the sphericity assumption for trial ($W = .01$, $p = <.001$), and the trial by location interaction, ($W = .01$, $p = <.001$); a Greenhouse-Geisser correction has been applied to those statistics.

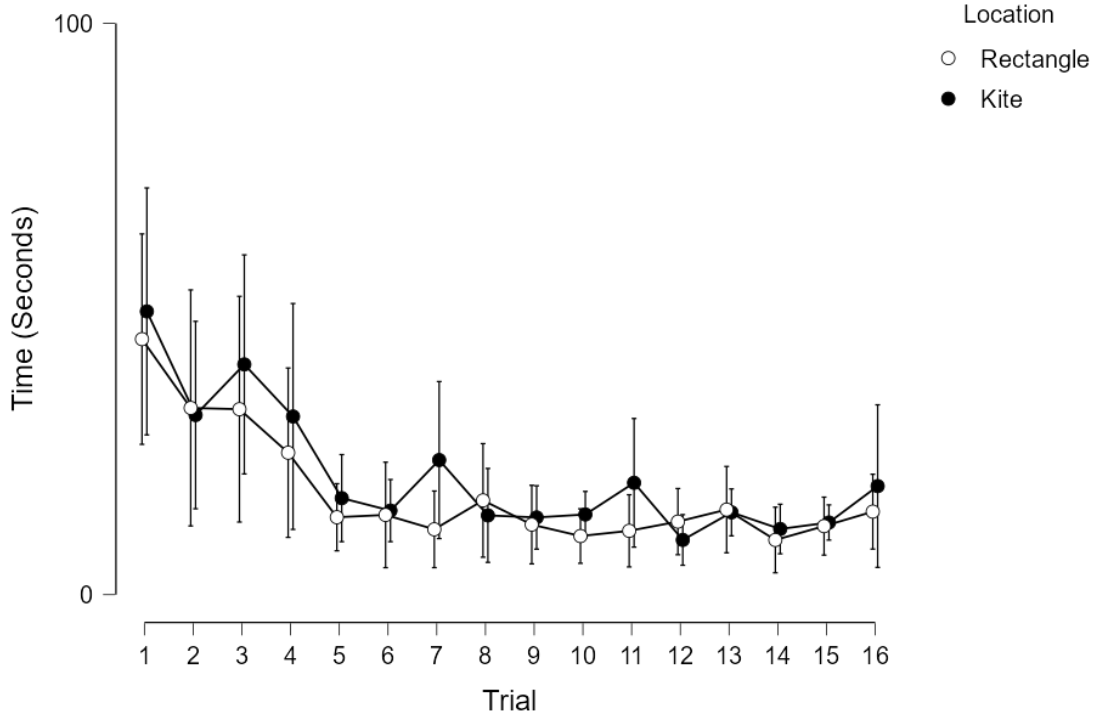
Figure 24.

Experiment V: The estimated mean latency to locate the hidden goal across each trial, split by condition (*A, B*) and shape.

A) Condition: Local Congruent.



B) Condition: Incongruent.



Note. Error bars represent +/-1 standard error of the mean.

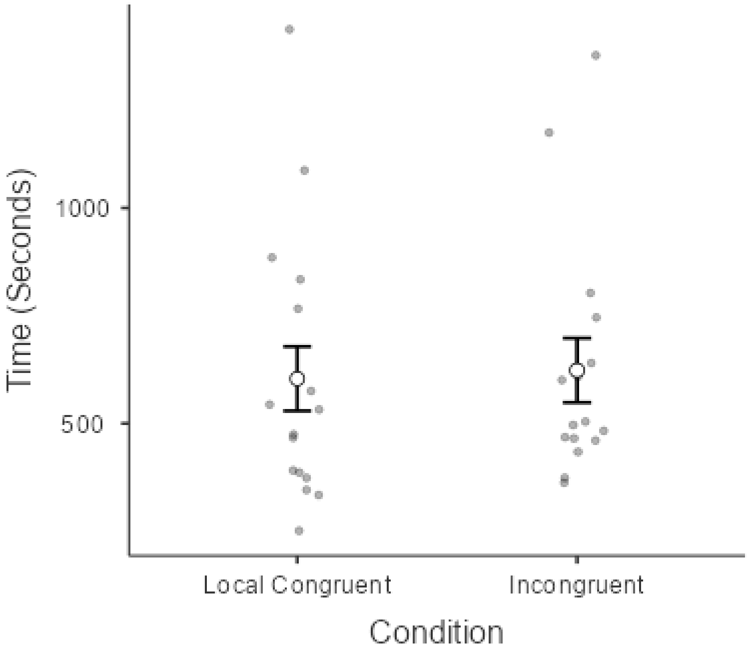
Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) suggest early trial learning, with latencies on the first trial being significantly longer to all other trials, *t*(930) = 7.878, *p* < .001, aside from trial 6, *t*(930) = 3.590, *p* = .173.

An inspection of figure 23 indicates that all participants spent the latter half of their trials at asymptote, this may have precluded the previous analysis from detecting a difference between the conditions. Consequently an identical analysis was run as reported above including only trials 1 to 8. Even so, results exactly followed the previously reported pattern.

As trials came to an end upon locating the connection area, the collapsed time for each group to complete the entire experiment can be seen below in in figure 25.

Figure 25.

Experiment V: Estimated mean time taken for participants to complete the experiment, split by condition (trials collapsed).



Note. Error bars represent +/-1 standard error of the mean. Dots represent individual observations.

4.1.4. *Discussion.*

During each trial in Experiment V, participants were required to find a hidden goal located in both a kite and a rectangle – intermixed on a trial-to-trial basis.

For half of our participants, the goal location in both kite and rectangle was at a local congruent location (e.g. *the goal was located at the corner with a short wall to the left and a long wall in both arenas*), while participants in the Incongruent group had an incongruent goal location (i.e. the goal was located where there is a *short wall on the left and a long on the right in one shape, whereas in the other it was located where there is short wall on the right and a long wall on the left).*Participants were counterbalanced to start their first trial in either kite or rectangle (within conditions). Performance was measured by exploring individual participants time to complete all trials.

The results revealed that participants located the hidden goal at equivalent rates as trials progressed, regardless of condition (local congruent or incongruent), or location (kite or rectangle). Again, post hoc analysis suggest that all participants were able to quickly learn the location of the hidden goals within their environments, consistent with a rapid-like learning of spatial information (Bast et al., 2009). Participants were able to complete both kite and rectangle trials in a statistically equivalent amount of time, regardless of condition. Similarly, both conditions were able to complete the experiment in a similar amount of time (trials collapsed).

Previous experimentation has shown how that training in one context alone results in egocentric transfer when a new shape is tested (e.g., Pearce et al., 2004), and from this we might predict that learning would transfer more successfully between trials for those in Group: Local congruent, resulting in a faster latency to locate the hidden goals across trials – a finding not reflected within the current results. However, as noted above, much of this experimentation has provided prior training in a consistent environment before a single test trial in another. One possible way of resolving these results to suggest that alternating exposure to different globally different environments does permit the encoding of an egocentric representation of the goal location, but that this is configured (e.g., Pearce, 1987) or associated with each of the two global representations. This form of representation can be likened to a "mental snapshot" (Cartwright & Collett, 1983) of the global plus the local features of the arena, and each trial within the arenas results in it being compared with a stored template of the arena from previous trials to determine whether the perceived pattern is the same. Under these circumstances we might not expect to observe a difference between the local congruent and incongruent groups as each has two different snapshots of the goal location stored in memory to base current performance upon.

In the following experiment, we aim to explore this finding further by combining over-training procedures in a single shape with the intermixed trial methodology introduced in Experiment V. Here, we first introduce pre-training trials in a single, consistent shaped arena, in the manner described by Buckley et al (2016b). Following this, participants will continue this training but now intermixed with additional training trials in a second shape, in a manner consistent with Experiment V. Previous studies has suggested that overtraining in a consistent environment in such a manner may promote the use of an egocentric navigation strategy (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996), perhaps, therefore, introducing different shaped environments so early in training in Experiment V, disrupted the use of this navigational strategy.

4.2. Experiment VI.

In the previous study reported in this chapter, participants received intermixed training in rectangular and kite shaped environment. Between arenas, the goal was located in a position that was either congruent with the local geometric features of the corner of the arena, or incongruent. Participants in both conditions were found to locate the goal at equivalent rates regardless of if the goal location in their two environments was at a local-congruent or incongruent location.

In Experiment VI, we aim to explore this effect further by introducing pre-training trials in a consistent shape. Following this training period, participants will have a new, second shape introduced in a manner consistent with Experiment V. Previous literature has suggested that overtraining in a consistent environment in such a manner may promote the use of an egocentric navigation strategy (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996). Consequently, we may find that participants in the local congruent condition transfer learning more successfully from one global context to another (i.e. from the rectangle to the kite), resulting in a shorter latency to complete the intermixed trials when compared to those in the incongruent condition – a result not reflected in the above Experiment V. Participants were counterbalanced within conditions to receive their initial 32 training trials in either the kite or rectangle, before the introduction the other shape.

4.2.1. Participants.

32 individuals were recruited from in and around The University of Nottingham – aged between 18 and 26 (*M* = 19.188, *SD* =2.32, *f* = 19). Participants were split equally into two experimental groups: local congruent (*M* = 19.313, *SD* =2.12, *f* = 10) and incongruent (*M* = 19.06, *SD* = 2.56, *f* = 9).

4.2.2. Procedure.

The materials and procedure used for this experiment were identical to Chapter Four: Experiment V with the following exceptions; Participants in the current Experiment received these revised instructions before the experiment began:

> *This study is assessing navigation using a computer-generated virtual environment. During this experiment, you will complete multiple trials. In each trial, you will be placed into a room that contains a connection area. You will not be able to see the connection area, however once you walk near it, an automatic message will pop up saying "Connected!". Your aim is to end the trials as quickly as possible by walking to the connection area.*
>
> *To start with, you may find that a connection area is difficult to find. However, it is possible to learn its specific location as the experiment progresses. It is a good idea to fully explore the environment during the first trial to become aware of your surroundings. This should help you in learning where the connection area is. If you have difficulty finding the area, a white flag will appear indicating its location.*

Participants then spent 32 trials navigating towards a hidden goal in the same shaped arena – either the rectangle or kite. On each trial, participants always began at a point halfway between the acute and obtuse corners of the kite-shaped arena, or the centre of the rectangle arena; the direction in which participants faced was randomized (around 0 and 259°) per trial.

Following this training in a consistent environment, a second shape was introduced in a trial-by-trial basis, consistent with the procedure reported in Experiment V (i.e., participants alternate between the kite and rectangle-shaped environments on a trial-by-trial basis for the remainder of the experiment (please see figure 22)). No time limits were imposed during these 32 trials (16 in each shape), and each trial only ended once the hidden goal had been located. Goal locations were again found at either a local congruent or incongruent condition For participants in the Local Congruent group, the goal location in both kite and rectangle was at an egocentric-congruent goal location (e.g. *the goal was located at the corner with a short wall to the left and a long wall in both arenas*) and was also congruent with the location of the goal from the previous consistent environment training stage, while participants in the Local Incongruent group the second half had an egocentric incongruent goal location (i.e. the goal was located where there is a *short wall on the left and a long on the right in one shape, whereas in the other it was located where there is short wall on the right and a long wall on the left). However, due to researcher error, participants only received 30 trials during this second stage (15 in each shape), rather than the 32 trials as described in Experiment V.*

No pre-warning of the introduction of the different shaped arena was provided, and participants were appropriately counterbalanced so that this new arena was either the kite or rectangle (within groups).

4.2.3. Results.

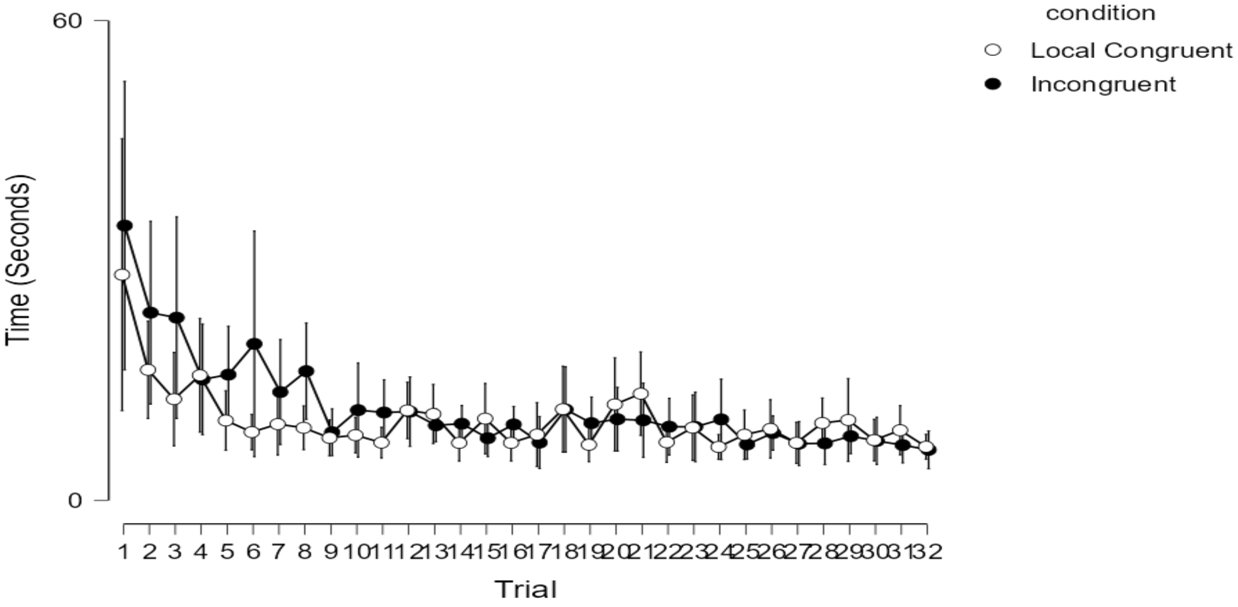
4.2.3.1. Acquisition.

Figure 26 displays the mean time taken for each group to complete the initial 32 training trials during stage 1. Not surprisingly, there was no difference between the conditions at this stage, as, during this point they were treated identically. This impression was confirmed with a repeated measures ANOVA with a within-subjects factor of trial (1 to 32) and between subjects factor of condition (local congruent or incongruent) reveals a significant main effect of trial, *F*(31,930) = 6.756, $p < .001$, $\eta^2_G = .162$, 95% CI [.11,.20], a non-significant main effect of condition, *F*(1,30) = 1.238, $p = .275$, $\eta^2_G < .01$, 95% CI [.00,.01], and no significant interaction, *F*(31, 930) = .993, *p* = ..27, $\eta^2_G = .02$, 95% CI [.00,.02].

Post-hoc Bonferroni adjusted pairwise comparisons suggest one-trial learning (Rock, 1957), with latencies on the first trial being significantly longer to all other trials, *t*(930) = 9.423, $p < .001$. No other comparisons were found to be significant.

Figure 26.

Experiment VI: Estimated mean latency to locate the hidden goal on each of the 32 pre-training trials.



Note. Error bars represent +/-1 standard error of the mean.

4.2.3.2. *Test.*

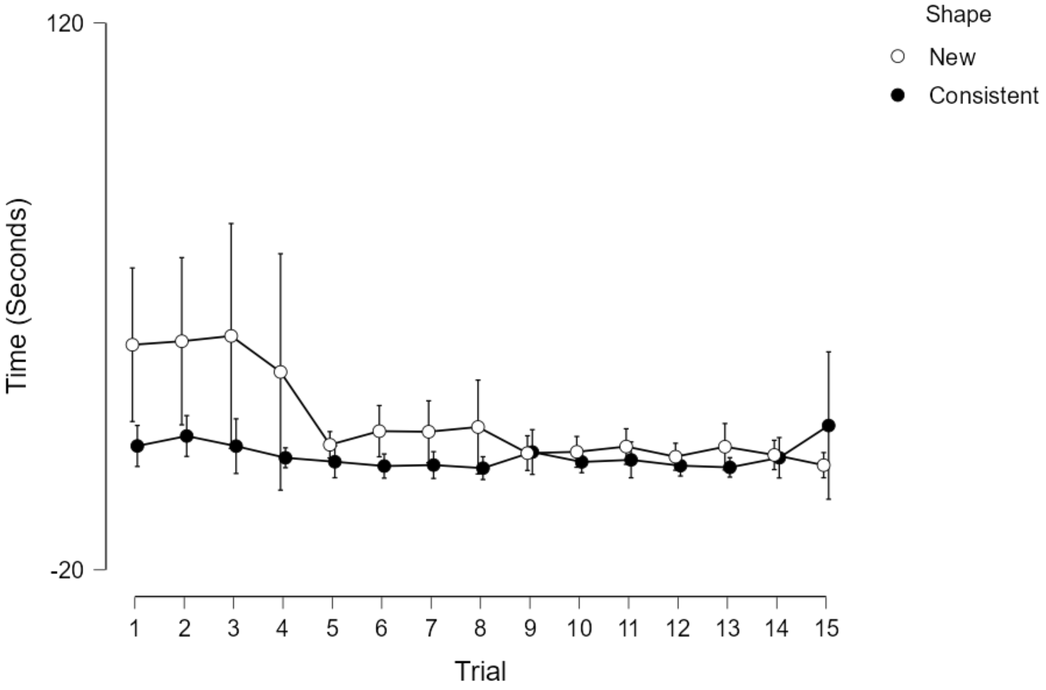
The time taken for participants in both conditions to complete trials in both the consistent (i.e., the same shape as their pre-training) and new shapes can be found in figure 27. A repeated measures ANOVA with within-subjects factors of trial (1 to 15), shape (consistent (with pre-training) or new), and between subjects factor of condition (local congruent or incongruent) reveals a significant main effect of trial, $F(4.71,152.17) = 14.134$, $p < .001$, $\eta^2_G = .182$, 95% CI [.12,.36], significant main effect of location, $F(1,420) = 91.188$, $p < .001$, $\eta^2_G = .09$, 95% CI [.16,.05], and significant main effect of condition, $F(1,30) = 4.48$, $p = .043$, $\eta^2_G = .01$, 95% CI [.00,.02]. Additionally, a three way interaction was also found to be significant, $F(14,420) = 2.146$, $p = .009$, $\eta^2_G < .02$, 95% CI [.00,.08]. Pre-analysis checks suggest a violation of the sphericity assumption for trial, $W < .01$, $p <.001$; Consequently, a Greenhouse-Geisser correction has been applied to these statistics.

As trials came to an end upon locating the connection area, the collapsed time for each group to complete the final 30 test trials can be seen below in in figure 28.

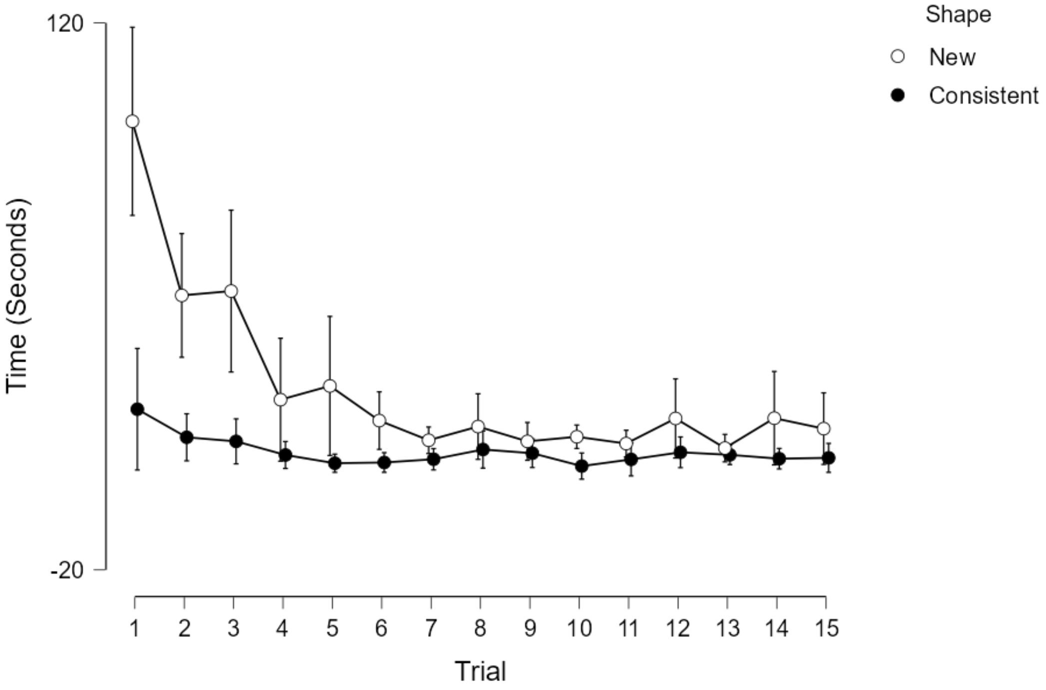
Figure 27.

Experiment VI: Estimated mean latency to locate the hidden goal during the final 30 trials in both consistent and shape, split by condition (A, B).

A) Condition: Local congruent.



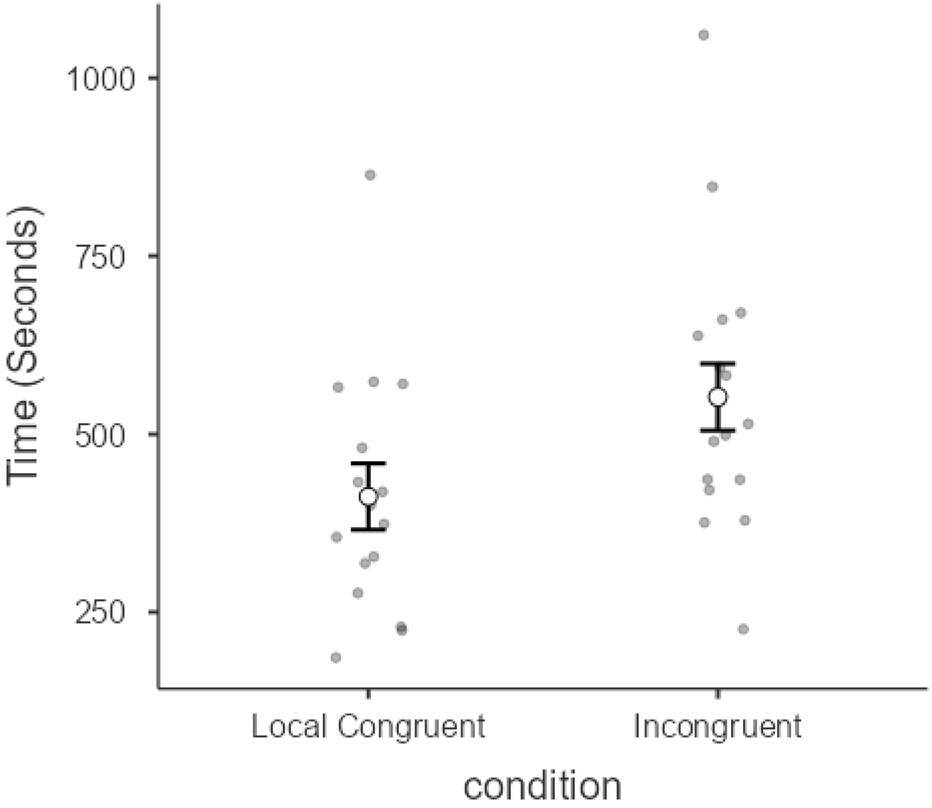
B) Condition: Incongruent.



Note: Error bars represent +/-1 standard deviation.

Figure 28.

Experiment VI: Estimated mean time taken for participants to complete the experiment, split by condition (trials collapsed).



Note. Error bars represent +/-1 standard error of the mean. Dots represent individual observations.

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) indicate a significant difference between conditions, with participants in the local congruent condition completing stage 2 significantly faster than those in the incongruent condition, *t*(30) = -2.12, *p* = .04. Additionally, participants completed trials in the old shape significantly faster than the newly introduced shape, *t*(30) = 9.549, *p* < .001.

An analysis of individual trials indicates that those in the incongruent condition had a significantly slower time to find the hidden goal during trial 1 relative to the local congruent condition, *t*(796) = -8.07, *p* < .001.Those in the local incongruent condition demonstrated early trial learning, with their second trial in the new shape being significantly faster than their first, *t*(833) = 6.52, *p* < .001. Similarly, their second and third trials in the new shape were significantly slower than trial 5 and onwards, *t*(796) = 5.57, *p* < .001.

Of additional note, participants in the local congruent condition did not significantly differ in their new shape trial completion times until a comparison of trial 1 vs. final trial, *t*(833) =4.51, *p* = .013. Additionally, no difference was found for trials completed in the old shape in both conditions across all trials, *t*(833) = -1.56, *p* = .99. No other noteworthy comparisons were found to be significant.

4.2.4. Discussion.

In Experiment VI we conducted a shape transformation procedure in which participants were required to find a hidden goal located in one corner of a kite and a rectangle – intermixed on a trial-to-trial basis. Before this, participants were trained to find the same goal within a consistent shape for 32 trials. For half of participants, the goal location in both kite and rectangle was at an egocentric-congruent goal location (i.e. *the goal is at the corner with a short wall on the left and a long wall on the right in both arenas*), while the remaining participants had an egocentric incongruent goal location (i.e. *short on the left, long on the right in one shape; short wall on the right and long wall on the left in the other).*

Previous experimentation has suggested that this form of overtraining is a reliable primer of more egocentric-based navigation strategies (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996). By introducing a second environmental context later into our procedure, we aimed to explore this type of navigation across multiple instances of re-orientation.

Our results again support the notion that navigators can isolate and navigate towards local cues - with those in the local congruent condition completing trials in the new shape significantly faster than their local incongruent counterparts. Furthermore, these results also support the idea of rapid spatial learning, with those in the incongruent condition displaying strong one trial learning for the late-introduced context (Bast et al., 2009, see also Chapter 3, Experiment III). This effect was not replicated for those in the local-congruent condition, suggesting some transfer of spatial learning focused upon local features of geometry from one global context to another.

Further still, aside from the difference in completion times for the first trial in the new shape, participants across both conditions displayed no significant difference in performance for the remainder of the trials. However, unlike Experiment V, participants in the current local congruent condition of the current study were able to complete the remainder of the experiment significantly faster than those in the incongruent condition – suggesting some transfer of spatial information across the independent global contexts.

Combined these results again suggest lengthy or repetitive navigation in a consistent environment does support the use of more egocentric based spatial reorientation (see Bohbot et al., 2012 for a clear demonstration of this effect). In the current Experiment VI we again see a shape transformation paradigm prompt orientation with regards to local shape cues, consistent with previous research measuring behaviour in a single test trial (e.g. Pearce et al., 2004, Buckley et al., 2016b). However, when subjected to an intermixed trial methodology, navigators only showed a statistically clear improvement in latency to find the goal when the introduction of the new, second shape was preceded by training in a consistent one (Experiment VI; condition: local congruent). Participants in

Experiment V displayed similar behaviour throughout their experiment, with navigators in both conditions completing the experiment in similar amounts of time, suggesting a less efficient transfer of spatial information across the intermixed global contexts.

In the final experiment reported in this chapter, we again use this intermixed trial methodology to explore reorientation beyond a single test trial. However, instead of applying it to aforementioned shape-transformation paradigms – traditionally thought to prompt egocentric, or local based navigation, we have applied it to a boundary transfer procedure (Buckley et al., 2019). Such boundary transfer procedures, in the absence of landmarks, are typically thought to encourage reorientation with regards to an allocentric, or global reference frame (Buckley et al., 2019, Holden et al., 2021, see also: Experiments I, II, III).

As informed by previous boundary transfer studies, we may expect that participants in the global congruent condition transfer learning more successfully from one context to another (i.e., inside to outside), when compared to those in the local congruent or incongruent conditions, resulting in a shorter latency to complete the procedure.

4.3. Experiment VII.

In the previous experiments reported in this chapter, we conducted shape transformation paradigms in a similar manner to papers in the spatial processing field (e.g. Pearce et al., 2004, Buckley et al., 2016b).In such studies, navigators are traditionally trained in a single shape - or global context - before a single test trial within a new shape. Combined, this research suggests that navigators are able to translate spatial information (such as a goal location) associated with unique features of local geometry to a new global context.

In the previously reported studies in this chapter, however, unlike prior experimentation, we adapt this traditional shape transformation methodology via use of virtual environments and human participants by having navigators alternative between shapes on a trial-by-trial basis. For half of participants in these experiments, the goal location in both kite and rectangle was at an egocentric-congruent goal location (i.e. *the goal is at the corner with a short wall on the left and a long wall on the right in both arenas*), while the remaining participants had an egocentric incongruent goal location (i.e. *short on the left, long on the right in one shape; short wall on the right and long wall on the left in the other).*

Consequently, we may expect that participants in the local congruent conditions to transfer learning more successfully from one global context to another (i.e., from the rectangle to the kite), when compared to those in the incongruent conditions – a result not reflected in the above Experiment V. However when this trial-by-trial methodology was preceded by extensive overtraining trials in a consistent shape - a form of navigation thought to prime egocentric reorientation (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996), participants in the local-congruent condition were able to complete the remainder of the experiment significantly faster than those in the incongruent condition (see Experiment VI).

In the following experiments, we again utilise this trial-by-trial context alternation procedure, however this time we apply it to a boundary transfer procedure, similar to those reported by Buckley et al., (2009), and Holden et al., (2021; see also Chapter 3). Using the cross maze, participants will alternate between the inside and the outside of the arena between trials. Like experiments V & VI, participants were split into separate experimental groups – however, due to the more complicated nature of this arena, four separate groups were formed. For those in the local congruent condition, the goal location for both internal and external trials was at the location which consistently and exactly matched local features of environmental geometry (for example *the goal is at the corner with a short wall on the left and a long wall on the right both inside and outside*); for those in the allocentric congruent condition, the external goal location was at the corner nearest to the internal goal location (i.e. *the other side of the corner which represented the internal goal). Additionally,* two incongruent conditions were constructed; For those in the (incongruent) angle congruent condition, the external goal location was incongruent with regards to both either egocentric or the allocentric spatial reference frame and at an opposite-angled corner (i.e. if the internal goal was at a concave corner with a short wall on the left and a long on the right, the external goal location was a convex corner with a short wall on the right and a long wall on the left . Similarly, those in the (incongruent) angle congruent condition had a consist corner type both inside and outside (e.g., if the internal goal location was found at a concave corner with a short wall on the left and a long wall on the right, the external goal location was found at a concave corner with a short wall on the right and a long wall on the left.; for a visualisation of these conditions, please see figure 29 below).

Here, we may expect that participants in the global congruent condition transfer learning more successfully from one context to another (i.e., inside to outside), when compared to those in the local congruent or incongruent conditions, resulting in a shorter latency to complete the procedure

4.3.1. Participants.

64 individuals were recruited from in and around The University of Nottingham – aged between 18 and 35 (*M* = 22.14, *SD* = 3.96, *f* = 44). Participants were split equally into four experimental groups:

Allocentric congruent (*M* = 23.93, *SD* =3.23, *f* = 12) egocentric congruent (*M* = 22.18, *SD* = 3.83, *f* = 8), incongruent (angle congruent), *M* = 23.31, *SD* = 4.52, *f* = 10, and incongruent (angle incongruent), *M* = 19.12, *SD* = 2.41, *f* = 14.

4.3.2. Procedure.

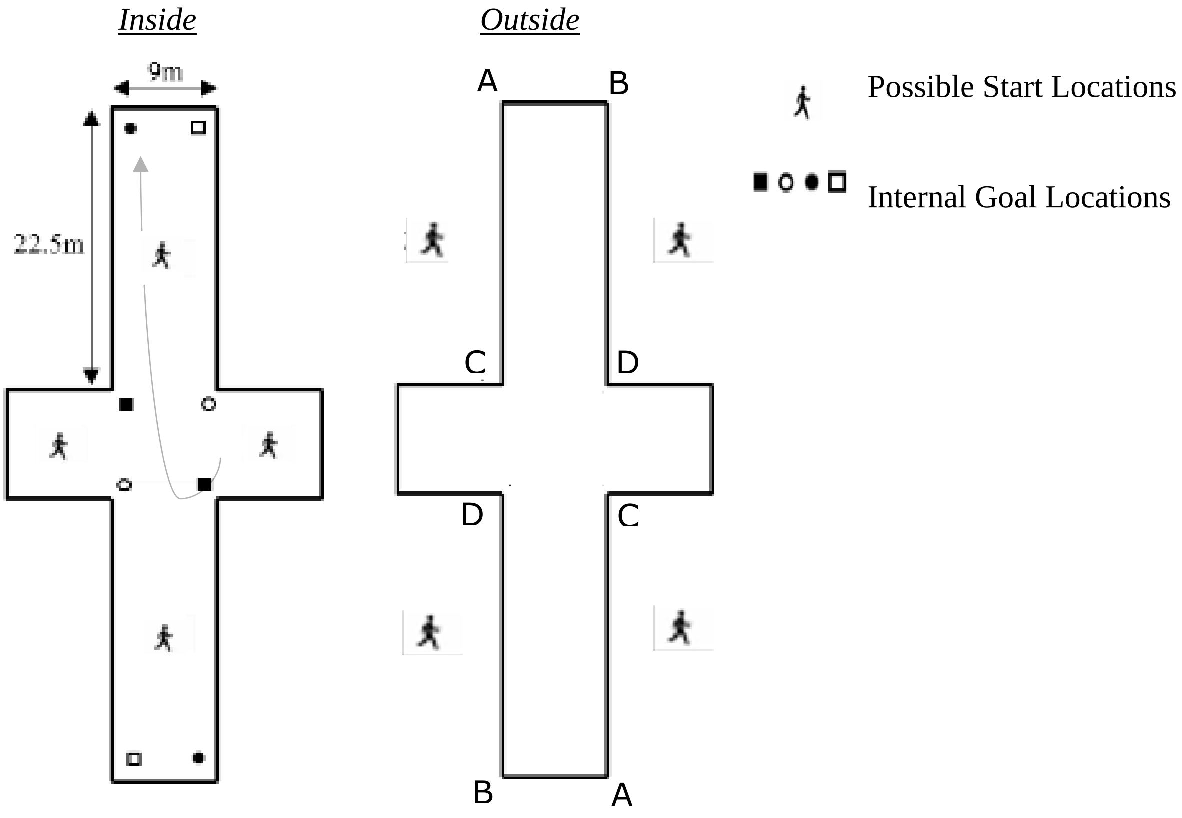
The procedure for Experiment VII is almost identical to the one reported earlier in this chapter (Experiment V), bar the following alterations:

On a trial-by-trial basis, participants alternated between the inside and outside of the cross maze for a total of 32 trials .Participants were split into four experimental groups: For those in the local congruent condition, the goal location for both internal and external trials was at the location which consistently and exactly matched local features of environmental geometry (for example *the goal is at the corner with a short wall on the left and a long wall on the right both inside and outside*); for those in the allocentric congruent condition, the external goal location was at the corner nearest to the internal goal location (i.e. *the other side of the corner which represented the internal goal). Additionally,* two incongruent conditions were constructed; For those in the (incongruent) angle congruent condition, the external goal location was both incongruent with regards to either egocentric or the allocentric spatial reference frame and at an opposite-angled corner (i.e. if the internal goal was at concave corner with a short wall on the left and a long on the right, the external goal location was a convex corner with a short wall on the right and a long wall on the left. Similarly, those in the (incongruent) angle congruent corner had a consist corner type both inside and outside (e.g., if the internal goal location was found at a concave corner with a short wall on the left and a long wall on the right, the external goal location was found at a concave corner with a short wall on the right and a long wall on the left.; for a visualisation of these conditions, please see figure 29). Participants were counterbalanced to start at each internal and external start location an equal number of times (counterbalanced within conditions), alongside starting either inside or outside equally.

In keeping with previously published perspective transformation studies (e.g. Buckley et al., 2016b), in which participants also navigated around the inside and outside of the same arena, it was necessary to increase the duration of external trials by 50% (to 180s).This is due to the fact that, when on the inside of an environment it is possible to establish orientation based on the shape of the environment by simply rotating around the *y*-axis to bring consecutive walls into view. When on the outside of an environment, 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 may take considerably longer compared to reorienting on the inside of an arena.

Figure 29.

Plan view of the cross maze. The arena is a simplified cruciform architecture.



Note. The schematic view of the cross maze arena This includes an example of an internal training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. With regard to this, when viewing the outside, "A" represents the goal external location for participants in the allocentric congruent condition, "B" represents the external goal location for those in the (incongruent) angle incongruent condition, "C" represents the external goal location for those in the egocentric congruent condition, and "D" represents the external goal location for those in the (incongruent) angle congruent condition.

4.3.3. Results.

Time taken for participants in all conditions to locate the hidden goal during the internal and external trials can be seen in figure 30. Here participants display a much longer latency to find the hidden goal on the first trial, regardless of condition or location (inside or outside). From here, patterns of latency are comparable.

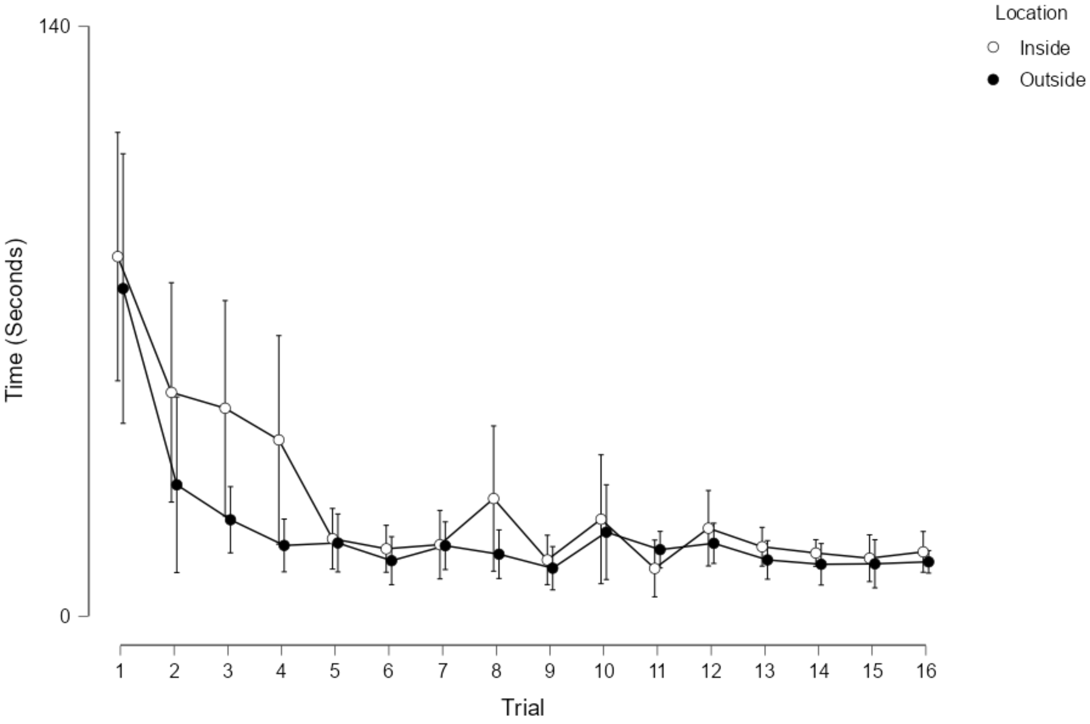
A repeated measures ANOVA with within-subject factors of location (inside or outside) and trial (1:16), and a between subjects factor of condition (allocentric congruent, egocentric congruent, incongruent (angles congruent) and incongruent (angles incongruent) reveals a significant main effect of location, $F(1,900) = 39.86$, $p < .001$, $\eta^2_G = .02$, 95% CI [.00,.02], a significant main effect of trial, $F(4.59,225.97) = 78.36$, $p < .001$, $\eta^2_G = .36$, 95% CI [.22,.59], and a non-significant main effect of condition, $F(3,60) = 1.39$, $p = .25$, $\eta^2_G < .01$, 95% CI [.00,.01]. Additionally, a location by trial interaction was also found to be significant, $F(3.76,225.97) = 4.36$, $p < .001$, $\eta^2_G = .02$, 95% CI [.00,.03]. Pre-analysis checks suggest a violation of the sphericity assumption for trial, $W < .01$, $p <.001$, and location by trial interaction, $W < .01$, $p <.001$; Consequently, a Greenhouse-Geisser correction has been applied to these statistics. No other interactions were found to be significant, $F (15,900) = .82$, $p = .48$, $\eta^2_G < .01$, 95% CI [.00,.01] .

As trials came to an end upon locating the connection area, the collapsed time for each group to complete the 32 test trials can be seen below in in figure 31.

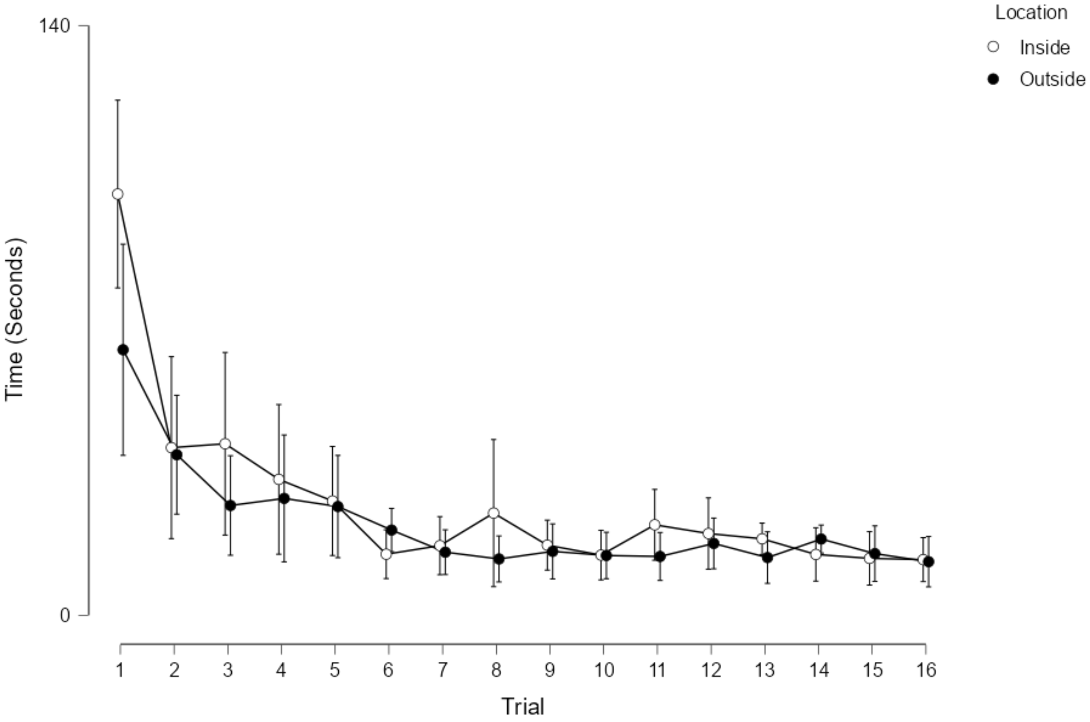
Figure 30.

Experiment VI: Estimated mean latency to locate the hidden goal on each of the internal and external trials, split by condition (A – D).

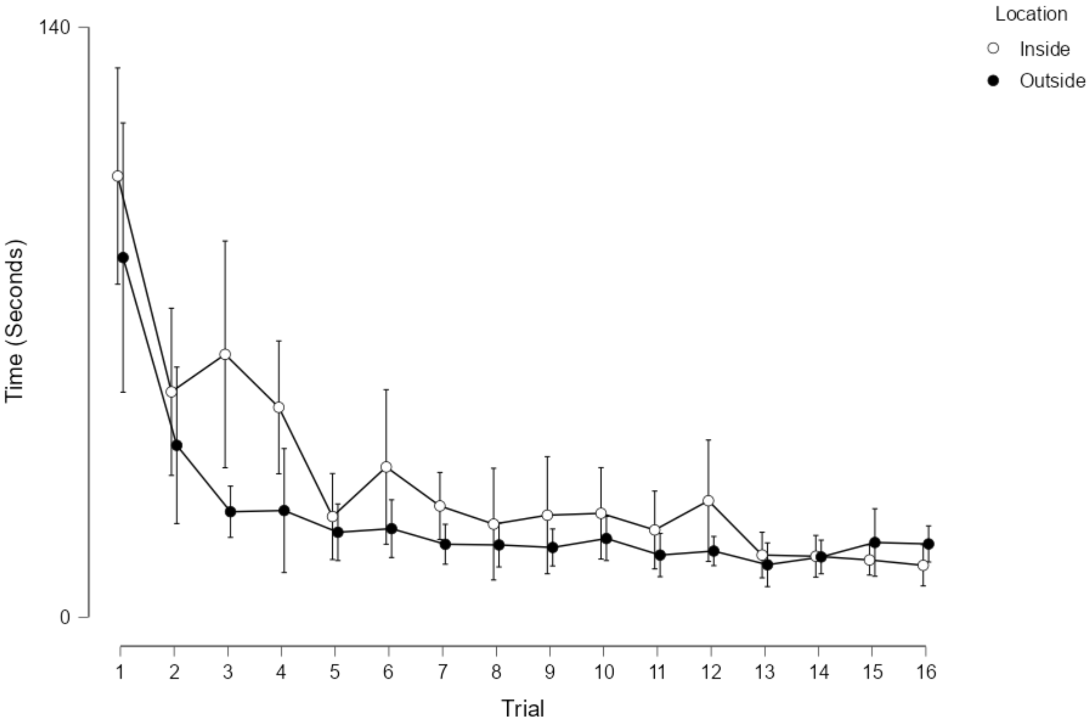
A) Condition: Local congruent.



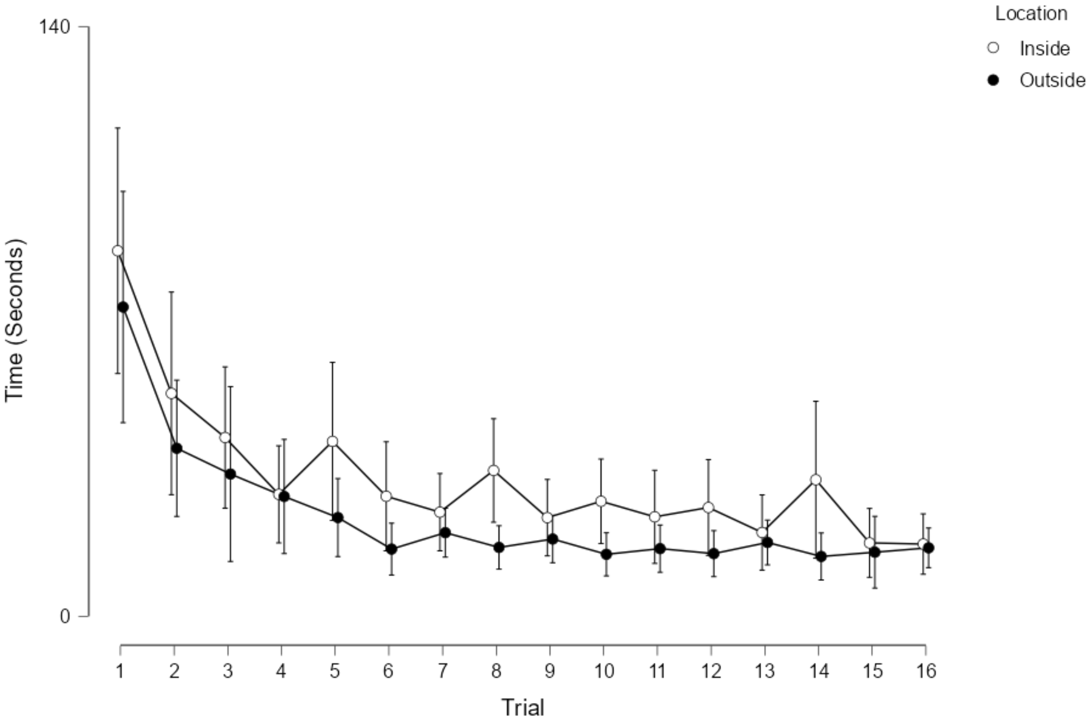
B) Condition: Global congruent.



C) Condition: Incongruent (angle congruent).



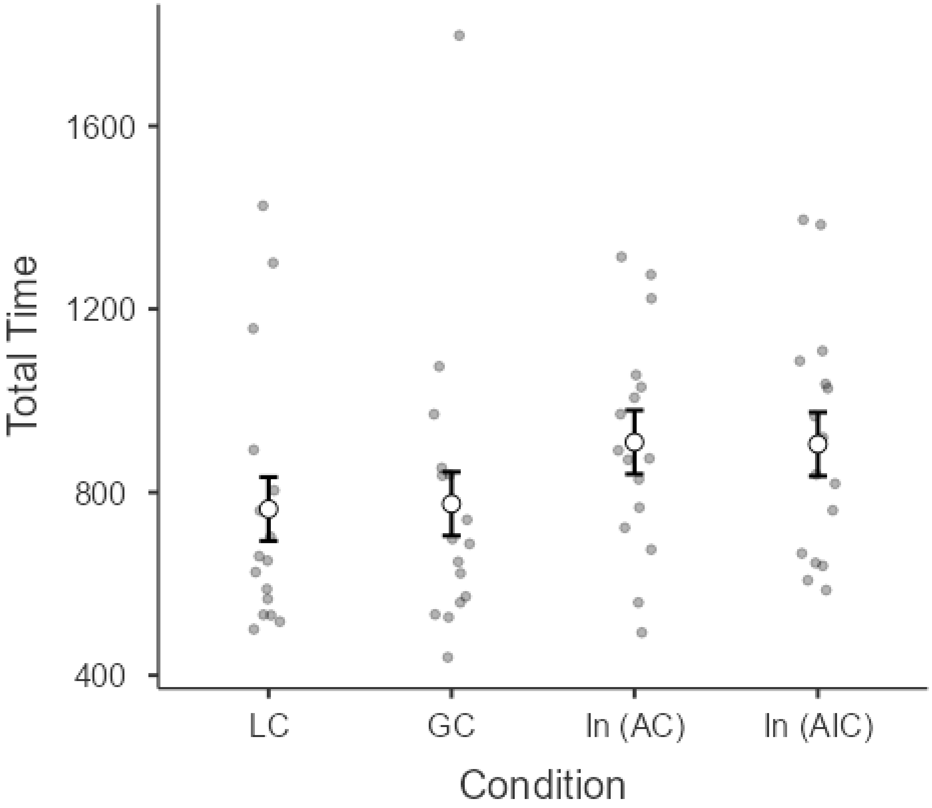
D) Condition: Incongruent (angle incongruent).



Note. Error bars represent +/-1 standard error of the mean.

Figure 31.

Experiment VII: Estimated mean time taken for participants to complete the experiment, split by condition (local congruent (LC), global congruent (GC), and incongruent (angle congruent (In AC) and incongruent (In AIC)); trials collapsed).



Note. Error bars represent +/-1 standard error of the mean. Dots represent individual observations.

Post-hoc Bonferroni adjusted pairwise comparisons suggests a noticeable learning rate, with latencies on the first trial being significantly longer to all other trials, *t*(900) = 24.64, *p* < .001. Additionally, trial 2 was found to be significantly longer than all subsequent trials, *t*(900) = 9.86 *p* < .001, aside from trials 3 & 4. Trial 3 was found to be significantly longer than all subsequent trials, bar trial 4, *t*(900) = 8.33, *p* < .001. And finally, trial 4 was found to be significantly faster than all subsequent other trials, *t*(900) = 6.46, *p* < .001. Additional post-hoc analysis indicates that internal trials were completed faster than external trials *t*(60) = 6.31, *p* < .001.

4.3.4. Discussion.

During each trial in Experiment VII, participants were required to find a hidden goal location on both the inside and outside of a cross shaped arena, with trials on the inside and outside being intermixed on a trial-to-trial basis.

Participants were split into four experimental groups: For those in the local congruent condition, the goal location for both internal and external trials was at the location which consistently and exactly matched local features of environmental geometry (for example *the goal is at the corner with a short wall on the left and a long wall on the right both inside and outside*); for those in the allocentric congruent condition, the external goal location was at the corner nearest to the internal goal location (i.e. *the other side of the corner which represented the internal goal). Additionally,* two incongruent conditions were constructed; For those in the (incongruent) angle congruent condition, the external goal location was both incongruent with regards to either egocentric or the allocentric spatial reference frame and at an opposite-angled corner (i.e. if the internal goal was at concave corner with a short wall on the left and a long on the right, the external goal location was a convex corner with a short wall on the right and a long wall on the left. Similarly, those in the (incongruent) angle congruent corner had a consist corner type both inside and outside (e.g., if the internal goal location was found at a concave corner with a short wall on the left and a long wall on the right, the external goal location was found at a concave corner with a short wall on the right and a long wall on the left.; for a visualisation of these conditions, please see figure 27)

In keeping with the results of Experiment V, participants again showed comparable learning rates in the four different conditions.

Participants in all conditions were able to complete the entire experiment in a similar amount of time, suggesting that the transfer of spatial information (either allocentric or egocentric) across the environmental boundary has either 1) not efficiently happened, or; 2) is just as viable as navigating with regards to two separate contexts (inside and outside).

4.4. Chapter Discussion.

In Experiments V, VI, & VII, we utilise an intermixed-context procedure to explore navigation surrounding boundary transfer and shape transformation paradigms.

Shape-transformation paradigms have revealed that many organisms can reorient on the basis of local-shape cues. (e.g. Pearce et al., 2004, Tommasi & Polli, 2004, Buckley et al., 2016b). This type of reorientation is widely considered to be egocentric in nature, as, crucially, allocentric spatial cues associated with the goal location during training are no longer present at test – such as global or Euclidian shape structure cues (Cheng & Newcombe, 2005; McGregor et al., 2006). For instance, following training to find a hidden goal in a rectangle-shaped arena where a short wall is to the left of a long wall, a test trial conducted in a kite-shaped arena will reveal a bias towards searching in the right-angled corner of the kite that shares the same local-shape cues that that were associated with the goal location in the rectangle (e.g., Pearce et al., 2004).

As this previous experimentation has consistently examined performance in a single test trial, it remains to be determined if the egocentric representation of the goal location influences performance beyond a single instance of re-orientation. Here in Experiments V & VI, unlike previous shape transformation experiments, participants rotate between environments on a trial-to-trial basis for the entirety of the experiment (32 trials; 16 in each shape). Half of the participants had a local congruent goal location across both environments (i.e., *the goal is at the corner with a short wall on the left and a long wall on the right in both shaped environments*.), while the other half had an incongruent goal location (i.e. *short on the left, long on the right in one shape; short wall on the right and long wall on the left in the other).* Participants either completed this procedure immediately (Experiment V), or after 32 trials of pre-training in a consistent shape before the introduction of a new shape in the above-described manner (Experiment VI). In both procedures, no pre-warning of a new global context was provided, and participants were appropriately counterbalanced so that this new global context was either the kite or rectangle (within respective experiments and conditions).

As informed by previous shape transformation studies, we may expect that participants in the local congruent condition transfer learning more successfully from one global context to another (i.e., from the rectangle to the kite), when compared to those in the incongruent condition, resulting in a shorter latency to complete the procedure – a result not reflected in the above Experiment V. Here, participants in both conditions were able to complete the entire experiment with no statistical difference in observable performance. However, when this trial-by-trial methodology was preceded by extensive overtraining trials in a consistent shape - a form of navigation thought to prime egocentric reorientation (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996) - participants in the local-congruent condition were able to complete the remainder of the experiment significantly faster than those in the incongruent condition (see Experiment VI).

Combined these results again suggest lengthy or repetitive navigation in a consistent environment does support the use of more egocentric based spatial reorientation (see Bohbot et al., 2012 for a clear demonstration of this effect). Again, we see a shape transformation paradigm prompt orientation with regards to local shape cues, consistent with previous research measuring behaviour in a single test trial (e.g. Pearce et al., 2004, Buckley et al., 2016b). However, when subjected to a intermixed trial methodology, navigators only showed a statistically clear improvement in latency to find the goal when the introduction of the new, second shape was preceded by training in a consistent one (Experiment VI; condition: local congruent). Participants in Experiment V displayed similar behaviour throughout their experiment, with navigators in both conditions completing the experiment in similar amounts of time, suggesting a less efficient transfer of spatial information across the intermixed global contexts.

In the final experiment reported in this chapter, we again use this intermixed trial methodology to explore reorientation beyond a single test trial. However, instead of applying it to aforementioned shape-transformation paradigms – traditionally thought to prompt egocentric-based navigation, we have applied it to a boundary transfer procedure (Buckley et al., 2019). Such boundary transfer procedures, in the absence of landmarks, are typically thought to resiliently prompt reorientation with regards to an allocentric reference frame (Buckley et al., 2019, Holden et al., 2021, see also: Experiments I, II, III).

Due to the more complicated nature of the arena used (cross maze; see previous figure 28), participants in Experiment VII were split into four separate groups; For those in the local congruent condition, the goal location for both internal and external trials was at the location which consistently and exactly matched local features of environmental geometry (for example *the goal is at the corner with a short wall on the left and a long wall on the right both inside and outside*); for those in the global congruent condition, the external goal location was at the corner nearest to the internal goal location (i.e. *the other side of the corner which represented the internal goal). Additionally,* two incongruent conditions were constructed; For those in the (incongruent) angle congruent condition, the external goal location was both incongruent with regards to either egocentric or the allocentric spatial reference frame and at an opposite-angled corner (i.e. if the internal goal was at concave corner with a short wall on the left and a long on the right, the external goal location was a convex corner with a short wall on the right and a long wall on the left. Similarly, those in the (incongruent) angle congruent corner had a consist corner type both inside and outside (e.g., if the internal goal location was found at a concave corner with a short wall on the left and a long wall on the right, the external goal location was found at a concave corner with a short wall on the right and a long wall on the).

As informed by previous boundary transfer studies, we may expect that participants in the global congruent condition transfer learning more successfully from one context to another (i.e., inside to outside), when compared to those in the local congruent or incongruent conditions, resulting in a shorter latency to complete the procedure – a result not reflected in the above Experiment VII. Here, all participants were able to complete the entire experiment with no statistical difference in observable performance between conditions.

One thing we may have to consider is that participants did not see the intermixed trial-by-trial contexts as connected, or the same, when not preceded by training in a consistent shape. Consequently, for participants in Experiments V & VI, we cannot be sure of reference frame use within any specific context; participants may be using an egocentric method for one context (e.g., inside), and an allocentric method for the other (e.g., outside) – regardless of condition or experiment. It is currently unclear how to discern reorientation strategy under such experimental conditions from observable behaviour alone. One possible way to infer reference-frame use via reverse inference would be to observe neurological markers at probe points throughout the procedure, with specific observation of caudate and hippocampal sub-regions – both associated with egocentric and allocentric-based spatial processing, respectively (Bohbot, et al., 2007; Guderian et al., 2015; Hartley et al., 2003; Iaria et al., 2003; Konishi et al., 2017; Packard & McGaugh, 1996; White & McDonald, 2002, Dudchenko, 2010).

Combined, however, results across this chapter suggest that reorientation strategies typically observed in a single test trial following training; such egocentric based reorientation following a shape transformation, or allocentric based reorientation following a boundary transfer, may again be task or experimental parameter dependant (see also; Experiment IV). When such paradigms are run utilising an intermixed trial-by-trial methodology, no observable difference in reorientation behaviour was found without the inclusion of pre-training in a consistent shape (Experiment VI). It is currently unclear how introducing pre-training trials in a consistent context to Experiment VII will affect behaviour upon the introduction of the other (i.e., training inside before the outside is introduced on a trial-by-trial basis). Here, participants in both contexts have equal access to local and global cues (e.g., inside and outside); while pre-training in such as manner is thought to prompt reorientation with regards to local cues (e.g., Pearce et al., 2004), engaging in a boundary transfer is typically thought to prompt reorientation with regards to global shape cues (e.g., Buckley et al., 2019, but see Experiment IV & VII). Consequently, it is currently unclear how navigators may behave under such conditions.

In the following, final chapter of this thesis, we again explore the boundary transfer effect introduced in Chapter 3. However, here we explore the effects of age on performance by using child participants throughout.

Chapter Five: Boundary Transfers (Developmental).

In Experiments I, II, III & IV, participants were required to locate a hidden goal that was always located adjacent to a right-angled corner within a cross-shaped virtual arena. Following training, participants were faced with a surprise test trial on the outside of this arena and tasked with finding the area on the outside that best corresponded to the location of the internal goal location. This cross-shaped arena was used as it provides identical features of geometry, from a first-person perspective both internally and externally. Consequently, at test, participants may re-orient themselves and search for the goal with regard to either an allocentric reference frame, or reorientate with regard to unique local features of environmental geometry in an egocentric manner (see also: Buckley et al., 2019; Holden, Whitt, & Haselgrove, 2021).

Combined, the results from Chapter three suggest that re-orientation takes place, following a boundary transfer, with respect to an allocentric, rather than an egocentric representation of the geometry of the arena, Furthermore, this effect was shown to be resilient to variables that might be expected to undermine it. For example, manipulations regarding the navigational exposure strategy used within the environment (Experiment II) and exposure time to the environment itself (number of trials; Experiment III). This effect is, however, susceptible to disruption. Results from Experiment IV showed that the inclusion of salient landmarks integrated into the environmental geometry itself may promote egocentric-based reorientation following a boundary transfer. However, of crucial note, when presented with a post-test shape recognition task, all participants in this study were able to accurately identify the global structure of their environment, regardless of condition. Further still, the inclusion of internal salient landmarks did not disrupt allocentric-based reorientation post boundary transfer, in the absence of those landmarks at test (condition: "no landmarks”), with all adult participants displaying a similar pattern of results (i.e., clear preference for the allocentric correct zone).

These results support the idea of a dual-processing model of spatial acquisition (Bodily et al., 2011; Dudchenko, 2010). Results further support the notion that both an allocentric and egocentric reference frames are encoded for active navigation, and participants may choose to behave with regards to either, depending on the navigational task at hand (Hartley et al., 2003; Iaria et al., 2003; Restle, 1957; Peer, Brunec, Newcombe, & Epstein, 2021).

Literature suggests that task parameter dependents range broadly, including the range of cues available to the navigator (such as landmarks (see Experiment IV), or the ability to match local features of geometry within a new environment (e.g., shape transformation paradigms such as Pearce et al., 2004). Similarly, how a navigator is exposed to an environment is also considered to affect reference frame use – with lengthy training or repetitive motion being suggested to prompt egocentric strategies (Morris et al., 1982; O’Keefe & Nadel, 1979; Packard & McGaugh, 1996, Hartley et al., 2003).

Additional key factors thought to have an impact over navigational performance are the idiosyncratic details related to the navigator themselves. Of particular note, the navigators age (for reviews, see Konishi, Mckenzie, Etchamendy, Roy, & Bohbot, 2017; Lester et al., 2017; Wills & Cacucci, 2014; Newcombe, 2019; León, Tascón, & Cimadevilla, 2016). Broadly speaking, literature suggests that younger children and older adults have a general bias towards navigational strategies thought to be more reliant on egocentric spatial processing (e.g., Bohbot et al., 2012).

However, it should be emphasised that data suggest children *may simply prefer* egocentric navigational strategies (often aligned with local-feature reorientation). Research suggests children are perfectly capable of demonstrating allocentric cognitive mapping in experimental situations - as young as 36 months old (Nardini et al., 2006, 2008). Of additional note, older children typically perform better in tasks of allocentric spatial processing, suggesting an chartable developmental trajectory (Bostelmann et al., 2020; Wills & Cacucci, 2014).

Combined this suggests that reference frame use for reorientation is, again, task or parameter dependant. For example, the boundary primary effect as introduced in Chapter 1 (Hermer & Spelke, 1996; Lee & Spelke, 2010; see also Cheng et al., 2003). Here, experimentation in which children were observed to rely on the ambiguous shape of the arena walls at test – instead of an unambiguously informing polarizing wall - has been taken as evidence that children rely on the global-shape (in a similar fashion to Cheng’s original rodents (1986; see also: Margules & Gallistel, 1988)). However these results may again be task parameter dependent; when the original Hermer and Spelke (1996) task was conducted in a larger rectangular arena (8 x 12 ft), children were able to use the polarising wall to reorient (Learmonth, Newcombe, and Huttenlocher, 2001; see also Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008). Children have also been shown to reorient using a polarising coloured wall in 7 x 7 ft rhombic space (Hupbach & Nadel, 2005), and in a large octagonal space (Newcombe et al., 2013). Finally, it has also been demonstrated that children are able to reorient using a local yellow polarising wall in a smaller rectangular arena (4 x 6 ft), providing they *are first given pre-training* in which they must find a hidden object in the centre of a yellow wall in an equilateral triangular arena (Twyman et al., 2007).

However, part of the problem in exploring how the shape of an environment is encoded during navigation is that it is not entirely clear how to dissociate reorientation based on global information from local information *when using shape alone.* In polarising wall experimentation such as those presented above, any local or egocentric elements are often aligned with *a landmark*, either isolated or integrated within a boundary itself (see also: Experiment IV; Herrera et al., 2022). Consequently, in the first experiment reported in this chapter we assess post-boundary reorientation in the absence of landmarks.

We again use the cross maze as described in chapters 1, 2, 3 and 4. Here, behaviour in a single test trial following a boundary transfer is measured. Unlike some previous boundary transfer experimentation (e.g., Buckley et al., 2016b), utilisation of this cross shape provides navigational circumstances in which reorientation based upon an egocentric spatial reference frame is not precluded, as exact features of local geometry can be matched internally and externally (Buckley et al., 2019; Holden et al., 2021). Under such experimental conditions typical adult participants display a strong preference for reorientation behaviour reliant on an allocentric reference frame – a strategy choice shown to be resilient to various manipulations (Experiments II & III). It is currently unclear how the reorientation behaviour of children may differ from this when tested under similar experimental circumstances; this is the focus of Experiment IIX.

In the subsequent and final experiment of this thesis - Experiment IX - we again introduce landmarks to the environmental boundaries in a manner consistent with Experiment IV (i.e., matched internally and externally for local features of geometry). Some authors have suggested that boundaries and geometric environmental information has a special status, in that encoding them does not follow general associative principles and are not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). However, these results may be task specific, with recent publications suggesting that the temporal and spatial contiguity between goal locations and landmarks may indeed influence test-behaviour reliant on global shape (Herrera et al., 2022; see also Experiment IV). With this in mind, it is unknown how participants in our landmarks condition will behave at test; will they respond to the overall allocentric structure or beacon towards the now-landmarked features of local geometry? Similarly, will the inclusion of landmarks during training interfere with encoding of the global structure for our no landmarks condition?

Finally, participants in Experiment IX were presented with a post-test shape recognition task (see methods section below). In this, subjects were asked if they could identify the global structure of the experimental arena from a selection of similar buildings. This final manipulation was introduced as a rudimentary test of allocentric processing. That is to say; participants, at test, may *only* choose to behaviourally respond in a manner consistent with either allocentric or egocentric strategies. For example, participants navigating with regard to an egocentric reference frame, at test, may still be undertaking allocentric spatial encoding processes and are simply not behaviourally expressing these due to the specific task demands. By introducing a post-test shape recognition task at this point we aim to further understand mechanisms to shape-encoding using procedure uniquely suited to humans.

5.1. Experiment IIX.

Previous research utilising the cross-maze revealed that following a boundary transfer, adults prefer to orient with regards to an allocentric representation of their environment (Buckley et al., 2019; Holden et al., 2021; see also Chapters 3 & 4). However, these results, as with many others in the spatial cognition field, may be specific task or parameter dependent. For example, when a similar boundary transfer experiment using the exact same structure was applied to a trial-by-trial procedure - instead of repetitive training followed by a single test – no clear preference for allocentric based orientation was found (Experiment VII).

The purpose of Experiment IX was to determine if children would display a similar preference when tested under a traditional 2 stage training-test paradigm. As discussed in the introduction; combined, previous shape transformation and boundary transfer studies to use child participants again support a dual processing model of spatial acquisition. Children as young as 36 months have displayed allocentric spatial processing in experimental settings (Nardini, Burgess, Breckenridge, & Atkinson, 2006; see also Hermer & Spelke, 1996, 1994). For example, in a series of six experiments, Huttenlocher, Newcombe, & Sandberg (1994) had children search for toys after seeing them buried in a rectangular sandbox (surrounded by a circular sheet) – in a similar manner to Cheng's rats (Cheng, 1986). Experiments include a number of manipulations, such as providing intramaze and extramaze cues that also signal the baited corner. Here, results suggest children have systematic bias towards orientation with regards to the their arena boundaries in an allocentric manner (see also: Newcombe, Huttenlocher, Drummey, & Wiley, 1998).

However these results may again be task specific. Many authors have suggested children have a bias towards navigation strategies considered more egocentric in nature. For example, children have empirically suggested preference towards using intramaze cues to orientate, despite either extramaze cues or environmental boundaries providing valid goal-related spatial information (Buckley, Haselgrove, & Smith, 2015; Bullens, Iglói, Berthoz, Postma, & Rondi-Reig, 2010; Laurance, Learmonth, Nadel, & Jacobs, 2003; See also: polarizing wall research above). Navigation with respect to intramaze cues in such a manner is thought to be egocentric in nature, with some authors claiming that children find it difficult to link the geometric properties of isolated extra-maze landmarks; consequently, children may be using these proximal intramaze landmarks to navigate in a egocentric view-matching manner (Gouteux & Spelke, 2001; Lee & Spelke, 2010b).

Many authors have put forward possible reasons for this general preference for egocentric strategies, suggesting underdeveloped neural architecture resulting in less precise and integrated cognitive maps (Lourenco & Huttenlocher, 2007; Piaget & Inhelder, 2013), and an inability correctly accurately integrate multiple sources of information, such as extra-maze cues and immediate boundary walls (Nardini et al., 2008).

What cannot be determined from many of these previous experiments, however, is the extent to which children rely on global- or local-shape representations when both types of representation can support reorientation. That is, in traditional shape transformation experiments, allocentric global-shape representations cannot be used to guide reorientation due to the change in the overall boundary-shape between training and test. Likewise, egocentrically encoded local-shape representations cannot be used to guide reorientation in boundary-transfer paradigms that use relatively regular shaped-arenas, such as kites and rectangles, because the transfer from the inside to the outside of the boundary shape between training and test reverses the spatial relationship between the relative wall lengths that signalled a goal location. By using a cross-shaped arena during training on the inside and then testing on the outside, we can place local and global reorientation cues into conflict following a boundary transfer

5.1.1. Participants.

For all experiments reported in this chapter, participants were recruited at a public engagement event held at the University of Nottingham (Psychology). Children were recruited at an annual event named "Summer Scientist Week" (for more details see summerscientist.org). Here children complete multiple "research games" in exchange for tokens – these can then be exchanged for additional games and activity participation (they enjoy it, I promise!). Participants also receive an additional gift bag for their attendance.

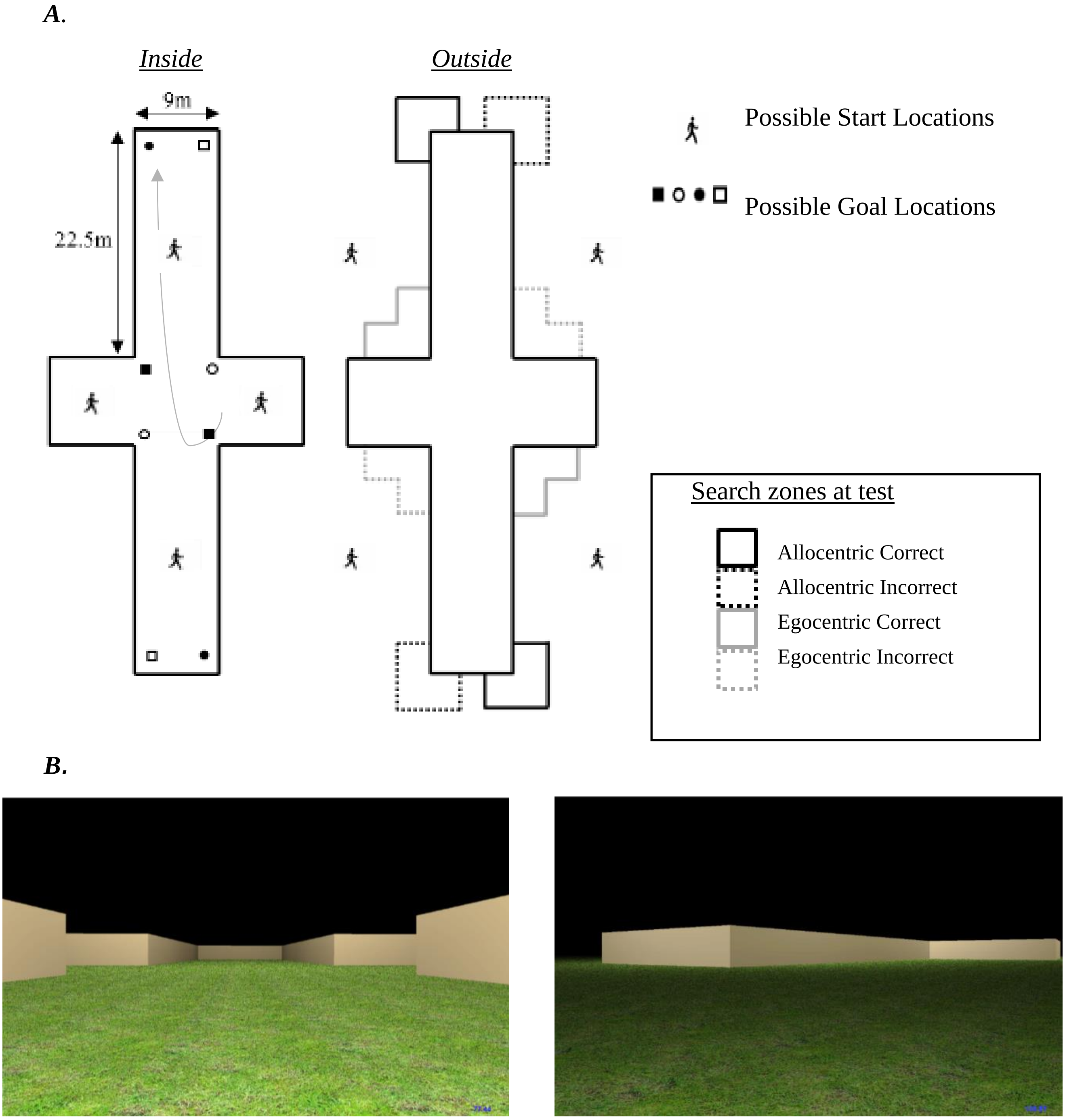
75 children took part in Experiment IIX – aged between 72.11 and 145.09 months (*M* = 109.16, *SD* = 19.65, *f* = 30). *i.e., between 6 and 12 years old.* All participants took part in the experiment as part of Summer Scientist Week (as described above). Participants were often tested alone, if older; parents frequently escort younger children but do not interfere.

5.1.2. Procedure.

The procedure, stimuli and materials for Experiment IX was identical to Chapter One: Experiment I. Thus, participants were first trained over 8 trials to locate a hidden goal that was locate adjacent to one of the right-angled corners on the inside of the cross shaped arena. Following this, a single test trial would begin in which participants were transferred to the outside of the structure. Unbeknownst to them, during this final trial there was no goal to find (see figure 32).

Figure 32.

Plan view of the cross maze. The arena is a simplified cruciform architecture.

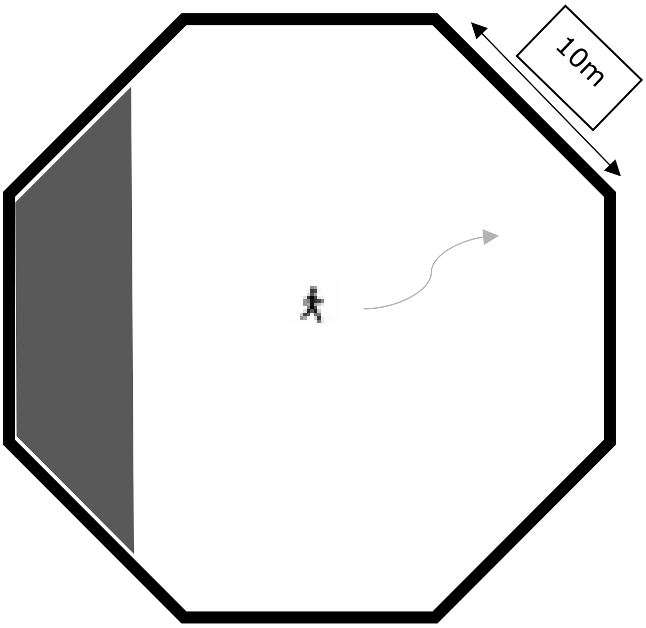


Note. A: The schematic view of the cross maze arena This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. External search zones are consistent with this training, as are all four goal locations (counterbalanced within studies). B: Sample screen captures taken from inside (left) and outside (right) of the structure.

Minor adjustments were made to the experiment to make the procedure more accessible to child participants. First, before the experiment began all children were permitted to explore a practice environment to familiarise themselves with the movement controls (see figure 33). This was a large regular octagon with 8 equal sides of 10m. Again, a wall height of 2.5 meters was used and a grassy and crème texture used for both the floor and walls. Participants started this training trial in the centre of the octagon and were able to freely move around. The training trial ended once they walked into the third of the environment directly behind them at the start of the trial, thus ensuring at least one 180-degree turn.

Figure 33.

Plan view of the octagon practice arena.



Note. Time in this practice arena ended upon entry of the grey-zone. Participants always started with this area behind them, ensuring at least one 180° turn.

For the main experiment, participants were told they would be playing a “Ghost Hunter” game, and each were given the same standardised instructions (both verbally and via text):

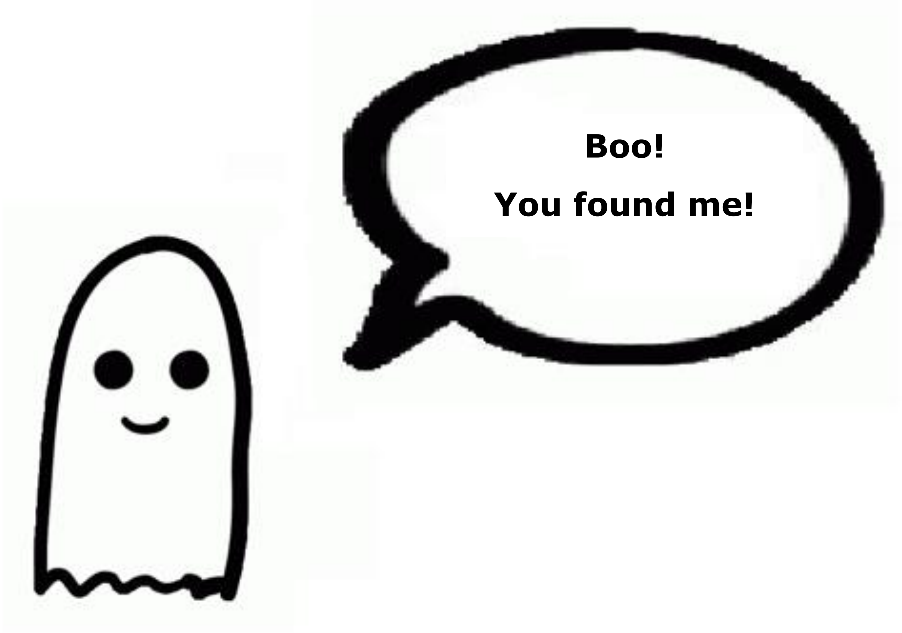
> *During this game, you are going to have to hunt down Gabby the Ghost!*
>
> *You are going to be placed into a room on the computer, and somewhere in that room is a ghost for you to find.*
>
> *Gabby is a ghost so you will not be able to see her; she is invisible. However if you go close her - if you go to the right place she will jump up on the screen.*
>
> *Your job is to keep hunting gabby down, keep getting to her as fast as you can. Once you have found her she will not move, but you might start in different places in the room. She will always be in the same place and you need to keep getting back to her as quickly as you can.*
>
> *Shall we have a practice first so you know what it is like?*

Participants would then complete the practice training trial as described above. Upon completion of this trial, “Gabby” the ghost would pop up on screen (see figure 34) with the caption “Boo! You found me!”.

Following successful completion of this initial practice training trial, participants began the main internal training trials. Each trail only ended once the hidden goal had been located, however if two minutes elapsed during one of these training trials, a small white flag would appear at the goal location. Once the goal had been found, participants would no longer be able to move and Gabby would appear on screen with the caption “Boo! You found me!”. After 3 seconds the next trial would begin. Previous studies (Buckley et al. 2019) have revealed that adult participants rapidly learn this task (16 trials). Indeed, Holden, et al. (2021) have shown that participants will successfully transfer their search behaviour to the appropriate global (allocentric) search zones at test following as few as 2 training trials on the inside of the cross-shaped arena. Consequently, to hopefully reduce any potential fatigue effects in our younger participants, the number of training trials was 8.

Figure 34.

The ghost image used to represent “Gabby the Ghost”.



Note. Image was “pop up” upon location of the hidden goal in each trial.

Participants started each training trial at one of two start locations within the arena: (a) at a point between the centre of the arena and the end of one of the long arms and (b) at a point between the centre of the arena and the end of one of the short arms (mirrored – again, see Figure 32). The direction that participants faced was chosen at random at the start of each trial. During training, participants began training equally frequently at each of the start locations. Once training was completed, the following instructions were presented on screen:

> *On this last go, Gabby will be really hard to find! She's also gone outside of the room, so we'll have to go outside too!*
> *Don't walk in circles around the building – Where do you think she might be?*

These instructions were also verbally presented to participants before the experimenter manually triggered a final 2-minute test trial on the outside of the structure. Here, we measure test-trial performance or navigational behaviour in extinction – i.e. where no hidden goal is present. To do this, we analyse time spent in L-shaped search zones placed outside the environment (long sides 6.48m, short sides 3.24). These were created and positioned around the convex and within the concave right-angled corners see figure 32.

Assessing spatial behaviour during extinction tests in such a manner is common in experiments conducted with both non-human animals (e.g. McGregor, Horne, Esber, & Pearce, 2009), human adults (Buckley et al., 2019; Holden et al., 2021; Redhead & Hamilton, 2009), and researchers have successfully used test trials without the presence of a hidden goal in navigational experiments with children previously (e.g. Buckley et al., 2015).

5.1.3. Results.

5.1.3.1. Acquisition.

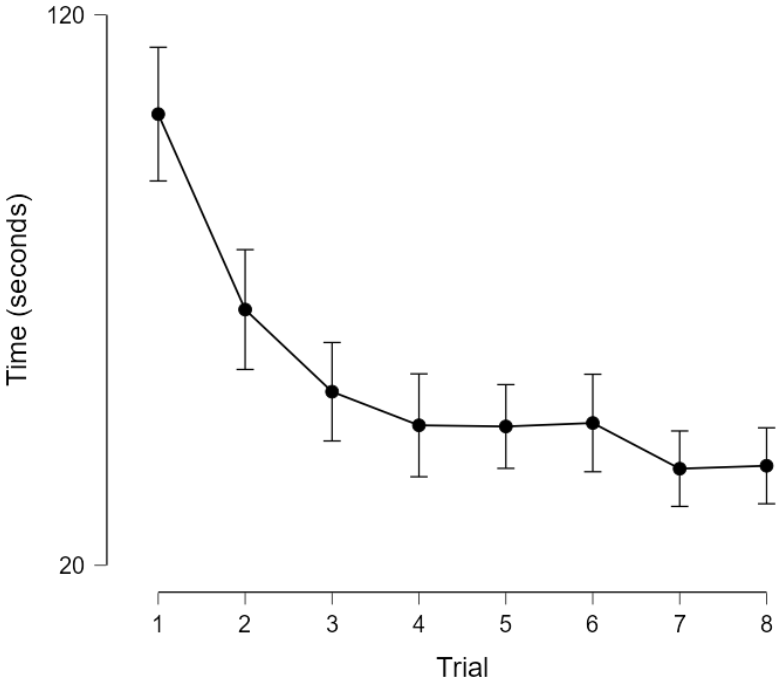
To analyse latencies to find the goal during training, we conducted analysis of covariance (ANCOVA), with trials (1-8) as a within-subjects factor, and age as a covariate. As noted in previous developmental research (e.g. Buckley et al., 2015), it is necessary to mean-centre the age covariate when performing these analyses, as it has been demonstrated that tests of within-subjects main effects are altered when the mean of a covariate differs from zero (see Delaney & Maxwell, 1981; Thomas et al., 2009). By mean centring age (subtracting the mean age of the entire sample from individual ages) the mean of the covariate becomes zero but, importantly, this rescaling does not influence tests of the main effect of, or interactions with, the covariate itself.

Figure 35 displays that the mean latencies for participants to find the hidden goal decreased as training progressed, indicating that children learned the task. A one-way ANCOVA with a within-subjects factor of trial (1-8), and a covariate of age (mean centred), revealed a significant within-subjects effect of trial, $F(5.48, 386.99) = 6257$, $p < .001$, $\eta_p^2 = .19$ [.09.28], a significant age covariate, $F(1, 71) = 41.15$, $p < .001$, $\eta_p^2 = .39$ [.23-.50], but no significant interaction between trial and age, $F(7, 497) = 1.78$, $p = .08$, $\eta_p^2 = .03$ [.00-.04]. Of note, Mauchly's test for sphericity suggests a violation of this assumption for trial, $W = .36$, $P < .001$; consequently, a Greenhouse-Geisser correction has been applied to these statistics.

Post-hoc Bonferroni adjusted pairwise comparisons (Welch's) suggest learning across individual trials, with latencies on the first trial being significantly longer to all other trials, $t(71) = 10.39$, $p < .001$. Time taken to locate the hidden goal during the second trial was also found to be significantly faster than the final two trials, *t*(71) = 4.42, *p* < .001; *t*(71) = 4.31, *p* < .001 (respectively). No other comparisons were found to be significant.

Figure 35.

Experiment IIX: The mean latency to locate the hidden goal during the eight internal training trials.



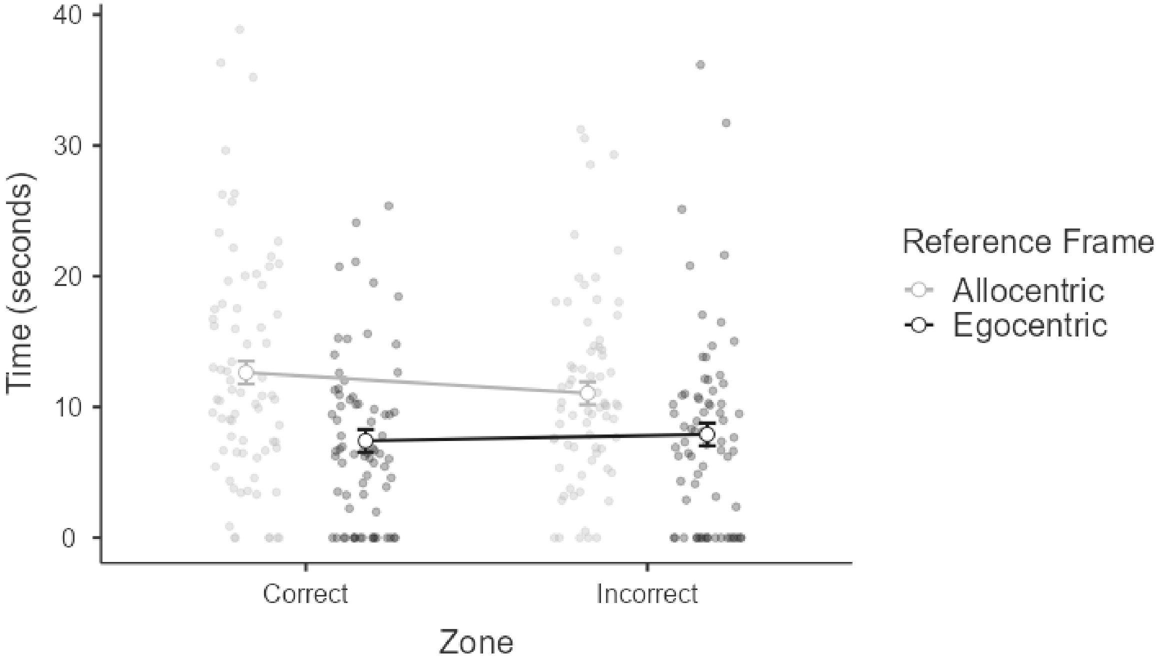
Note. Error bars represent +/-1 standard error of the mean.

5.1.3.2. *Test.*

Please see figure 36 for total mean time spent in each external search zone. For consistency with previous experimentation using the cross maze, a 2 (reference frame: allocentric or egocentric) x 2 (zone: correct or incorrect) ANOVA was used to conduct a preliminary analysis of the test data. Here, reference frame is the only significant main effect, *F*(1, 288) = 23.15, *p* < .001, η^2_P = .08, 95% CI [.01,.17], with post-hoc pairwise comparisons (Welch's) suggesting participants spent more time searching in allocentric relative to the egocentric zones at test, *t*(288) = 4.81, *p* < .001. There was no significant main effect of zone, *F*(1,288) = 21.72, *p* = *.53,* η^2_P = .001, 95% CI [.00,.00], nor any significant interaction between zone and reference frame, *F*(1, 288) = 1.42, *p* = .23, η^2_P = .005, 95% CI [.01,.00].

Figure 36.

Experiment IIX: Estimated mean time spent within each of the external search zones during the final test trial.



Note. Individual data points represent raw observed scores. Error bars represent +/-1 standard error of the pooled model mean.

5.1.3.3. *Developmental Trajectory Analysis.*

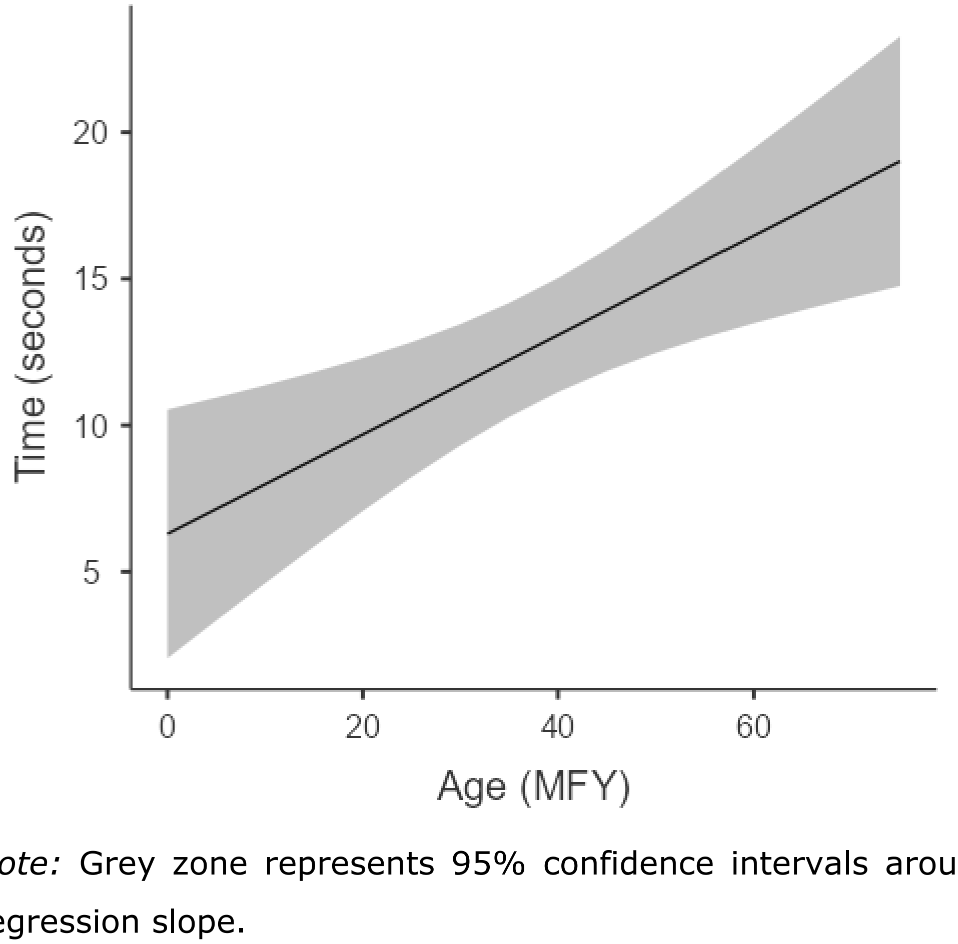
Here, to assess whether age predicted test performance, individual ages were regressed onto time spent within each of the 4 external zones (A – D). Following Thomas et al. (2009: see also Buckley et al., 2015), we rescaled the age predictor to reflect the months from the youngest age (MFY) tested within our sample. Rescaling ages in the manner does not alter the predictive ability of age, but does adjust the y-intercept of the regression model such that it occurs at the youngest age within our sample.

A) Allocentric correct.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 2.21. *p* = .48, and collinearity statistics report acceptable tolerances, *tolerance* = .1, *VIF* = 1. Age is able to significantly predict time spent within this zone, *R* = .36, *Adjusted R²* = .12, *F(1,71)* = 11.18, *p* < .001; *b* = .17, *t* = 3.34, see figure 37.

Figure 37.

Experiment IIX: Regression model for time spent within the allocentric correct zone, by age (months from youngest within sample).



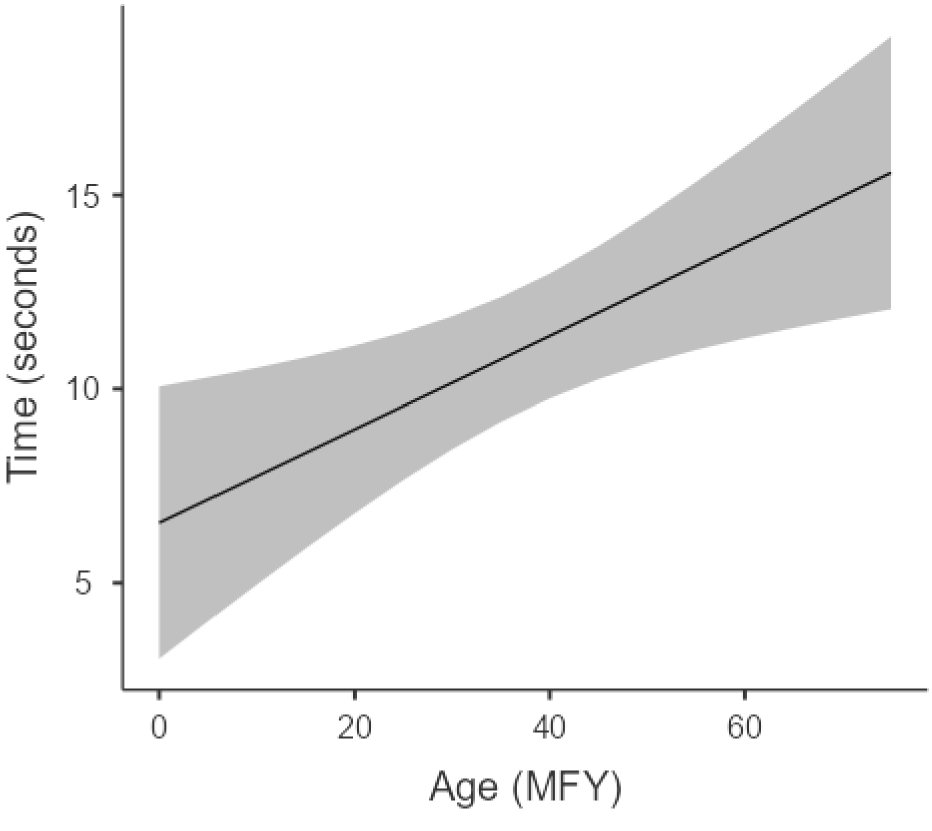
Note: Grey zone represents 95% confidence intervals around the regression slope.

B) Allocentric incorrect.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 1.72. *p* = .16, and collinearity statistics report acceptable tolerances, *tolerance* = .1, *VIF* = 1. Age is able to significantly predict time spent within this zone, *R* = .32, *Adjusted R²* = .09, *F(1,71)* = 8.24, *p* = .005; *b* = .12, *t* = 2.87, see figure 38.

Figure 38.

Experiment IIX: Regression model for time spent within the allocentric correct zone, by age (months from youngest within sample).



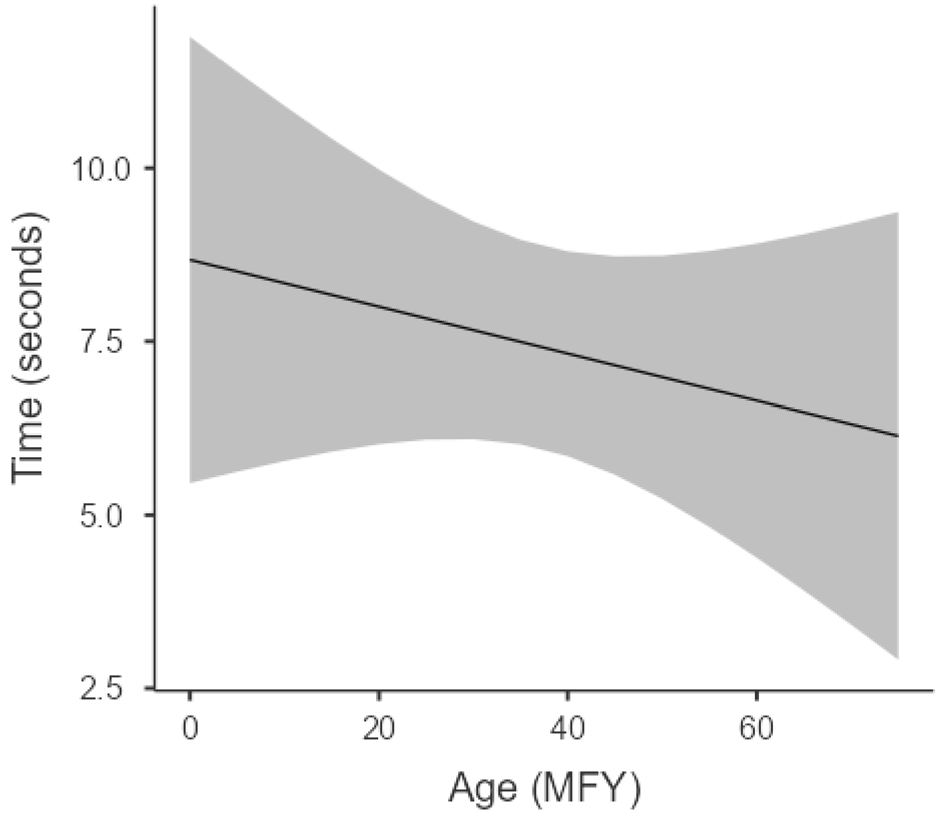
Note: Grey zone represents 95% confidence intervals around the regression slope.

C) Egocentric Correct.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 2.05. *p* = .97, and collinearity statistics report acceptable tolerances, *tolerance* = .1, *VIF* = 1. Age is not able to significantly predict time spent within this zone, *R* = .10, *Adjusted R²* = .01, *F(1,71)* = .77, *p* = .38; *b* < .01, *t* = -.88, see figure 39.

Figure 39.

Experiment IIX: Regression model for time spent within the allocentric correct zone, by age (months from youngest within sample).



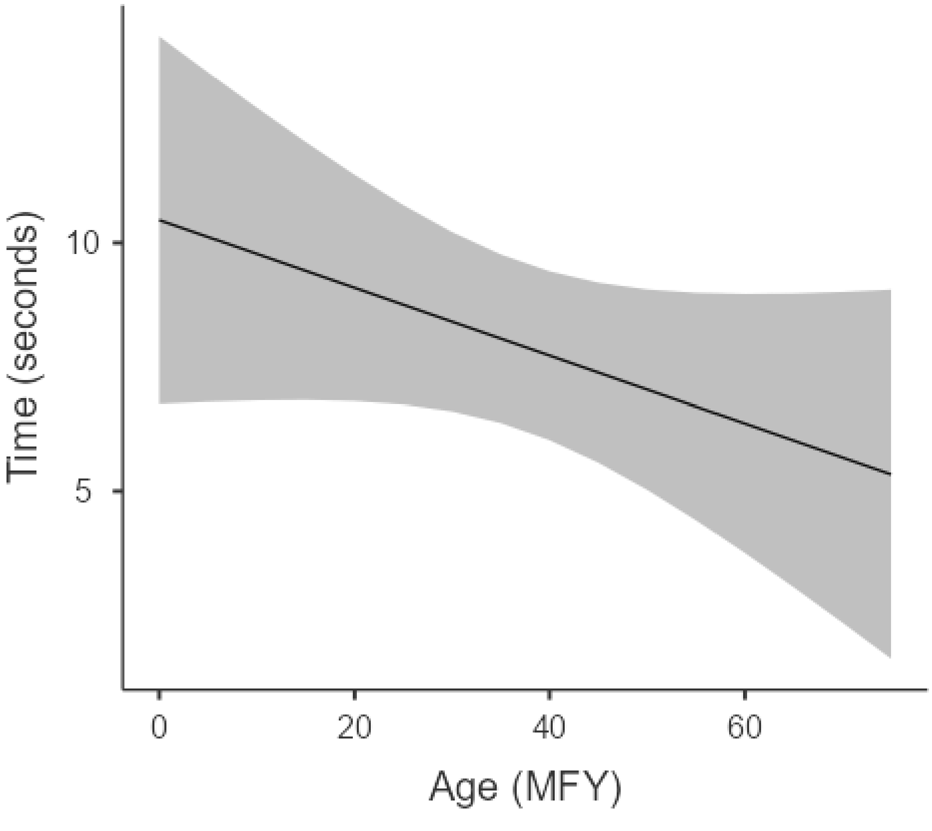
Note: Grey zone represents 95% confidence intervals around the regression slope.

D) Egocentric Incorrect.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 1.89. *p* = .55, and collinearity statistics report acceptable tolerances, *tolerance* = .1, *VIF* = 1. Age is not able to significantly predict time spent within this zone, *R* = .18, *Adjusted R²* = .01, *F(1,71)* = 2.38, *p* = .13; *b* < .01, *t* = -1.54, see figure 40.

Figure 40.

Experiment IIX: Regression model for time spent within the allocentric correct zone, by age (months from youngest within sample).



Note: Grey zone represents 95% confidence intervals around the regression slope.

5.1.4. Discussion.

In Experiment IIX, children were trained to find a hidden goal on the inside of a cross-shaped arena, before receiving a test trial conducted on the outside of the same arena. During test, both the global- and local-shape cues that signalled the goal location during training were present; however, reorientation behaviour based upon these representations was placed into conflict (see also, Chapters 3 & 4; Buckley et al., 2019; Holden et al., 2021).

In line with the experiments conducted with adult participants reported in Chapter 3, and also described by Buckley et al (2019), children spent more time searching within the allocentric correct and incorrect zones relative to the egocentric correct and incorrect zones at test. Children, however, did not significantly prefer the allocentric correct search zone over the allocentric incorrect zone – a finding inconsistent with adult participants.

A possible reason for this difference in behaviour, at test, may be that children are thought to be less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007). Under such assumptions, it is possible that our younger participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal representation with the current, new, external – an idea previously voiced in developmental research (i.e. Nardini et al., 2008).

Further regression analyses revealed that age was a significant predictor of the proportion of time spent searching in the allocentric zones, but not the egocentric zones at test, with older children spending significantly more time in the allocentric zones. No preference was found for the egocentric search zones, with the majority of all participants spending minimal time in these zones (<10s).

This general lack of time spent within egocentric search zones amongst our younger participants again suggests that the specific act of crossing an environmental boundary resiliently prompts allocentric-based navigation under traditional test-trial procedures (see also; Experiments I, II, III; Buckley et al., 2019). Our data suggests this preference in navigation strategy is unaffected by a potential developmental bias for navigation based upon an egocentric reference frame.

In the final experiment reported in this chapter *and* thesis, Experiment IX, we again introduce landmarks to the internal and external side of the cross maze – in a manner consistent with Experiment IV. Landmarks were present for all participants during internal training trials. However, during the final test trial participants were split into two experimental groups. For half of the participants, the landmarks were again present during this final trial at locations congruent with the internal features of geometry. For example, if the corner at which a long wall was on the left of a short wall was blue inside; it was blue outside (group landmarks). For these participants, allocentric and egocentric spatial reference frames may potentially be placed into conflict upon this final trial. The remaining participants faced a test trial identical to previous versions – i.e. no external panels, with a crème texture applied throughout (group: no landmarks).

Some authors have suggested that boundaries and geometric environmental information has a special status, in that encoding them does not follow general associative principles and are not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). However some research has suggested that the introduction of landmarks can interfere with navigation by, and recognition of global shape in a standard intradimensional-extradimensional shift (ID-ED; Buckley et al., 2014) and OS/blocking paradigms (Buckley, Smith, et al., 2015). However, these results may be task specific, with recent publications suggesting that the temporal and spatial contiguity between goal locations and landmarks may influence test-behaviour (Herrera et al., 2022).

Further still, as discussed above, children specifically have been noted to have bias towards landmark related reorientation, and will generally navigate with regards to a polarizing wall (Learmonth et al., 2001; 2002; 2008; Hupbach & Nadel, 2005; Newcombe, Ratliff, Shallcross, & Twyman, 2013; Twyman, Friedman, & Spetch, 2007; but see Hermer and Spelke, 1996; Cheng 1986). With this in mind, it is unknown how participants in our landmarks condition will behave at test; will they respond to the overall allocentric structure or beacon towards the now-landmarked features of local geometry? Similarly, will the inclusion of landmarks during training interfere with encoding of the global structure for our no landmarks condition? To aid with further interpretation of this last point, we again use the post-test shape recognition task. In this, subjects were asked if they could identify the global structure of the experimental arena from a selection of similar buildings. This final manipulation was introduced as a rudimentary test of allocentric processing. That is to say; participants, at test, may *only* choose to behaviourally respond in a manner consistent with either allocentric or egocentric strategies. For example, participants navigating with regard to an egocentric reference frame may still be undertaking allocentric spatial encoding processes and are simply not behaviourally expressing these at test due to the specific task demands. By introducing a post-test shape recognition task we aim to further understand mechanisms to shape-encoding using procedure uniquely suited to humans.

5.2. Experiment IX.

In the final experiment reported in this chapter, we again adopt a boundary transfer procedure in which child participants are trained on the inside of a cross maze arena over multiple training trials. Following training, participants are given a single test trial on the outside of the same arena in which, unbeknownst to them, there is no goal to find. During this final trial their search behaviour is measured in the same four external search regions as used previously (e.g., experiment IIX).

In previous experiments, during this final trial, adult participants typically spend more time in the zone that is consistent with them having encoded an allocentric representation of their environment (i.e., the allocentric correct zone; Buckley et al., 2019, Holden et al., 2021). This boundary transfer effect seems resistant to manipulations in training length and internal navigation style (see experiments II & III). However, we have previously broke this effect by introducing landmarks to the arena – defined as coloured panels situated upon 90-degree corners within the arena, in a manner consistent with Buckley et al., 2014; Herrera et al., 2022; see experiment IV. Here, for half of participants, landmarks were present during this final trial at locations congruent with the internal features of local geometry. That is to say, if -during training - the hidden goal was located at a blue coloured corner where a long wall was on the left of a short wall, then the blue panel was located on an identical corner on the outside (group: landmarks). For these participants, allocentric and egocentric spatial reference frames are potentially placed into conflict upon this final trial, depending on how they had encoded the internal goal location. The remaining participants faced a test trial identical to previous versions – i.e. no external panels with a crème texture applied throughout (group: no landmarks).

When adults are tested under such conditions, participants in the landmarks group, following boundary transfer, spend significantly more time at the egocentric-correct zone at test (i.e. they again go to the landmark). For the remainder of participants, reorientation behaviour follows the established pattern of results consistent amongst adults (i.e., spending more time in the allocentric zones, with specific preference for the allocentric-correct). These findings may prove contrary to the notion that boundaries and geometric environmental information has a special status, in that encoding them does not follow general associative principles and are not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). However, it should be explicitly noted that when presented with a post-test shape recognition task, *all* participants, regardless of condition, were able to accurately identify the global structure of the test arena (see: experiment IV), suggesting some elements of global boundary encoding had occurred.

Here, we adopt this procedure for use with child participants. When tested in the absence of landmarks, at test, children show preference for the allocentric zones – but not specific preference for the allocentric-correct (see: experiment IIX). A possible reason for this difference in behaviour at test may be that children are thought to be less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007). Under such assumptions, it is possible that younger participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal representation with their current, new, external – an idea previously voiced in developmental research (i.e. Nardini et al., 2008).

Further still, children specifically have been noted to have bias towards landmark related reorientation, and will generally navigate with regards to a polarizing wall (Learmonth et al., 2001; 2002; 2008; Hupbach & Nadel, 2005; Newcombe, Ratliff, Shallcross, & Twyman, 2013; Twyman, Friedman, & Spetch, 2007; but see Hermer and Spelke, 1996; Cheng 1986). With this in mind, it is unknown how participants in our landmarks and no landmarks conditions will behave at test; will those in the no landmarks condition show complimentary results to participants in experiment IIX, or will internal landmarks interfere with navigation by, or recognition of global shape (Buckley et al., 2014; 2015). Similarly, will those in the landmarks condition respond to the overall global structure or beacon towards the now-landmarked features of local geometry, in a manner consistent with adults?

To further aid with interpretation, we again present participants with a post-test shape recognition task. In this, subjects were asked if they could identify the global structure of the experimental arena from a selection of similar buildings (see methods section below). This final manipulation was introduced as a rudimentary test of allocentric processing. That is to say; participants, at test, may *only* choose to behaviourally respond in a manner consistent with either allocentric or egocentric strategies. For example, participants navigating with regard to landmarks may still be undertaking allocentric spatial encoding processes and are simply not behaviourally expressing these at test due to the specific task demands. By introducing a post-test shape recognition task we aim to further understand mechanisms to shape-encoding using procedure uniquely suited to human participants.

5.2.1. Participants.

82 children took part in Experiment XI – aged between 50.44 and 143.21 months (*M* = 104.35, *SD* = 23.84, *f* = 32). *i.e., between 4 and 12 years old.* Participants were again recruited at the public engagement event "Summer Scientist Week" at The University of

Nottingham (SummerScientist.org), and were split equally into two experimental groups; landmarks (*M* = 104.17, *SD* = 22.95, *f* = 16) and no landmarks (*M* = 104.81, *SD* = 24.91, *f* = 18). Groups did not differ significantly in their age, *t*(81) = 0.05, *p* = .996.

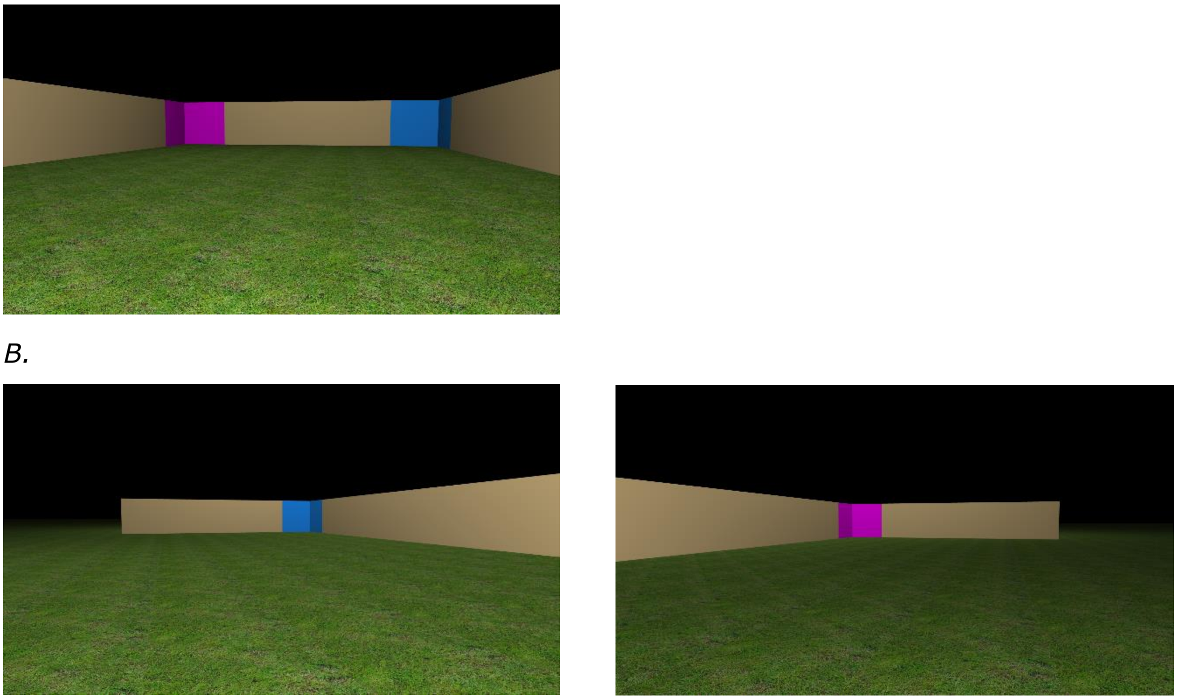
5.2.2. Procedure.

For half of participants (group: no landmarks) The materials and procedure used for the maze task within this experiment were near identical to Experiment IIX – with coloured landmarks being introduced to *internal* training trial corners (see also: experiment IV). For the second half of participants, procedure was identical to that presented in the previous Experiment IIX with the following key manipulations:

During all internal training trials, uniquely coloured panel landmarks were placed over the corners (matched upon lines of symmetry to allow for rotational errors in the cross-maze). Colours used were always blue and magenta, and landmarks were placed over both concave and convex corners (see figure 41). Landmarks were again present during the final external test trial at locations locally-consistent with their internal orientation. For example, if a concave corner with a short wall on the left and a long wall on the right was blue internally, it was blue externally (see figure 41).

Figure 41.

Landmarks introduced for Experiment IX; Condition: Landmarks.



A.

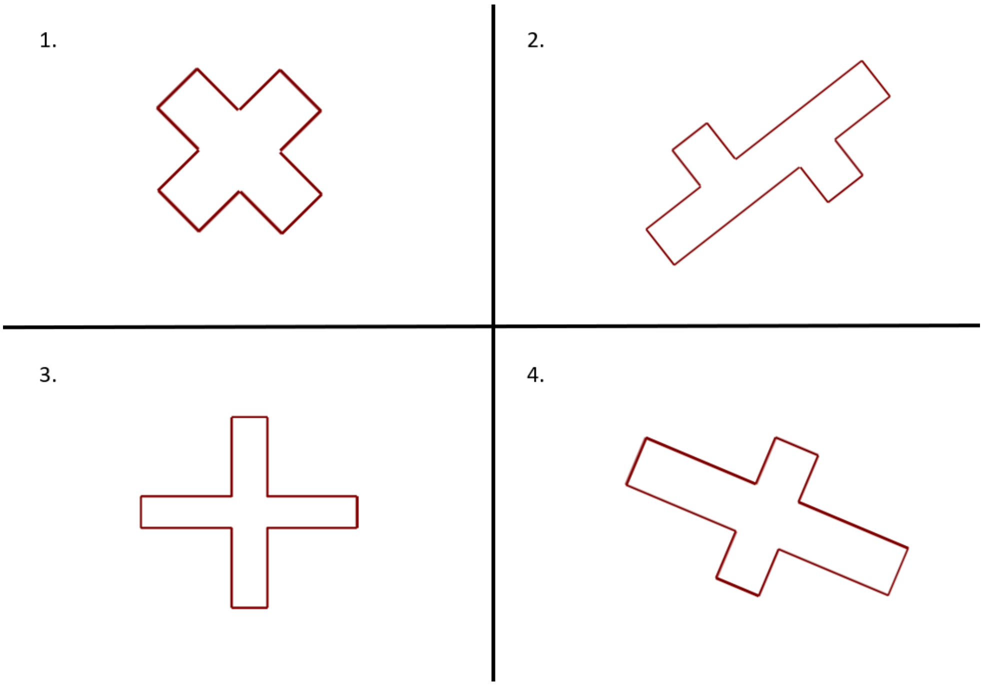
B.

Note. A. & B. represents landmarks used both internally (top) and externally (bottom). In this example, landmarks are considered locally-congruent across the boundary transfer; for example, the blue landmark is at the concave corner at which a short wall is on the left of a long wall both internally and externally.

Following this maze task, participants were presented with the shape recognition task, in which they are asked to identify the shape of the arena that they had just been traversing from multiple similar options (see figure 42). Presentation order of these options was counterbalanced within this study.

Figure 42.

The post-test shape recognition task options presented to participants navigating the cross shaped arena.



Note. Presentation order was counterbalanced across participants; here, the correct answer is option 4.

5.2.3. Results.

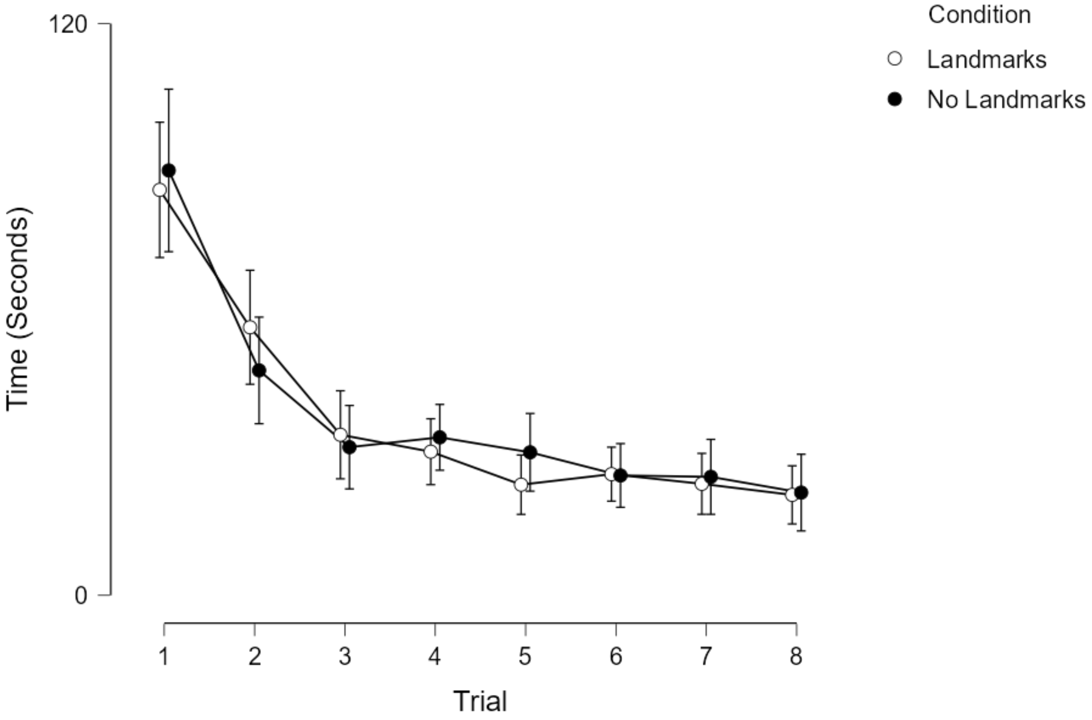
5.2.3.1. <u>Acquisition.</u>

To analyse latencies to find the goal during training, we conducted analysis of covariance (ANCOVA), with trials (1-8) as a within-subjects factor, condition as a between-subjects factor and age as a covariate. As noted in previous developmental research (e.g. Buckley et al., 2015), it is necessary to mean-centre the age covariate when performing these analyses, as it has been demonstrated that tests of within-subjects main effects are altered when the mean of a covariate differs from zero (see Delaney & Maxwell, 1981; Thomas et al., 2009). By mean centring age (subtracting the mean age of the entire sample from individual ages) the mean of the covariate becomes zero but, importantly, this rescaling does not influence tests of the main effect of, or interactions with, the covariate itself.

Figure 43 displays that the mean latencies for participants to find the hidden goal decreased as training trials progressed, indicating that children in both conditions learned the task.

Figure 43.

Experiment IX: Mean time taken to locate the hidden goal for each condition during each internal training trial.



Note. Error bars represent +/-1 standard error of the mean

Pre-analysis checks suggest a violation of the sphericity assumption for trial (W = .01, P = <.001), and a Greenhouse-Geisser correction has been applied to these statistics. Repeated measures ANCOVA with a within-subjects factor of trial (1-8), a between subjects factor of condition (landmarks or no landmarks), and a covariate of age revealed a significant main effect of trial, $F(3.92,306.49) = 46.74$, $p < .001$, $\eta^2_G = .08$, 95% CI [.00, .12], a non-significant main effect of condition, $F(1,78) = .36$, $p = .851$, η^2_G

< .001, 95% CI [.00,.00], and no significant interaction, *F*(7,546) = .554, $p = .793$, $\eta^2_G < .001$, 95% CI[.00,.00]. Both age, *F*(7,546) = 23.74, $p < .001$, $\eta^2_G = .047$, 95% CI[.03,.05], and the age by trial interaction, *F*(7,546) = 3.41, $p < .001$, $\eta^2_G = .032$, 95% CI[.02,.00], were found to be significant.

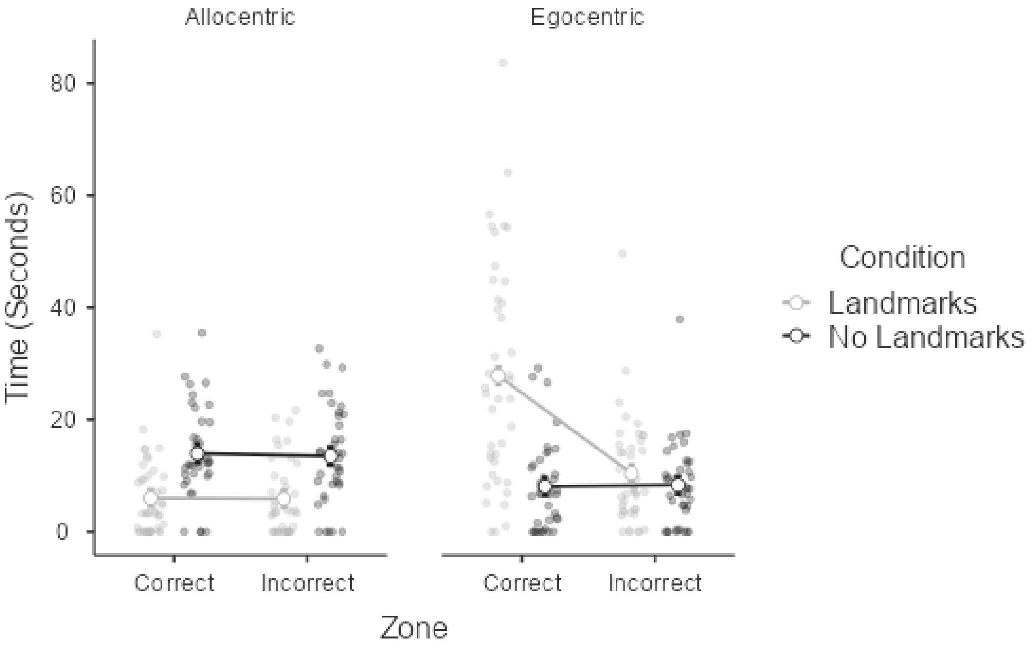
Post-hoc pairwise comparisons (Welch's) suggests learning across individual training trials, with the first trial being significantly faster than all other trials, *t*(78) = 10.42, $p < .001$. Similarly, trial 2 was faster than all subsequent trials, *t*(78) = 6.61, $p < .001$. No other comparisons were found to be significant. Please see section 5.2.3.3. for additional age by trial analysis.

5.2.3.2. *Test.*

Figure 44 displays estimated marginal means for time, in seconds, spent by each group in each external search zone. Participants in the no landmarks condition display a pattern of search behaviour consistent with experiment IIX. Specifically, participants spent more time in the allocentric search zones when compared to the egocentric. However, of crucial note, participants in the landmarks condition do not replicate this pattern of results. Instead, here, participants show clear preference for the egocentric correct zone above all else. Differences in time spent in each of the other three zones appears quite minimal.

Figure 44.

Experiment IX: Estimated mean time spent within each of the external search zones during the final test trial, split by condition.



Note. Error bars represent +/-1 standard error of the mean.

A 2(condition: landmarks or no landmarks) x 2(reference frame: allocentric or egocentric) x 2(zone: correct or incorrect) ANOVA reveals a non-significant main effect of condition, *F*(1,316) = 1.89, $p = .171$, $\eta^2_G = .004$, 95% CI[.00,.00], a significant main effect of reference frame, *F*(1,316) = 11.29, $p < .001$, $\eta^2_G < .025$, 95% CI[.01,.02], and significant main effect of zone, *F*(1,316) = 15.24, $p < .001$, $\eta^2_G < .033$, 95% CI[.02,.03]. All interactions involving these three main effects were also found to be significant; condition by reference frame, *F*(1,316) = 67.78, $p < .001$, $\eta^2_G < .149$, 95% CI[.09,.21]; condition by zone, *F*(1,316) = 14.52, $p < .001$, $\eta^2_G < .032$, 95% CI[.02,.03]; reference frame by zone, *F*(1,316) = 13.51, $p < .001$, $\eta^2_G < .029$, 95% CI[.02,.03]. Additionally, a three way interaction between these main effects was also found to be significant, *F*(1,316) = 15.67, $p < .001$, $\eta^2_G < .034$, 95% CI[.02,.03].

Post-hoc pairwise comparisons (Welch's) were conducted to further explore this significant 3-way interaction. Here, we can see that those in condition: no landmarks, at test, significantly preferred the allocentric zones, when compared to the egocentric, $t(316) = 3.38$, $p = .005$. However, no preference was shown for the allocentric correct zone over the allocentric incorrect, $t(316) =.196$, $p > .999$ – reproducing the pattern of results expressed by those in the previously reported experiment IIX (i.e. when trained in the absence of internal landmarks). For participants with locally matched internal and external landmarks, however, participants spent significantly more time in the egocentric zones when compared to the allocentric, $t(316) = -8.35$, $p < .001$. Further still, participants in this condition show a significantly increased amount of time specifically in the egocentric correct zone, when compared to the incorrect, $t(316) = 7.81$, $p < .001$; indeed, no significant difference was found for time spent within the other three zones within this condition, $t(316) = -1.97$, $p > .999$.

5.2.3.3. *Developmental trajectory Analysis.*

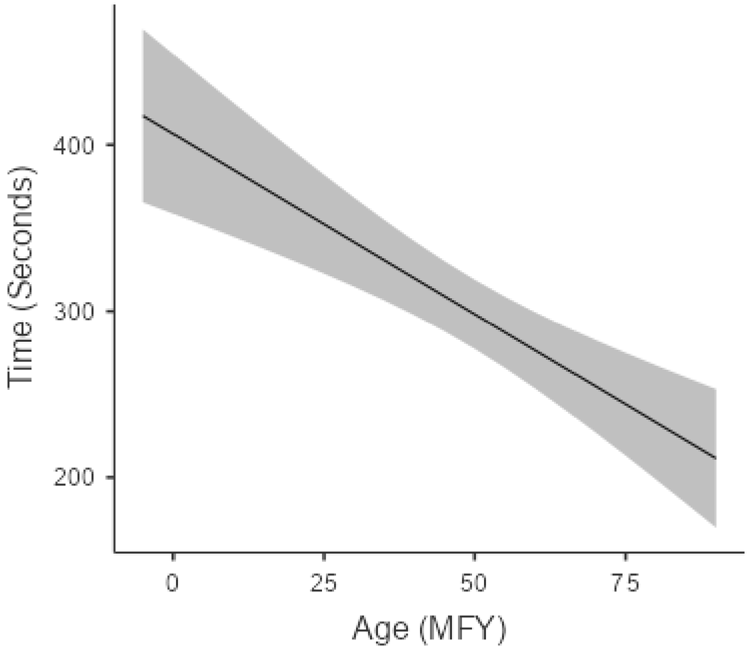
First, we use linear regression to assess the significant interaction of age and trial during internal training (A). Here, age is directly regressed with the total time for participants to complete the 8 internal training trials (collapsed). Following this, to assess whether age predicted test performance, individual ages were regressed onto time spent within each of the 4 external zones (B – E), with condition (landmarks vs. no landmarks) entered into the model as a factor. Following Thomas et al. (2009: see also Buckley et al., 2015), we rescaled the age predictor to reflect the months from the youngest age (MFY) tested within our sample. Rescaling ages in the manner does not alter the predictive ability of age, but does adjust the y-intercept of the regression model such that it occurs at the youngest age within our sample.

A) Training trials.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 1.92. *p* = .726, and collinearity statistics report acceptable tolerances, *tolerance* = .1, *VIF* = 1. Age is able to significantly predict time spent taken to complete the 8 internal training trials, *R* = .48, *Adjusted* R^2 = .23, *F(1,79)* = 24.03, *p* < .001; *b* = -.48, *t* = -4.91, suggesting older children were able to complete the internal training trials significantly faster, see figure 45.

Figure 45.

Experiment IX: Collapsed time taken to complete the 8 internal training trials, by age (months from youngest in sample).



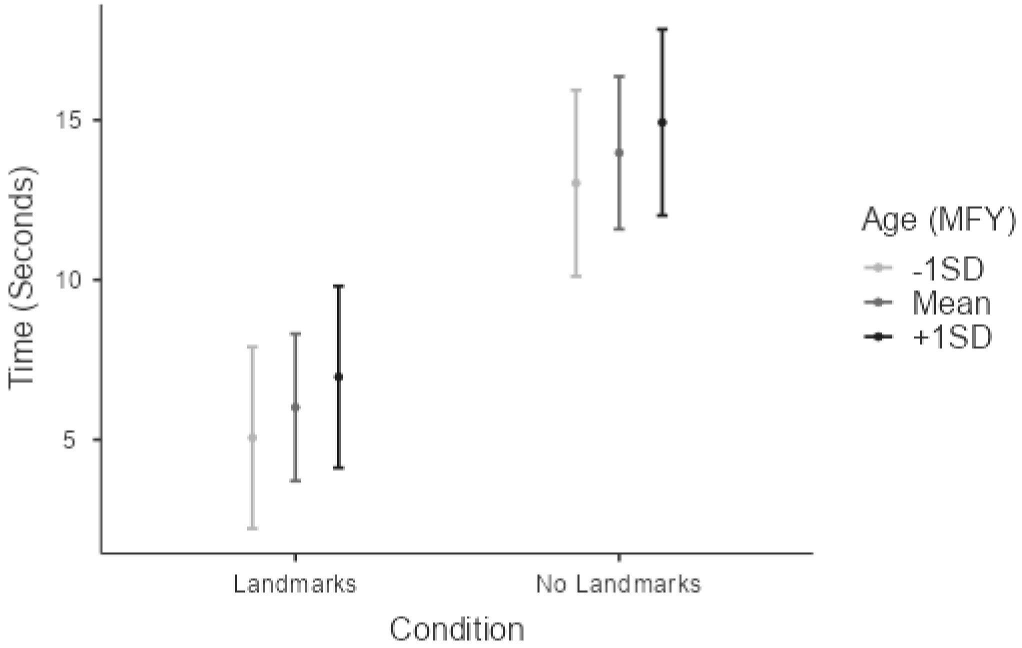
Note: Grey zone represents 95% confidence intervals around the regression slope.

B) Allocentric correct

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 2.14. *p* = .59, and collinearity statistics report acceptable tolerances for age, *tolerance* = 1, *VIF* = 1, and condition, *tolerance* = 1, *VIF* = 1. Here, overall model fit is significant, *R* = .48, *Adjusted R²* = .27, *F(2,78)* = 12.06, *p* < .001. However, condition is the only significant coefficient, *b* =7.96, *β* = .94, *t* = 4.78, *p< .001*. Age was not found to be a significant predictor, *b* =.04, *β* = .11, *t* = 1.13, *p = .26*, see figure 46.

Figure 46.

Experiment IX: Regression model for time spent within the allocentric correct zone, by age (months from youngest in sample) and condition.



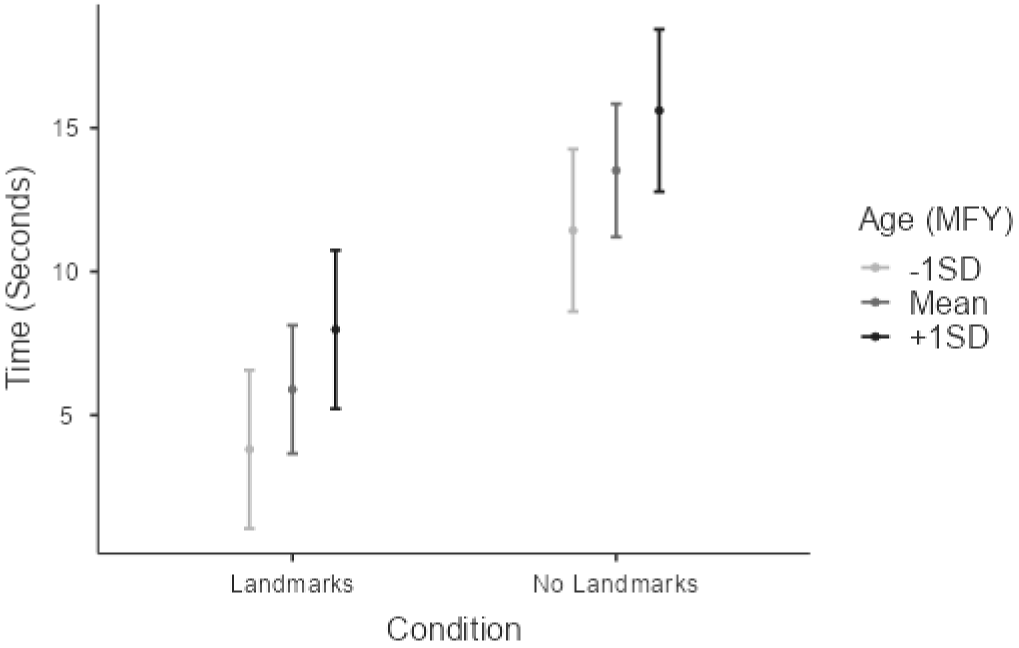
Note. Error bars represent 95% confidence intervals of the pooled model mean.

C) Allocentric incorrect.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 2.22. *p* = .34, and collinearity statistics report acceptable tolerances for age, *tolerance* = 1, *VIF* = 1, and condition, *tolerance* = 1, *VIF* = 1. Here, overall model fit is significant, *R* = .52, *Adjusted R²* = .25, *F(2,78)* = 14.42, *p* < .001. Both condition, *b* =7.96, *β* = .94, *t* = 4.78, *p< .001*, and age, *b* =.04, *β* = .11, *t* = 1.13, *p* = *.26*, were found to be significant predictors of time spent within this zone - see figure 47.

Figure 47.

Experiment IX: Regression model for time spent within the allocentric incorrect zone, by age (months from youngest in sample) and condition.



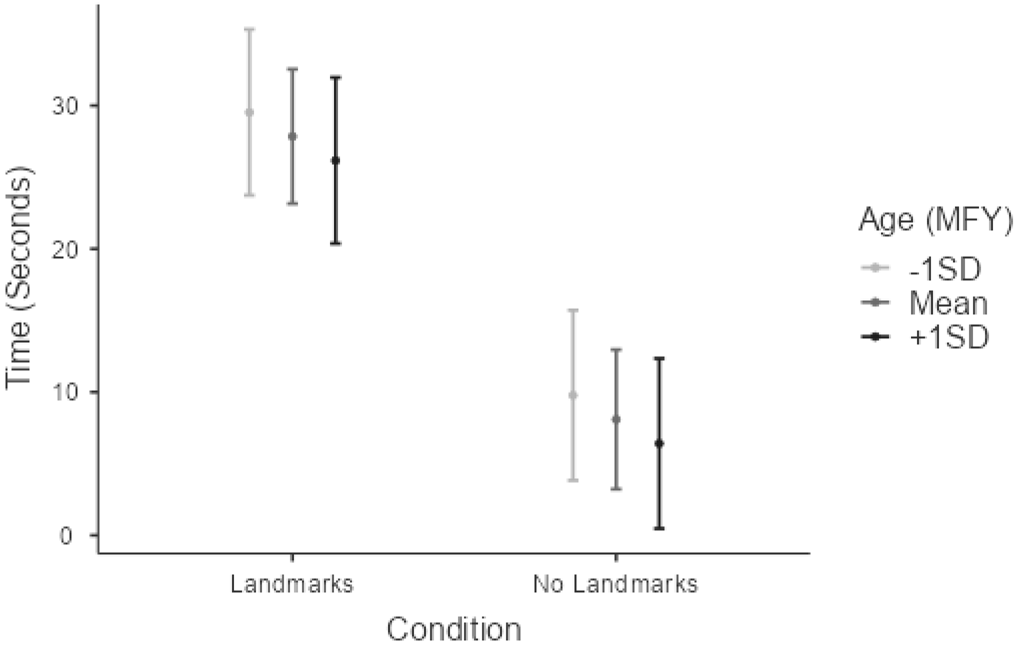
Note. Error bars represent 95% confidence intervals of the pooled model mean.

D) Egocentric correct.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 1.76. *p* = .24, and collinearity statistics report acceptable tolerances for age, *tolerance* = 1, *VIF* = 1, and condition, *tolerance* = 1, *VIF* = 1. Here, overall model fit is significant, *R* = .55, *Adjusted R²* = .29, *F(2,78)* = 17.40, *p* < .001. However, condition is the only significant coefficient, *b* =-.07, *β* = -1.08, *t* = -5.81, *p*< *.001*. Age was not found to be a significant predictor, *b* =-.07, *β* = -.09, *t* =-.98, *p* = *.32*, see figure 48.

Figure 48.

Experiment IX: Regression model for time spent within the egocentric correct zone, by age (months from youngest in sample) and condition.



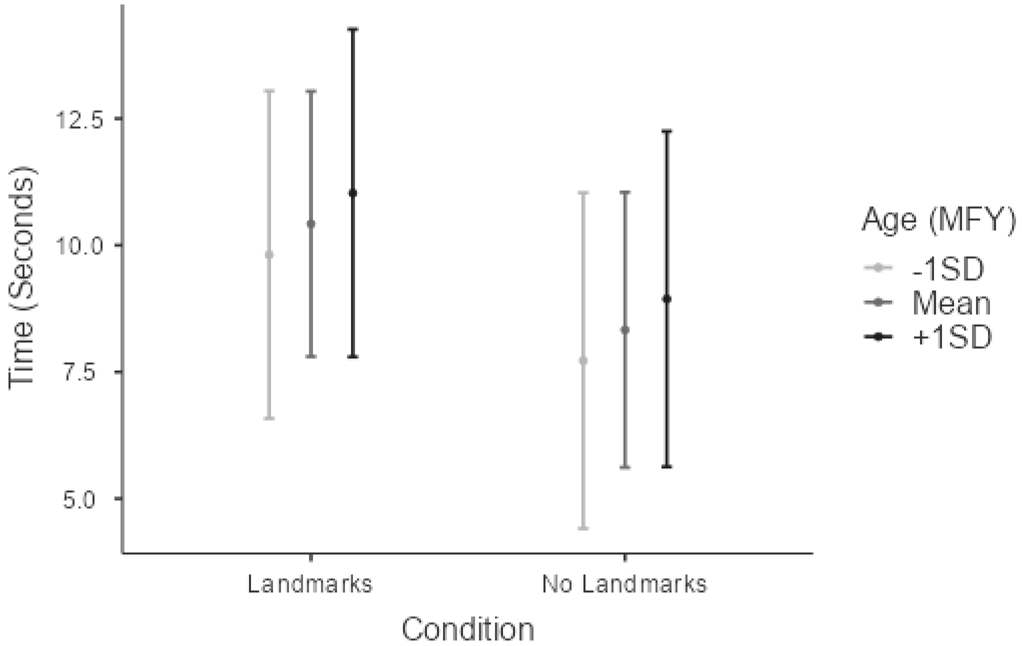
Note. Error bars represent 95% confidence intervals of the pooled model mean.

E) Egocentric incorrect.

Pre-analysis checks (Durbin-Watson) suggest no evidence of autocorrelation, *DW* = 1.73. *p* = .17, and collinearity statistics report acceptable tolerances for age, *tolerance* = 1, *VIF* = 1, and condition, *tolerance* = 1, *VIF* = 1. Here, overall model fit is not significant, *R* = .14, *Adjusted R²* = -.05, *F(2,78)* = .81, *p* = .448. Neither condition, *b* = -2.09, *β* = -.24, *t* = -1.11, *p* = *.273*, nor age was found to be a significant predictor for time spent within this zone, *b* =.02, *β* = .07, *t* = .63, *p* = *.529*, see figure 49.

Figure 49.

Experiment IX: Regression model for time spent within the egocentric incorrect zone, by age (months from youngest in sample). and condition.



Note. Error bars represent 95% confidence intervals of the pooled model mean.

5.2.3.4. *Shape Recognition Task.*

Table 2 displays the number of participants who chose each option for the post-navigation shape recognition task. Here, clear preference is shown for the correct shape choice, with over half of participants choosing this shape. Chi squared analysis suggests that all participants showed preference for the correct response (equal variance assumed; X^2 (3, N = 82) = 47.8, p < .001.), regardless of condition (X^2 (3, N = 82) = 2.01, p = .572).

Table 2: Shape choices made by participants during the post-test shape recognition task in experiment IX.

	Condition		
Shape Choice	**Landmarks**	**No Landmarks**	**Total**
1	10	8	18
2	4	1	5
3	6	7	13
4 (correct)	21	25	46
Total	41	41	82

Note. Option 4 denotes the correct choice. Shape choice order is consistent with the order presented in above Figure 40, however the presentation order was counterbalanced within this individual study.

5.2.4. Discussion.

During each training trial, participants in Experiment IX were required to a hidden goal location inside a cross shaped arena. Following this, participants faced a surprise final test trial on the outside of said arena in which there was no goal to find. Navigational behaviour on this final test trial was measured by their time spent in 4 external search zones.

Landmarks were present for all participants during internal training trials. However, during the final test trial participants were split into two experimental groups. For half of the participants, the landmarks were again present during this final trial at locations congruent with the internal features of geometry. For example, if the corner at which a long wall was on the left of a short wall was blue inside; it was blue outside (group landmarks). For these participants, allocentric and egocentric spatial reference frames may potentially be placed into conflict upon this final trial. The remaining participants faced a test trial identical to previous versions – i.e., no external panels, with a crème texture applied throughout (group: no landmarks).

An analysis of acquisition data suggests that during internal training, no differences were found between groups with regards to latency to find the hidden goal – as expected (as no manipulations had been made at this stage). Children were able to learn the goal location, resulting in a general decrease in trial completion latency as trials progressed. Regressing navigator age against the total time taken for participants to complete the training trials suggests that age is a reliable predictor, with the oldest children within our sample able to complete the trials almost twice as fast as the youngest. To save on undue repetition, comparisons with experiment IIX will be confined to the chapter discussion.

At test, a significant three-way interaction was found between condition, reference frame and zone. Participants in the no landmarks conditions were found to spend more time in the allocentric search zones, in keeping with results shown in Experiment IIX (see also: Buckley et al., 2016b, 2019), and the notion that boundary transfer procedures following a single test trial paradigm resiliently prompt reorientation with regard to allocentric spatial processing (see also: experiments I, II & III; Holden et al., 2021). Consistent with adult participants examined under similar experimental conditions (experiment IV), child participants in our no landmarks condition show no significant preference for the allocentric correct corner over the incorrect.

These findings perhaps further suggest that the inclusion of landmarks may interfere with or influence reorientation with reference to a *precise* allocentric reference frame (Buckley et al., 2014; see also: Herrera et al., 2022). Alternatively, it may be the case that children are less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007); Under such assumptions, it is possible that our younger participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal representation with the current, new, external (Nardini et al., 2008).

For those in condition: landmarks, the inclusion of landmarks during *both* internal acquisition and the final test trial further modified behaviour. Unlike all other previous boundary transfer experiments, participants in this group spent more time in the egocentric correct zone when compared to all other zones. This result suggests that the inclusion of salient landmarks during both internal training and external test trial can significantly modify behaviour following boundary transfer. Participants in this condition expressed behaviour consistent with egocentric spatial processing, by, it is assumed, associating the goal location with the salient local feature.

Generally speaking, results from other spatial navigation studies suggest the inclusion of landmarks at or near a hidden goal may block or overshadow spatial learning based upon the geometry of the arena (Buckley et al., 2014), a result which could be explained under traditional cue-competition paradigms (e.g., Rescorla & Wagner, 1972). Typically, such cue competition effects are expected to occur when stimuli are in competition with each other as signals for a specific outcome (e.g. an invisible connection area). However, it is possible that local features within the global environment serve as additional signposts *alongside the global geometry*, rather than as separate cues competing for association with an outcome (the connection area). Under these conditions, there is no theoretical reason to expect the shape of an arena to compete with landmarks for control over behaviour (but see Herrera et al., 2022).

With this in mind, it is interesting to note that when faced with the post-test shape recognition task, participants in both the landmarks and no landmarks condition were able to accurately identify the global structure of the arena. This suggests that although participants in the landmarks condition display reorientation behaviour in a manner that was consistent with egocentric spatial processing at test, elements of global shape were still encoded (Bast et al., 2009).

Further regression analysis suggests that condition (landmarks vs. no landmarks) is generally the largest predictor of zone choice at test. Inspections of figures 44 through 47 suggest a general trend of time spent within each external search zone, with older children typically spending more time in the allocentric zones, and less in the egocentric. Indeed, children again spend very little time in the egocentric search zones at test (roughly 10s), with only those in the landmarks condition spending significant time here (roughly 30s).

This general lack of time spent within egocentric search zones amongst our younger participants again suggests that the specific act of crossing an environmental boundary resiliently prompts allocentric-based navigation under traditional trial-test procedures (see also; Experiments I, II, III; Buckley et al., 2019). Our data suggests this preference in navigation strategy is unaffected by a potential developmental bias for navigation based upon an egocentric reference frame.

5.3. Chapter Discussion.

In experiments IIX & IX we again assess reorientation behaviour following a boundary transfer using a cross-shaped arena. As with many previously reported boundary transfer paradigms, participants are trained for multiple trials on one side of the test arena before a single test trial on the other (in extinction).

When tested under similar conditions, adult participants show resilient reorientation reliant on allocentric processing (Buckley et al., 2019; Holden et al., 2021; but see experiment IV). In experiment IIX, we adapt the Buckley et al., (2019; see also experiment I) procedure for use with child participants. Following this, in experiment IX we adapt the previously reported experiment IV procedure for use with child participants. Here, during all internal training trials, uniquely coloured panel landmarks are placed over the corners (matched upon lines of symmetry to allow for rotational errors in the cross-maze). Colours used were always blue and magenta, and landmarks were placed over both concave and convex corners (see above figure 39). For half of participants - condition: landmarks - landmarks were again present during the final external test trial at locations locally-consistent with their internal orientation. For example, if a concave corner with a short wall on the left and a long wall on the right was blue internally, it was blue externally. For the remainder of participants – condition: no landmarks – no landmarks were present for this final test trial (consistent with the previously reported experiment IIX).

Analysis of experiments IIX & IX acquisition data suggests that, over training, all children were able to learn the goal location as trials progressed. It should be noted that when trained in the absence of landmarks (experiment IIX), no significant age by trial interaction was found. However, for participants navigating towards a goal location signposted by local landmark (experiment IX; both conditions), a significant age by trial interaction was found, with regression analysis suggesting that older children are predicted to complete the internal training trials much faster than their younger counterparts. The underlying reason for this statistical discrepancy is currently unclear; It is possible that, in general, towards an explicitly landmark signposted goal is much easier than navigation with regards to boundary structure alone (as landmarks may prompt an egocentric beacon strategy (Bohbot et al., 2012; Learmonth et al., 2002; Lee, Shusterman, & Spelke, 2006). Consequently, for children in experiment IX, measurements of training trial time may be explained as a refined reflection of procedure interface capabilities (i.e., individual navigator abilities with regard to physically moving around the arena). With this in mind, for future experimentation we may wish to include measures of video game experience to our procedure – which we can add to any subsequent regression model. Experience here has previously been linked with better performance in tasks of virtual navigation (Murias et al., 2016; Van Mier & Jiao, 2020).

At test, child participants in experiment IIX show statistical preference for allocentric search zones (collapsed). Unlike adult participants (e.g. Buckley et al, 2019; Holden et al., 2021), children show no preference for the specific correct zone over the incorrect. One possible reason for this difference in navigational behaviour is that children are thought to be less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007). Under such assumptions, it is possible that our child participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal representation with the current, new, external (Nardini et al., 2008). Further regression analyses revealed that age was a significant predictor of the proportion of time spent searching in the allocentric zones, but not the egocentric zones at test. Here older children are predicted to spend significantly more time in the allocentric search zones. No preference was found for the egocentric search zones, with the majority of participants spending minimal time in these zones (<10s). These findings further bolster the notion that older children typically perform better in tasks of allocentric spatial processing (Bostelmann et al., 2020; Wills & Cacucci, 2014).

For participants in experiment IX, test behaviour varied by condition. Participants in the no landmarks condition were found to spend more time in the allocentric search zones at test, in keeping with the pattern of results displayed by participants in experiment IIX (see also: Buckley et al., 2016b, 2019), and the notion that boundary transfer procedures utilising single test trial paradigms resiliently prompt reorientation with regard to allocentric spatial processing (see also: experiments I, II & III; Holden et al., 2021). Consistent with adult participants examined under similar experimental conditions (experiment IV), child participants in our no landmarks condition show no significant preference for the allocentric correct corner over the incorrect.

These findings *perhaps* further suggest that the inclusion of landmarks may interfere with or influence reorientation with reference to a *precise* allocentric reference frame (Buckley et al., 2014; see also: Herrera et al., 2022). Alternatively, it may indeed be the case that children are less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007); under such assumptions, it is possible that our participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal goal representation with the current, new, external (Nardini et al., 2008).

For those in condition: landmarks, the inclusion of landmarks during *both* internal acquisition and the final test trial further modified behaviour. Unlike other previous boundary transfer experiments (e.g., experiments I:III; Buckley et al., 2019) participants in this group spent more time in the egocentric correct zone when compared to all other zones (see also: experiment IV). This result suggests that the inclusion of salient landmarks during both internal training and external test trial can significantly modify behaviour following boundary transfer. Participants in this condition expressed behaviour consistent with egocentric spatial processing, by, it is assumed, associating the goal location with the salient local feature.

Generally speaking, results from spatial navigation studies suggest the inclusion of landmarks at or near a hidden goal may block or overshadow spatial learning based upon the geometry of the arena (Buckley et al., 2014), a result which could be explained under traditional cue-competition paradigms (e.g., Rescorla & Wagner, 1972). Typically, such cue competition effects are expected to occur when stimuli are in competition with each other as signals for a specific outcome (e.g. an invisible connection area). However, it is possible that local features within the global environment serve as additional signposts *alongside the global geometry*, rather than as separate cues competing for association with an outcome (the connection area). Under these conditions, there is no theoretical reason to expect the shape of an arena to compete with landmarks for control over behaviour (but see Herrera et al., 2022).

With this in mind, it is interesting to note that when faced with the post-test shape recognition task, navigators in both conditions were able to accurately identify the global structure of the arena. This suggests that although participants in the landmarks condition display reorientation behaviour in a manner that was consistent with egocentric spatial processing at test, elements of global shape were still encoded (Bast et al., 2009).

Further regression analysis suggests that the inclusion of landmarks (condition: landmarks vs. no landmarks) is generally the largest predictor of zone choice at test. Inspections of figures 44 through 47 suggest a general trend of time spent within each external search zone, with older children typically predicted to spend more time in the allocentric zones, and less in the egocentric. Indeed, children again spend very little time in the egocentric search zones at test (roughly 10s), with only those in the landmarks condition spending significant time here (roughly 30s).

This general lack of time spent within egocentric search zones amongst our younger participants again suggests that the specific act of crossing an environmental boundary resiliently prompts allocentric-based navigation under traditional trial-test procedures (see also; Experiments I, II, III; Buckley et al., 2019). Our data suggests this preference in navigation strategy is unaffected by a potential developmental bias for navigation based upon an egocentric reference frame. Unlike adults, however, children show no specific preference for the correct allocentric zone over the incorrect – suggesting a comparatively imprecise allocentric representation of the global structure of their environment when compared to adults (Nazareth et al., 2018).

Chapter Six: General Discussion.

Across nine experiments we have explored properties of reorientation surrounding boundary transfer and shape transformation procedures. In Experiments I, II, III & IV (chapter three), human participants were required to locate a hidden goal that was always located adjacent to a right-angled corner within a cross-shaped virtual arena. Following this training, participants were faced with a surprise test trial on the outside of this arena and tasked with finding the area on the outside that best corresponded to the location of the internal goal location. This cross-shaped arena was used as it provides identical features of geometry, from a first-person perspective both internally and externally. Consequently, at test, participants may re-orient themselves and search for the goal with regard to either an allocentric reference frame, or individual egocentric features.

Experiment I replicated the boundary transfer experiment reported by Buckley et al., (2019) but with a minor modification to 8, rather than 16 training trials. Following a boundary transfer, participants again spent significantly more time in external search zones that suggest the use of an allocentric spatial reference frame for navigation. Subsequent studies in this chapter explored this effect by making procedural adaptations to increase the probability of using either a local, or egocentric frame of reference.

Experiment II tested the idea that restricting the number of routes taken by participants on each training trial would bias them into a more egocentric frame of reference – a bias that would be revealed at test by influencing how much time was spent at the allocentric and egocentric search zones. Unlike previous research (Experiment I, Buckley et al., 2019), participants during each training trial started at a single central start location – resulting in a navigation strategy that may be more akin to egocentric-route following as opposed to allocentric-wayfinding (Hartley et al., 2003).

Despite this manipulation, participants were found to spend significantly more time in the zone consistent with them having encoded an allocentric representation of their environment. Moreover, participants spent significantly more time in the correct allocentric zone, suggesting this representation is relative precise. No preference was shown for time spent in the egocentric-correct search zone over the incorrect, replicating the pattern of results reported by Buckley et al., (2019) and in Experiment I.

In Experiment III, we explored whether restricting the amount of training to either two, four or sixteen trials inside the arena would result in differences in the amount of exploration, at test, in the allocentric and egocentric search zones. In all conditions, participants rapidly learned to find the hidden goal. More importantly, at test, participants across all conditions preferred to search in the allocentric-correct zones over any other external search zones. This pattern of results is consistent with those reported by Buckley et al., (2019, 2016b) and suggests that participants had encoded an allocentric representation of their environment and subsequently used this as the basis of reorientation following a boundary transfer. More importantly, this allocentric frame of representation is, apparently, relatively resilient to variations in training that might be anticipated to undermine it; neither restricting the path from start location to goal (Experiment II) or restricting the amount of training (Experiment III) during initial training primed egocentric-based orientation following boundary transfer.

During Experiment IV, the final experiment of chapter three, multiple salient landmarks were introduced during internal trials for all participants at locations spatially congruent and incongruent with the invisible goal locations (i.e. directly next to them, and at adjacent corners; coloured panels). For half of the participants, these landmarks were again present during this final trial at locations that were congruent with the local geometry of the inside of the arena. Thus, for example, if a landmark was located at the convex corner which had a long wall to the left of a short wall then the landmark was located at an identical corner on the outside (group: landmarks). The remaining participants faced a test trial identical to Experiments I, II and III. It has been suggested that boundaries and geometric environmental information has a special status, in that its encoding does not follow general associative principles and is not susceptible to interference from local landmark information (Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990). Results from our Experiment IV conflict with these proposals. Participants in the "no landmarks" group were found to orientate with regards to the global structure in a manner consistent with previous experiments reported in chapter three (i.e., experiments I, II & III). Participants in group "local landmarks", however, were found to significantly prefer searching at the external areas congruent with their internal landmark location. Of note, when faced with a shape recognition task, all participants across both groups were able to correctly identify the global structure of the environment they had just been exposed to. This suggests that the inclusion of salient landmarks during internal training trials did not disrupt allocentric spatial information acquisition. Rather, it influenced the expression of behaviour specific to this task (see also: (Hayward et al., 2004; Herrera et al., 2022).

Combined, the results of chapter three support the idea of a dual-processing model of spatial encoding. That is to say, results support the notion that both an allocentric and egocentric reference frame are encoded for active navigation, and participants may choose to behave with regards to either, depending on the task at hand (Bodily et al., 2011; Dudchenko, 2010; Han & Becker, 2014;

Hartley et al., 2003; Iaria et al., 2003; Kelly & McNamara, 2010; Restle, 1957). With this in mind, these findings suggest that the act of crossing an environmental boundary encourages the use of an allocentric reference frame for orientation, and that its use is particular resistance to manipulations that may be expected to undermine it (see: Experiments II & III).

Additionally, participants in all experiments displayed 1-trial learning (as defined by Rock (1957); see also: Roediger & Arnold, 2012), suggesting that the formation of these spatial representations is relatively immediate – indeed just under 40% of participants in the 2-trial group of Experiment III spent less than 90s within the arena, and yet still this condition revealed a pattern of reorientation consistent with the acquisition of a cognitive map. When the data from the from the test trial of Experiment II were compared to the test data of Experiment 2 reported by Buckley et al., (2019), then there was some evidence that restricting the number of start locations attenuated the amount of time spent in the allocentric search zones. Interestingly, in this comparison, there was no specific effect on the allocentric-correct zone. That is to say, participants in the current Experiment II reduced the amount of time they spent in both the allocentric correct and incorrect zones. This raises the possibility that if there is an impoverishment in the representation of the allocentric shape of the environment then it is an impoverishment of a relatively imprecise representation – a “fuzzy” spatial map (Kosko, 1986).

However, all the experiments noted in this initial experimental chapter have adopted a procedure in which a goal is hidden in a consistent location in the same shaped environment over a series of trials, before a final test trial - in which the conditions of training are changed by placing participants into a new context. For example, at test participants may be placed in a novel-shaped environment, or instead onto the outside of the training arena for a single test trial - and the transfer of spatial behaviour is examined. However, an alternative method of assessing the transfer of spatial behaviour is possible, which removes the need for a final (and single) test trial and instead examines the rate at which the location of a goal is learned over successive trials.

In the following experimental chapter – chapter four - we utilise an intermixed-context procedure to explore navigation surrounding boundary transfer and shape transformation procedures. Traditional training-test procedures have revealed that many organisms can reorient on the basis of local-shape cues. (e.g. Pearce et al., 2004, Tommasi & Polli, 2004, Buckley et al., 2016b). This type of reorientation is widely considered to be egocentric in nature, as, crucially, allocentric spatial cues associated with the goal location during training are no longer present at test – such as global or Euclidian shape structure cues (Cheng & Newcombe, 2005; McGregor et al., 2006). For instance, following training to find a hidden goal in a rectangle-shaped arena where a short wall is to the left of a long wall, a test trial conducted in a kite-shaped arena will reveal a bias towards searching in the right-angled corner of the kite that shares the same local-shape cues that that were associated with the goal location in the rectangle (e.g. Pearce et al., 2004).

As this previous experimentation has consistently examined performance in a single test trial, and it remains to be determined if the egocentric representation of the goal location influences performance beyond a single instance of re-orientation. Here, in chapter 3; Experiments V & VI, participants swap between environments on a trial-to-trial basis for the entirety of the experiment (32 trials; 16 in each shape). Half of the participants had a local congruent goal location across both environments (i.e. *the goal is at the corner with a short wall on the left and a long wall on* *the right in both shaped environments*.), while the other half had an incongruent goal location (i.e. *short on the left, long on the right in one shape; short wall on the right and long wall on the left in the other).* Participants either completed this procedure immediately (Experiment V), or after 32 trials of pre-training in a consistent shape before the introduction of a new shape in the above-described manner (Experiment VI). In both procedures, no pre-warning of a new global context was provided, and participants were appropriately counterbalanced so that this new global context was either the kite or rectangle (within respective experiments and conditions).

As informed by previous shape transformation studies, we may expect that participants in the local congruent condition transfer learning more successfully from one global context to another (i.e. from the rectangle to the kite), when compared to those in the incongruent condition, resulting in a shorter latency to complete the procedure – a result not reflected in Experiment V. Here, participants in both conditions were able to complete the entire experiment with no statistical difference in observable performance. However, when this trial-by-trial methodology was preceded by extensive overtraining trials in a consistent shape - a form of navigation thought to prime egocentric reorientation (Bohbot et al., 2012; Cook & Kesner, 1988; Hartley et al., 2003; Morris et al., 1982; Packard & McGaugh, 1996) - participants in the local-congruent condition were able to complete the remainder of the experiment significantly faster than those in the incongruent condition (see Experiment VI).

These results again suggest lengthy or repetitive navigation in a consistent environment does support the use of more egocentric based spatial reorientation (see Bohbot et al., 2012 for a clear demonstration of this effect). Again, we see a shape transformation paradigm prompt orientation with regards to local shape cues, consistent with previous research measuring behaviour in a single test trial (e.g. Pearce et al., 2004, Buckley et al., 2016b). However, when subjected to a intermixed trial methodology, navigators only showed a statistically clear improvement in latency to find the goal when the introduction of the new, second shape was preceded by training in a consistent one (Experiment VI; condition: local congruent). Participants in Experiment V displayed similar behaviour throughout their experiment, with navigators in both conditions completing the experiment in similar amounts of time, suggesting a less efficient transfer of spatial information across the intermixed global contexts.

In the final experiment reported in chapter four, we again use this intermixed trial methodology to explore reorientation beyond a single test trial. However, instead of applying it to aforementioned shape-transformation paradigms – traditionally thought to prompt egocentric based navigation, we have applied it to a boundary transfer procedure (Buckley et al., 2019). Such boundary transfer procedures, in the absence of landmarks, are typically thought to resiliently prompt reorientation with regards to an allocentric reference frame (Buckley et al., 2019, Holden et al., 2020, see also: Experiments I, II & III).

Due to the more complicated nature of the arena used (cross maze; see previous figures), participants in Experiment VII were split into four separate groups; For those in the local congruent condition, the goal location for both internal and external trials was at the location which consistently and exactly matched local features of environmental geometry (for example *the goal is at the corner with a short wall on the left and a long wall on the right both inside and outside*); for those in the global congruent condition, the external goal location was at the corner nearest to the internal goal location (i.e. *the other side of the corner which represented the* *internal goal). Additionally,* two incongruent conditions were constructed; For those in the (incongruent) angle congruent condition, the external goal location was both incongruent with regards to either egocentric or the allocentric spatial reference frame and at an opposite-angled corner (i.e. if the internal goal was at concave corner with a short wall on the left and a long on the right, the external goal location was a convex corner with a short wall on the right and a long wall on the left. Similarly, those in the (incongruent) angle congruent corner had a consist corner type both inside and outside (e.g., if the internal goal location was found at a concave corner with a short wall on the left and a long wall on the right, the external goal location was found at a concave corner with a short wall on the right and a long wall on the).

As informed by previous boundary transfer studies, we may expect that participants in the global congruent condition transfer learning more successfully from one context to another (i.e. inside to outside), when compared to those in the local congruent or incongruent conditions, resulting in a shorter latency to complete the procedure – a result not reflected in the above Experiment VII. Here, all participants in all conditions were able to complete the entire experiment with no statistical difference in observable performance between conditions.

One thing we may have to consider is that participants did not see the intermixed trial-by-trial contexts as connected when not preceded by training in a consistent shape. Consequently, for participants in Experiments V & VI, we cannot be sure of reference frame use within any specific context; participants may be using an egocentric method for one context (e.g., inside), and an allocentric method for the other (e.g., outside) – regardless of condition or experiment. It is currently unclear how to discern reorientation strategy under such experimental conditions from observable behaviour alone. One possible way to infer reference-frame use would be to observe neurological markers at probe points throughout the procedure (in a similar manner to Bohbot et al., 2012), with specific observation of caudate and hippocampal sub-regions – both associated with egocentric and allocentric-based processing, respectively (Bohbot, et al., 2007; Guderian et al., 2015; Hartley et al., 2003; Iaria et al., 2003; Konishi et al., 2017; Packard & McGaugh, 1996; White & McDonald, 2002, Dudchenko, 2010).

Combined, however, results across chapter four suggest that reorientation strategies typically observed in a single test trial following training; such egocentric based reorientation following a shape transformation, or allocentric based reorientation following a boundary transfer, may again be task or experimental parameter dependant (see also; Experiment IV). When such paradigms are run utilising an intermixed trial-by-trial methodology, no observable difference in reorientation behaviour was found without the inclusion of pre-training in a consistent shape (Experiment VI). It is currently unclear how introducing pre-training trials in a consistent context to Experiment VII will affect behaviour upon the introduction of the other (i.e. training inside before the outside is introduced on a trial by trial basis). Here, participants in both contexts have equal access to local and global cues (e.g., inside and outside); while pre-training in such as manner is thought to prompt reorientation with regards to local cues (e.g. Pearce et al., 2004), engaging in a boundary transfer is typically thought to prompt reorientation with regards to global shape cues (e.g. Buckley et al., 2019, but see Experiment IV & VII). Consequently, it is currently unclear how navigators may behave under such conditions.

In the final experimental chapter reported in this thesis we explore task parameter dependants beyond the range of cues available to navigators and environmental exposure styles. Additional key factors thought to have an impact over navigational performance are the interpersonal details related to the navigator themselves. Of note: the navigators age (for reviews, see Bohbot et al., 2012; Konishi, Mckenzie, Etchamendy, Roy, & Bohbot, 2017; Lester et al., 2017; Wills & Cacucci, 2014; Newcombe, 2019; León, Tascón, & Cimadevilla, 2016). Broadly, this literature suggests that younger children and older adults have a bias towards navigational strategies thought to be more reliant on egocentric spatial processing.

In chapter five, experiments IIX & IX, we again assess reorientation behaviour following a boundary transfer using a cross-shaped arena. As with many previously reported boundary transfer paradigms, participants are trained for multiple trials on one side of the test arena before a single test trial on the other (in extinction). As noted above, when tested under similar conditions adult participants show resilient reorientation reliant on allocentric processing (Buckley et al., 2019; Holden et al., 2021; but see experiment IV). In experiment IIX, we adapt the Buckley et al., (2019; see also experiment I) procedure for use with child participants. Following this, in experiment IX we adapt the previously reported experiment IV procedure for use with child participants. Here, during all internal training trials, uniquely coloured panel landmarks are placed over the corners (matched upon lines of symmetry to allow for rotational errors in the cross-maze). Colours used were always blue and magenta, and landmarks were again placed over both concave and convex corners. For half of participants - condition: landmarks - landmarks were present during the final external test trial at locations locally-consistent with their internal orientation. For example, if a concave corner with a short wall on the left and a long wall on the right was blue internally, it was blue externally. For the remainder of participants – condition: no landmarks – no landmarks were present for this final test trial (consistent with the previously reported experiment IIX).

Analysis of experiments IIX & IX acquisition data suggests that, over training, all children were able to learn the goal location as trials progressed. It should be noted that when trained in the absence of landmarks (experiment IIX), no significant age by trial interaction was found. However, for participants navigating towards a goal location signposted by local landmark (experiment IX; both conditions), a significant age by trial interaction was found, with regression analysis suggesting that older children are predicted to complete the internal training trials much faster than their younger counterparts. The underlying reason for this statistical discrepancy is currently unclear; It is possible that, in general, towards an explicitly landmark signposted goal is much easier than navigation with regards to boundary structure alone (as landmarks may prompt an egocentric beacon strategy (Bohbot et al., 2012; Learmonth et al., 2002; Lee, Shusterman, & Spelke, 2006). Consequently, for children in experiment IX, measurements of training trial time may be explained as a refined reflection of procedure interface capabilities (i.e., individual navigator abilities with regard to physically moving around the arena). With this in mind, for future experimentation we may wish to include measures of video game experience to our procedure – which we can add to any subsequent regression model. Experience here has previously been linked with better performance in tasks of virtual navigation (Murias et al., 2016; Van Mier & Jiao, 2020).

At test, child participants in experiment IIX show statistical preference for allocentric search zones (collapsed). Unlike adult participants (e.g., Buckley et al, 2019; Holden et al., 2021), children show no preference for the specific correct zone over the incorrect.

One possible reason for this difference in navigational behaviour is that children are thought to be less capable of creating precise and interconnected cognitive maps (Lourenco & Huttenlocher, 2007). Under such assumptions, it is possible that our child participants could not differentiate between correct and incorrect zones at test, as, following boundary transfer, they were unable to integrate the previously encoded internal representation with the current, new, external (Nardini et al., 2008). Further regression analyses revealed that age was a significant predictor of the proportion of time spent searching in the allocentric zones, but not the egocentric zones at test. Here older children are predicted to spend significantly more time in the allocentric search zones. No preference was found for the egocentric search zones, with the majority of participants spending minimal time in these zones (<10s). These findings further bolster the notion that older children typically perform better in tasks of allocentric spatial processing (Bostelmann et al., 2020; Wills & Cacucci, 2014).

For participants in experiment IX, test behaviour varied by condition. Participants in the no landmarks condition were found to spend more time in the allocentric search zones at test, in keeping with the pattern of results displayed by participants in experiment IIX (see also: Buckley et al., 2016b, 2019), and the notion that boundary transfer procedures utilising single test trial paradigms resiliently prompt reorientation with regard to allocentric spatial processing (see also: experiments I, II & III; Holden et al., 2021). Consistent with adult participants examined under similar experimental conditions (experiment IV), child participants in our no landmarks condition show no significant preference for the allocentric correct corner over the incorrect.

These findings *perhaps* again further suggest that the inclusion of landmarks may interfere with or influence reorientation with reference to a *precise* allocentric reference frame (Buckley et al., 2014; see also: Herrera et al., 2022). Alternatively, it may indeed be the case that children are less capable of creating precise and interconnected cognitive maps, as outlined above (Lourenco & Huttenlocher, 2007). For those in condition: landmarks, the inclusion of landmarks during *both* internal acquisition and the final test trial further modified behaviour. Unlike other previous boundary transfer experiments (e.g., experiments I:III; Buckley et al., 2019) participants in this group spent more time in the egocentric correct zone when compared to all other zones (see also: experiment IV). This result suggests that the inclusion of salient landmarks during both internal training and external test trial can significantly modify behaviour following boundary transfer. Participants in this condition expressed behaviour consistent with egocentric spatial processing, by, it is assumed, associating the goal location with the salient local feature.

Generally speaking, results from spatial navigation studies suggest the inclusion of landmarks at or near a hidden goal may block or overshadow spatial learning based upon the geometry of the arena (Buckley et al., 2014), a result which could be explained under traditional cue-competition paradigms (e.g., Rescorla & Wagner, 1972). Typically, such cue competition effects are expected to occur when stimuli are in competition with each other as signals for a specific outcome (e.g., an invisible connection area). However, it is possible that local features within the global environment serve as additional signposts *alongside the global geometry*, rather than as separate cues competing for association with an outcome (the connection area). Under these conditions, there is no theoretical reason to expect the shape of an arena to compete with landmarks for control over behaviour (but see Herrera et al., 2022). With this in mind, it is interesting to note that when faced with the post-test shape recognition task, navigators in both conditions were able to accurately identify the global structure of the arena. This suggests that although participants in the landmarks condition display reorientation behaviour in a manner that was consistent with egocentric spatial processing at test, elements of global shape were still encoded (Bast et al., 2009).

Further regression analysis suggests that the inclusion of landmarks (condition: landmarks vs. no landmarks) is generally the largest predictor of zone choice at test. Inspections of figures 44 through 47 suggest a general trend of time spent within each external search zone, with older children typically predicted to spend more time in the allocentric zones, and less in the egocentric. Indeed, children again spend very little time in the egocentric search zones at test (roughly 10s), with only those in the landmarks condition spending significant time here (roughly 30s).

This general lack of time spent within egocentric search zones amongst our younger participants again suggests that the specific act of crossing an environmental boundary resiliently prompts allocentric-based navigation under traditional trial-test procedures (see also; Experiments I, II, III; Buckley et al., 2019). Our data suggests this preference in navigation strategy is unaffected by a potential developmental bias for navigation based upon an egocentric reference frame. Unlike adults, however, children show no specific preference for the correct allocentric zone over the incorrect – suggesting a comparatively imprecise allocentric representation of the global structure of their environment when compared to adults (Nazareth et al., 2018).

6.1. Directions for Future Research.

6.1.1. Exploring the Navigator.

As noted multiple times above, when it comes to identifying the personal factors associated with individual navigator performance our procedures could be more robust. Additionally, by capturing additional participant data – beyond age - we may explore further factors which may predict or influence navigator behaviour. For example, with child participants specifically, we may wish to include measures of video game experience, mental rotation, and mathematical abilities to our procedures. Here, meta-analysis suggests that higher ability within each of these domains is individually and positively correlated with improved performance in tasks spatial cognition (Mix et al., 2016; Tosto et al., 2014; Van Mier & Jiao, 2020; Young, Levine, & Mix, 2018). By including measures of these variables, we may produce developmental trajectory analysis which capture more variance within our datasets.

Speaking more broadly, we may wish to include measures of stress, anxiety and depression to our procedures. Here, literature provides very mixed results; for example, many articles suggest acute stress prompts allocentric spatial strategies (e.g., Chan et al., 2016), while others suggest the opposite (e.g., Brown et al., 2020). Articles such as Thomas et al., (2010) suggest that stress specifically impairs allocentric spatial abilities in females, whereas Duncko et al., (2007) conclude that spatial ability is enhanced in males when under stress. Further still, research from van Gerven et al., (2016) concludes that stress levels had no impact on navigational performance, and that gender was not a modulating factor (see also: Guenzel, Wolf, & Schwabe, 2014). With this in mind, we may wish to integrate standardised questionnaires such as the State Trait Inventory for Cognitive and Somatic Anxiety for adults (STISCA; see Julian, 2011 for review), and measures such as the Spence

Children's Anxiety Scale (CAS; Chorpita, Yim, Moffitt, Umemoto, & Francis, 2000) or Trier Social Stress Task (TSST; Kudielka, Hellhammer, & Kirschbaum, 2007) for children in attempt to cast further light on these mixed findings.

Further still, with adult participants we may wish to capture data regarding how much time they spend driving (associated with improved navigation performance (Weisberg, Newcombe, & Chatterjee, 2019)), or spend using Global Positioning Systems (GPS; associated with poorer navigational performance (Gramann, Hoepner, & Karrer-Gauss, 2017)). Additionally, a recent article by Coutrot et al., (2022; reviewed by Warren, 2022) found that the type of hometown an individual lived in whilst growing up has significant predictive value when regressed against spatial cognition ability in multiple domains. Here, people from more rural areas are thought to be superior at tasks of allocentric spatial processing when compared to those from suburban regions. With this in mind, we may wish to enquire about this information within our procedures.

Standardised self-report measures such as the Santa Barabara Sense of Direction Scale (SBSODS; Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002) may also provide further insight into navigational behaviour. For example, research has found that self-report sense of direction positively correlates with improved ability for following directions (Hund & Padgitt, 2010), managing orientation precision in complex environments (Sholl & DellaPorta, 2006; Burte & Hegarty, 2012), and, most notably, accuracy of finding locations (Takeuchi, 1992). However caution must be taken when utilizing such self-report methods; recent publication by Weisberg et al., (2014) conclude that self-report measures do not predict navigation ability. Further research in this area, such as Thorndyke & Goldin (1983), and Kato & Takeuchi (2003) has drawn similar conclusions, reporting that questionnaires regarding sense of direction do not differentiate between good and poor cognitive mapping ability effectively.

With regard to participant choice, we may wish to explore reorientation behaviour using the cross maze and older adults. Older age is also thought to drastically influence spatial processing ability, and an age-linked decline in spatial navigation is a well-known cognitive issue (see Lester et al., 2017 for review). Indeed, senescence based deficits in spatial learning & memory evident in a number of mammalian species (Barnes, McNaughton, & O'Keefe, 1983; Ingram, 1988; León, Tascón, & Cimadevilla, 2016; Moffat et al., 2002). Specifically, this deficit seems to be focused upon allocentric-based navigation capabilities and has been demonstrated in both real world and virtual settings (Gazova et al., 2013; Moffat et al., 2002; Morris, 1984; Newman & Kaszniak, 2000; Rodgers et al., 2012).

Multiple reasons have been proposed to explain this spatial deficit, including typical age related neural atrophy (Moffat, Elkins, & Resnick, 2006), and a general behavioural preference for egocentric strategies (Veronique D. Bohbot et al., 2012). It has been suggested that this shift towards egocentric strategies may be a compensatory mechanism to allow for more efficient navigation in later years (Etchamendy, Konishi, Pike, Marighetto, & Bohbot, 2012). Alternatively, some have suggested it to be the consequence of an overall increased use of response strategies in older adults (Balram et al., 2010), as the automation of such processing has been found to improve performance during some navigational tasks (e.g. Iaria et al., 2003).

To the best of our knowledge, there is currently no literature specifically looking at the use of environmental features of geometry in older human adults (in which geometry alone signifies goal locations). As this sub-section of the population is known to exhibit deficits in allocentric-based navigation, it is currently unknown how they will perform at test in our cross-shaped arena when compared to younger adults and young children.

6.1.2. Exploring Spatial Cues and Exposure.

Beyond self-report methods associated with individual navigator factors and covariates, I believe further investigation into cue competition is warranted. For example, further investigation into the effect of landmark *type* within blocking and overshadowing procedures, and further investigation into the specific strategy use of landmarks by navigators during reorientation procedures.

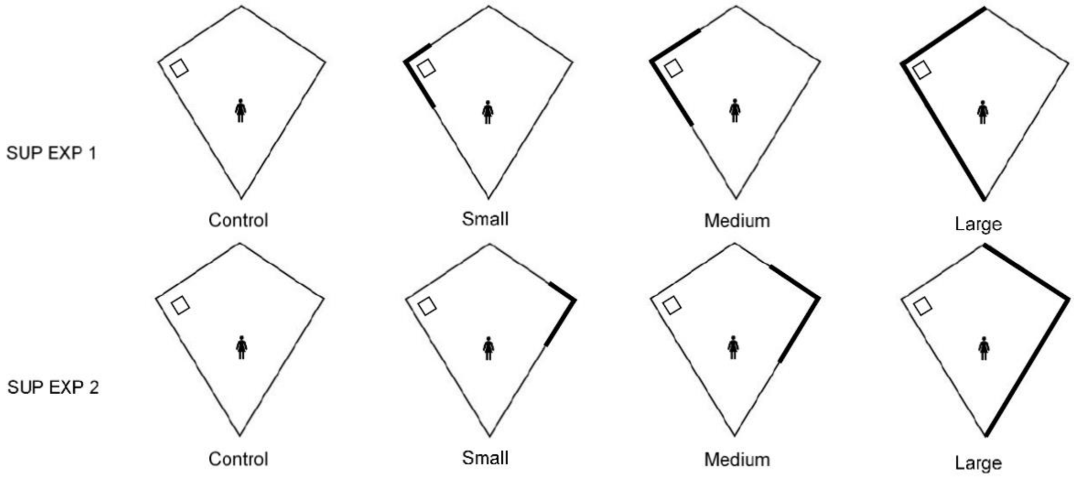
Broadly speaking, the observed use of landmarks (either integrated, proximal or distal) for reorientation is often aligned with egocentric strategies within the spatial cognition field. However, caution is stressed when directly correlating the use of landmark cues with either egocentric or allocentric based navigation (respectively). For example, in Buckley et al., (2015) Experiment 1, participants in both the intramaze and extramaze landmark groups are able to complete the navigational task with regards to either their allocentric or egocentric reference frame. Those in the intramaze group may encoded the goal location allocentrically (using the landmark-boarder relationship), and those in the extramaze group may have used an egocentric beacon or view-match strategy to locate the hidden goal (Bohbot et al., 2012; Sturzl & Zeil, 2007). Currently, it seems unclear for how to procedurally assess landmark use from behaviour alone; probe questions similar to that of Iaria et al., (2003) could be directly introduced to procedures. Here, if a participant directly describes using a sole landmark or local geometric feature to reorientate, it could defined as non-spatial use (egocentric), and if a participant mentioned the use the overall environmental boundaries, or the use of *at least two* landmarks or local features they could be categorised as spatial (allocentric).

Similarly, the types of landmarks used within procedures may provide different results (boundary-integrated, proximal or distal). For example, literature suggest that the encoding of boundary-integrated landmarks may differ to that of isolated landmarks (either intra or extra-maze; Horner, Bisby, Wang, Bogus, & Burgess, 2016; Lee, 2017). With single-cell literature suggesting that boundary-integrated landmarks may serve as a "true" barrier to movement, and, consequently, may provide different relative salience compared to isolated landmarks (Barry et al., 2006; Kosaki, Austen, & McGregor, 2013).

With this in mind, a replication of the Herrera et al., (2022) study with different landmark-type conditions may prove insightful. Here, adult human participants were trained within a kite (with landmarks), before being tested in a kite. During training, coloured panel landmarks were introduced, varying in size and proximity to the goal location (see figure 50).

Figure 50.

The arenas used by Herrera et al, (2022; supplementary experiments 1 & 2).



Note. Figure adapted from Herrera et al., (2022). Bold walls represent the landmark location and length (small, medium or large), whereas the square represents the goal location.

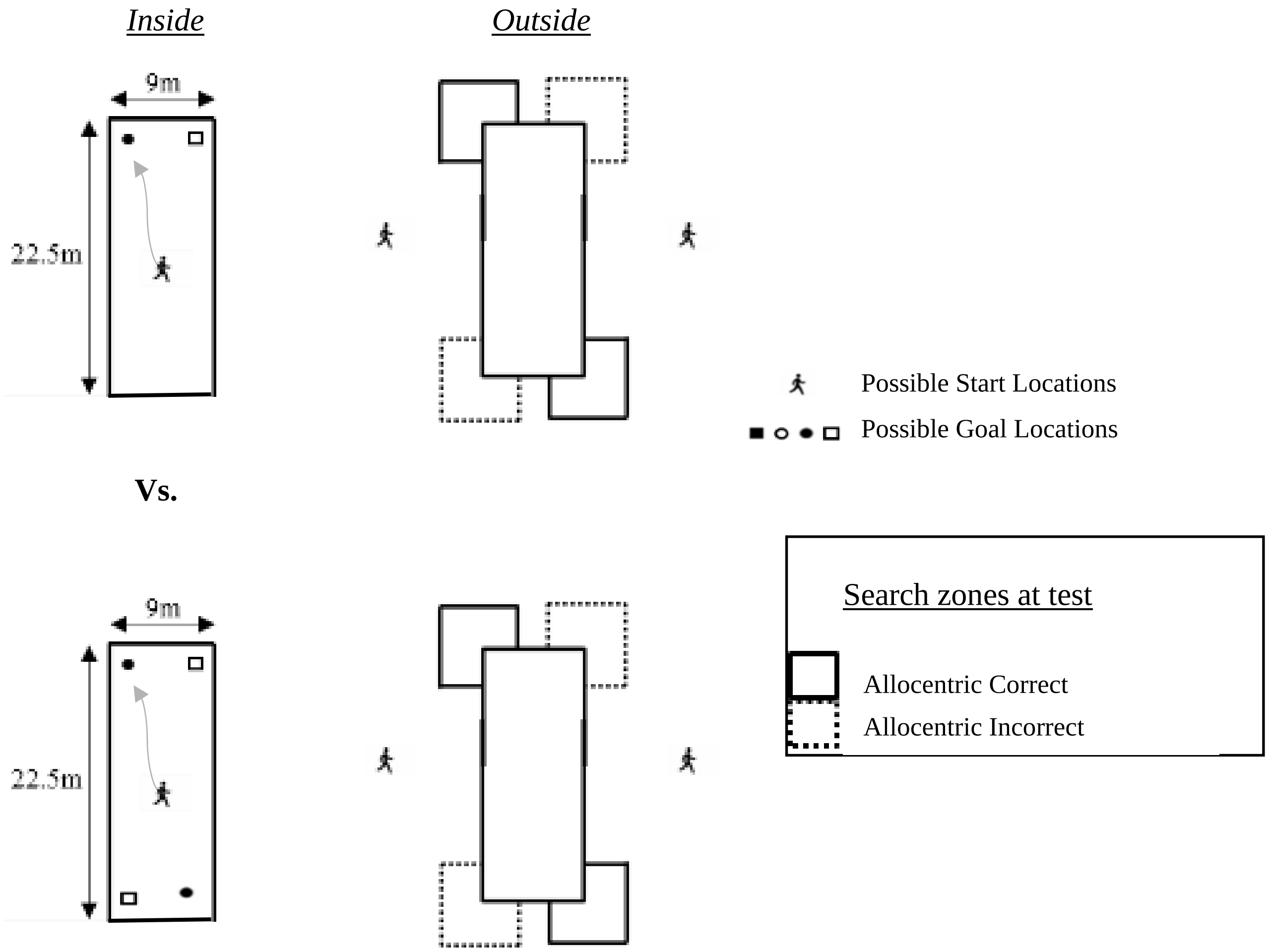
It is currently unclear if the overshadowing effect reported by Herrera and colleagues at test would be replicated were the integrated landmarks replaced with isolated intra-maze or extra-maze cues (of varying sizes).

Finally, it cannot go without mention that in the majority of shape transformation or boundary transfer procedures reported within this thesis, participants are required to navigate around relatively small and simple structures under fully reinforced conditions (e.g., kite, rectangle & cross-maze with multiple goals along symmetry lines). Initial exploration of spatial reinforcement literature suggests that levels of reinforcement may vastly affect acquisition and subsequent reorientation behaviour – however results must be interpreted with caution. For example, Gonzalez, Kolb, & Whishaw, (2000) performed a standard Morris water maze task where rats were trained to locate a hidden escape platform over multiple trials. Of key note, this platform was present on either 100%, 75% or only 50% of trials, depending on condition. Rodents in this final group failed to display learning, with greater levels of learning found in higher reinforcement conditions. However these results were not replicated when the procedure was conducted on dry land; here, the 50% condition performed slightly higher than the 100% condition – a result consistent with non-spatial reinforcement literature (e.g., skinner box; Cole & Van Fleet, 1976).

With this in mind, it is currently unclear how adult participants would compare under partially reinforced spatial acquisition conditions. This may be procedurally explored by a reduction of goal locations for some participants during internal training (see figure 51). Alternatively, internal extinction trials could be introduced, in which there is no goal to find. These could be coded to end after a certain amount of time had elapsed; following training, performance in a single external test trial would be compared.

Figure 51.

Plan view of proposed reinforcement study.

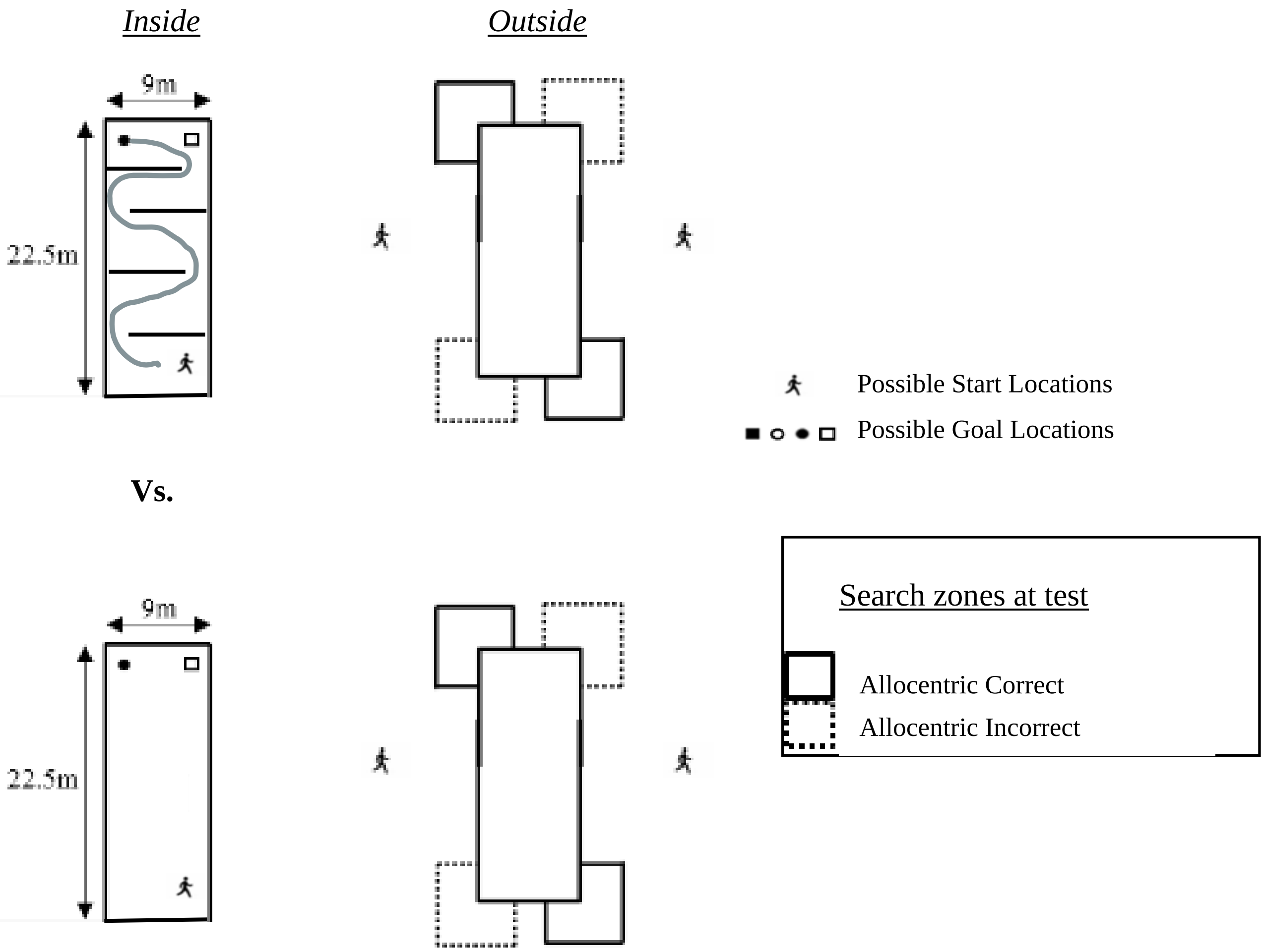


Note. The schematic view of a rectangle arena. This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. Top represents a partially reinforced condition, in which goal locations are not reflected upon lines of arena symmetry. External search zones are consistent with this training, as are all goal locations (counterbalanced within studies). The geometry of this structure is identical to those used in Buckley et al., 2016a, 2016b.

In a similar manner, the complexity of an environment is thought to vastly affect spatial acquisition and navigational ability (see Maguire et al., 1999 for review). Here, more complex environments are thought to prompt less precise navigational performance and acquisition. With this in mind, the introduction of internal walls in a manner consistent with figure 52 may produce marked differences in spatial reorientation at test. Here, at test, we may expect those in the walled condition to spend significantly less time in the allocentric correct zone when compared to their non-walled counterparts.

Figure 52.

Plan view of proposed environmental complexity study.



Note. The schematic view of a rectangle arena. This includes an example training trial (grey arrow) in which the goal was located at a concave corner where a long wall was to the left of a short wall. Top represents a more environmentally complex condition, in which internal walls divide the space.

External search zones are consistent with this training, as are all goal locations (counterbalanced within studies). The geometry of this structure is identical to those used in Buckley et al., 2016a, 2016b.

6.2. General Conclusions.

To conclude, recent cue competition literature, such as Buckley, Smith & Haselgrove (2016a), and Herrera et al., (2022), have challenged the notion that learning about the geometric properties of an environment is processed in an encapsulated module. Here, the encoding of spatial features, such as arena boundaries, is thought to be prevented from interaction with non-spatial cues (e.g., landmarks), and therefore immune to standard overshadowing and blocking effects (Gallistel, 1990). Work presented in this thesis aimed to further explore the malleability of this idea by exploring properties of reorientation – sometimes in the presence of landmarks (see experiments IV & IX).

Similarly, this thesis aimed to build upon the work of Buckley et al., (2016b), which broadly suggests that reorientation behaviour is based upon allocentric or global spatial processing following an arena boundary transfer; however, as alluded to above, many results within the spatial cognition field may indeed be task or procedure specific. Here, we further test this idea by assessing navigational behaviour following boundary transfers under procedural conditions in which no reorientation methods are precluded (experiments I, II, III, VII, IIX & IX; see also: Buckley et al., 2019).

Results reported within provide further evidence that under typical training-to-test paradigms, reorientation behaviour following a boundary transfer is indeed resiliently reliant on allocentric or global processing (experiments I:III). This effect can be broken thought the inclusion of landmarks (internal and external: see experiments IV & IX), however, of crucial note, navigators within these experiments were able to accurately identify the global structure of their environment when faced with a post-test shape recognition task. Further results suggest this resilient effect may be specific to typical training-to-test paradigms; when faced with intermixed internal and external trials in the same arena, navigators show no preference for reorientation based upon any spatial reference frame (see chapter IV).

In the final experimental chapter reported in this thesis, we explore a potential developmental trajectory of this resilient effect through the use of child participants (see chapter V). Here, navigators again typically navigate with regard to global shape structure when faced with training-to-test boundary transfer procedures. Unlike adult participants, however, children's reorientation behaviour is less precise, potentially highlighting impaired or underdeveloped allocentric spatial processing abilities.

References.

Amrhein, V., Greenland, S., Mcshane, B., Wasserstein, R. L., Schirm, A. L., & Lazar, N. A. (2019). Moving to a World Beyond " *p* < 0.05." *The American Statistician*.

Andersen, P., Morris, R., Amaral, D., Bliss, T., & O' Keefe, J. (2009). *The hippocampus book*. Oxford University Press, USA. https://doi.org/10.1093/acprof:oso/9780195100273.001.0001

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. https://doi.org/10.3758/BRM.40.1.353

Barnes, C. A., McNaughton, B. L., & O'Keefe, J. (1983). Loss of place specificity in hippocampal complex spike cells of senescent rat. *Neurobiology of Aging*. https://doi.org/10.1016/0197-4580(83)90034-9

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., & Keefe, J. O. (2006). The Boundary Vector Cell Model of Place Cell Firing and Spatial Memory, *I*(1), 71–98.

Bast, T., Wilson, L. A., Witter, M. P., & Morris, R. G. M. (2009). From rapid place learning to behavioral performance: A key role for the intermediate hippocampus. *PLoS Biology*. https://doi.org/10.1371/journal.pbio.1000089

Bertin, R. J. V, Graf, W., Guillot, A., Collet, C., Vienne, F., & Espié, S. (2005). Objective measurement and the role of visual-vestibular conflict situations. In *DSC 2005*.

Biocca, F. (1992). Will Simulation Sickness Slow Down the Diffusion of Virtual Environment Technology? *Presence: Teleoperators and Virtual Environments*. https://doi.org/10.1162/pres.1992.1.3.334

blender.org. (2015). blender.org - Home of the Blender project -

Free and Open 3D Creation Software.

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. https://doi.org/10.1007/s10071-011-0401-x

Bohbot, V. D., Lerch, J., Thorndycraft, B., Iaria, G., & Zijdenbos, A. P. (2007). Gray Matter Differences Correlate with Spontaneous Strategies in a Human Virtual Navigation Task. *Journal of Neuroscience*, *27*(38), 10078–10083. https://doi.org/10.1523/JNEUROSCI.1763-07.2007

Bohbot, Veronique D., McKenzie, S., Konishi, K., Fouquet, C., Kurdi, V., Schachar, R., … Robaey, P. (2012). Virtual navigation strategies from childhood to senescence: Evidence for changes across the life span. *Frontiers in Aging Neuroscience*, *4*(OCT), 1–10. https://doi.org/10.3389/fnagi.2012.00028

Bostelmann, M., Lavenex, P., & Banta Lavenex, P. (2020). Children five-to-nine years old can use path integration to build a cognitive map without vision. *Cognitive Psychology*. https://doi.org/10.1016/j.cogpsych.2020.101307

Brodbeck, D. R., & Tanninen, S. E. (2012). Place Learning and Spatial Navigation. In *Encyclopedia of the Sciences of Learning*. https://doi.org/10.1007/978-1-4419-1428-6_43

Brookhuis, K. A., de Waard, D., & Janssen, W. H. (2001). Behavioural impacts of advanced driver assistance systems–an overview. *European Journal of Transport and Infrastructure Research*.

Brown, T. I., Gagnon, S. A., & Wagner, A. D. (2020). Stress Disrupts Human Hippocampal-Prefrontal Function during Prospective Spatial Navigation and Hinders Flexible Behavior. *Current Biology*, *30*(10), 1821-1833.e8. https://doi.org/10.1016/j.cub.2020.03.006

Buckley, M. G., Haselgrove, M., & Smith, A. D. (2015). The developmental trajectory of intramaze and extramaze landmark biases in spatial navigation: An unexpected journey. *Developmental Psychology*. https://doi.org/10.1037/a0039054

Buckley, M. G., Holden, L. J., Spicer, S. G., Smith, A. D., & Haselgrove, M. (2019). Crossing boundaries: Global reorientation following transfer from the inside to the outside of an arena. *Journal of Experimental Psychology: Animal Learning and Cognition*, *45*(3), 322–337. https://doi.org/10.1037/xan0000206

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. https://doi.org/10.1037/a0034901

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. https://doi.org/10.1080/17470218.2014.977925

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016a). Blocking spatial navigation across environments that have a different shape. *Journal of Experimental Psychology: Animal Learning and Cognition*, *42*(1), 51–66. https://doi.org/10.1037/xan0000084

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016b). Thinking outside of the box: Transfer of shape-based reorientation across the boundary of an arena. *Cognitive Psychology*, *87*, 53–87. https://doi.org/10.1016/j.cogpsych.2016.04.001

Bullens, J., Iglói, K., Berthoz, A., Postma, A., & Rondi-Reig, L. (2010). Developmental time course of the acquisition of sequential egocentric and allocentric navigation strategies.

Journal of Experimental Child Psychology, *107*(3), 337–350. https://doi.org/10.1016/j.jecp.2010.05.010

Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Sciences*, *10*(12), 551–557. https://doi.org/10.1016/j.tics.2006.10.005

Cambridge University Press. (2020). Cambridge Dictionary: English Dictionary, Translations & Thesaurus. *Cambridge University Press*.

Carsten, O., Merat, N., Janssen, W., Johansson, E., Fowkes, M., & Brookhuis, K. (2005). HASTE: Final Report. *Human Machine Interface And the Safety of Traffic in Europe*.

Chamizo, V. D., Aznar-Casanova, J. A., & Artigas, A. A. (2003). Human overshadowing in a virtual pool: Simple guidance is a good competitor against locale learning. *Learning and Motivation*. https://doi.org/10.1016/S0023-9690(03)00020-1

Chamizo, V. D., Manteiga, R. D., Rodrigo, T., & MacKintosh, N. J. (2006). Competition between landmarks in spatial learning: The role of proximity to the goal. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2005.11.003

Chan, D., Gallaher, L. M., Moodley, K., Minati, L., Burgess, N., Hartley, T., … Jeffery, K. J. K. J. (2016). Acute stress switches spatial navigation strategy from egocentric to allocentric in a virtual Morris water maze. *Cognition*, *40*(3), 1–10. https://doi.org/10.1016/j.nlm.2016.05.003

Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D. M., Gallistel, C. R., … Menzel, R. (2014). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1408039111

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

https://doi.org/10.1016/0010-0277(86)90041-7

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. https://doi.org/10.3758/BF03196346

Cheng, Ken, Huttenlocher, J., & Newcombe, N. S. (2013). 25 years of research on the use of geometry in spatial reorientation: A current theoretical perspective. *Psychonomic Bulletin and Review*, *20*(6), 1033–1054. https://doi.org/10.3758/s13423-013-0416-1

Chorpita, B. F., Yim, L., Moffitt, C., Umemoto, L. A., & Francis, S. E. (2000). Assessment of symptoms of DSM-IV anxiety and depression in children: A revised child anxiety and depression scale. *Behaviour Research and Therapy*. https://doi.org/10.1016/S0005-7967(99)00130-8

Chrastil, E. R., & Warren, W. H. (2013). Active and passive spatial learning in human navigation: Acquisition of survey knowledge. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/a0032382

Cole, M., & Van Fleet, F. M. (1976). Partial reinforcement of discrete-trial responding in the Skinner box. *Psychological Reports*. https://doi.org/10.2466/pr0.1976.38.3.791

Conrad, C. D., Galea, L. A. M., Kuroda, Y., & McEwen, B. S. (1996). Chronic stress impairs rat spatial memory on the Y maze, and this effect is blocked by tianeptine pretreatment. *Behavioral Neuroscience*, *110*(6), 1321–1334. https://doi.org/10.1037/0735-7044.110.6.1321

Cook, D., & Kesner, R. P. (1988). Caudate nucleus and memory for egocentric localization. *Behavioral and Neural Biology*. https://doi.org/10.1016/S0163-1047(88)90338-X

Coughlan, G., Hort, J., & Hornberger, M. (2018). Spatial navigation deficits — overlooked cognitive marker for preclinical Alzheimer disease?, (July). https://doi.org/10.1038/s41582-018-0031-x

Coughlan, G., Laczó, J., Hort, J., Minihane, A. M., & Hornberger, M. (2018). Spatial navigation deficits — Overlooked cognitive marker for preclinical Alzheimer disease? *Nature Reviews Neurology*. https://doi.org/10.1038/s41582-018-0031-x

Coutrot, A., Manley, E., Goodroe, S., Gahnstrom, C., Filomena, G., Yesiltepe, D., … Spiers, H. J. (2022). Entropy of city street networks linked to future spatial navigation ability. *Nature*, *604*(7904), 104–110. https://doi.org/10.1038/s41586-022-04486-7

Dan, J. (2010). A weird view of human nature skews psychologists' studies. *Science*. https://doi.org/10.1126/science.328.5986.1627

Delaney, H. D., & Maxwell, S. E. (1981). On using analysis of covariance in repeated measures designs. *Multivariate Behavioral Research*. https://doi.org/10.1207/s15327906mbr1601_6

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

Domjan, M. (1998). *The principles of learning and behavior (4th ed.). The principles of learning and behavior (4th ed.).*

Dudchenko, P. (2010). *Why People Get Lost: The Psychology and Neuroscience of Spatial Cognition*. Oxford University Press, USA. https://doi.org/10.1093/acprof:oso/9780199210862.001.0001

Duncko, R., Cornwell, B., Cui, L., Merikangas, K. R., & Grillon, C. (2007). Acute exposure to stress improves performance in trace eyeblink conditioning and spatial learning tasks in healthy men. *Learning and Memory*. https://doi.org/10.1101/lm.483807

Engström, J., Johansson, E., & Östlund, J. (2005). Effects of visual and cognitive load in real and simulated motorway driving. *Transportation Research Part F: Traffic Psychology and Behaviour*. https://doi.org/10.1016/j.trf.2005.04.012

Etchamendy, N., Konishi, K., Pike, G. B., Marighetto, A., & Bohbot, V. D. (2012). Evidence for a virtual human analog of a rodent relational memory task: A study of aging and fMRI in young adults. *Hippocampus*, *22*(4), 869–880. https://doi.org/10.1002/hipo.20948

Filimon, F. (2015). Are all spatial reference frames egocentric? Reinterpreting evidence for allocentric, object-centered, or world-centered reference frames. *Frontiers in Human Neuroscience*, *9*(December), 648. https://doi.org/10.3389/fnhum.2015.00648

Franchak, J. M., & Adolph, K. E. (2010). Visually guided navigation: Head-mounted eye-tracking of natural locomotion in children and adults. *Vision Research*, *50*(24), 2766–2774. https://doi.org/10.1016/j.visres.2010.09.024

Frost, J. (2019). Hypothesis Testing: An intuitive guide for making data driven decisions. *Journal of Chemical Information and Modeling*.

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

Gazova, I., Laczó, J., Rubinova, E., Mokrisova, I., Hyncicova, E., Andel, R., … Hort, J. (2013). Spatial navigation in young versus older adults. *Frontiers in Aging Neuroscience*. https://doi.org/10.3389/fnagi.2013.00094

Golledge, R. G. (1999). Wayfinding behavior: Cognitive mapping and other spatial processes. *Psycoloquy*.

Golledge, R. G. (2003). Human wayfinding and cognitive maps. In *The Colonization of Unfamiliar Landscapes: The Archaeology of Adaptation*. https://doi.org/10.4324/9780203422908

Gonzalez, C. L. R., Kolb, B., & Whishaw, I. Q. (2000). A cautionary note regarding drug and brain lesion studies that use swimming pool tasks: Partial reinforcement impairs acquisition of place learning in a swimming pool but not on dry land. *Behavioural Brain Research*. https://doi.org/10.1016/S0166-4328(00)00162-5

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

Gouteux, Stéphane, & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition*. https://doi.org/10.1016/S0010-0277(01)00128-7

Gramann, K., Hoepner, P., & Karrer-Gauss, K. (2017). Modified navigation instructions for spatial navigation assistance systems lead to incidental spatial learning. *Frontiers in Psychology*, *8*(FEB), 1–10. https://doi.org/10.3389/fpsyg.2017.00193

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*. https://doi.org/10.1098/rsbl.2005.0347

Grieves, R. M., & Jeffery, K. J. (2017). The representation of space in the brain. *Behavioural Processes*, *135*, 113–131. https://doi.org/10.1016/j.beproc.2016.12.012

Guderian, S., Dzieciol, A. M., Gadian, D. G., Jentschke, S., Doeller, C. F., Burgess, N., … Vargha-Khadem, F. (2015). Hippocampal Volume Reduction in Humans Predicts Impaired Allocentric Spatial Memory in Virtual-Reality Navigation. *Journal of Neuroscience*, *35*(42), 14123–14131. https://doi.org/10.1523/JNEUROSCI.0801-15.2015

Guenzel, F. M., Wolf, O. T., & Schwabe, L. (2014). Sex differences in stress effects on response and spatial memory formation. *Neurobiology of Learning and Memory*. https://doi.org/10.1016/j.nlm.2013.11.020

Han, X., & Becker, S. (2014). One spatial map or many? Spatial coding of connected environments. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/a0035259

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*(5), 877–888. https://doi.org/10.1016/S0896-6273(03)00095-3

Haselgrove, M. (2012). *Learning: A Very Short Introduction*. Oxford University Press, USA. https://doi.org/10.1086/698069

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*. https://doi.org/10.1080/02724990344000150

Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*. https://doi.org/10.1016/S0160-2896(02)00116-2

Henrich, J., Heine, S. J., & Norenzayan, A. (2010a). Beyond WEIRD: Towards a broad-based behavioral science. *Behavioral and Brain Sciences*. https://doi.org/10.1017/S0140525X10000725

Henrich, J., Heine, S. J., & Norenzayan, A. (2010b). Most people are not WEIRD. *Nature*. https://doi.org/10.1038/466029a

Hermer, L., & Spelke, E. (1996a). Modularity and development: The case of spatial reorientation. *Cognition*, *61*(3), 195–232. https://doi.org/10.1016/S0010-0277(96)00714-7

Hermer, L., & Spelke, E. (1996b). Modularity and development: The case of spatial reorientation. *Cognition*, *61*(3), 195–232. https://doi.org/10.1016/S0010-0277(96)00714-7

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial orientation in young children. *Nature*, *370*, 57–59. https://doi.org/10.1038/370057a0

Herrera, E., Alcalá, J. A., Tazumi, T., Buckley, M. G., Prados, J., & Urcelay, G. P. (2022). Temporal and Spatial Contiguity Are Necessary for Competition Between Events, *48*(3), 321–347.

Holden, L. J., Whitt, E. J., & Haselgrove, M. (2021). EXPRESS: Resilient allocentric reorientation following transfer from the inside to the outside of an arena. *Quarterly Journal of Experimental Psychology*. https://doi.org/10.1177/17470218211021344

Horne, M. R., Gilroy, K. E., Cuell, S. F., & Pearce, J. M. (2012). Latent spatial learning in an environment with a distinctive shape. *Journal of Experimental Psychology: Animal Behavior Processes*. https://doi.org/10.1037/a0027288

Horner, A. J., Bisby, J. A., Zotow, E., Bush, D., & Burgess, N. (2016). Grid-like processing of imagined navigation. *Current Biology*, *26*(6), 842–847. https://doi.org/10.1016/j.cub.2016.01.042

Hu, Q., Yang, Y., Huang, Z., & Shao, Y. (2018). Children and adults prefer the egocentric representation to the allocentric representation. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2018.01522

Hubbard, T. (2018). *Spatial Biases in Perception and Cognition*. *Spatial Biases in Perception and Cognition*. https://doi.org/10.1017/9781316651247

Hund, A. M., & Padgitt, A. J. (2010). Direction giving and following in the service of wayfinding in a complex indoor environment. *Journal of Environmental Psychology*. https://doi.org/10.1016/j.jenvp.2010.01.002

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

Huttenlocher, J., Newcombe, N., & Sandberg, E. H. (1994). The coding of spatial location in young children. *Cognitive Psychology*. https://doi.org/10.1006/cogp.1994.1014

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *23*(13), 5945–5952. https://doi.org/23/13/5945 [pii]

Ingram, D. K. (1988). Complex maze learning in rodents as a model of age-related memory impairment. *Neurobiology of Aging*. https://doi.org/10.1016/S0197-4580(88)80101-5

Jain, D., Jakhalekar, I. R., & Deshmukh, S. S. (2017). Navigational Strategies and Their Neural Correlates. *Journal of the Indian Institute of Science*. https://doi.org/10.1007/s41745-017-0053-1

Jeffery, K. J. (2010). Theoretical accounts of spatial learning: a neurobiological view (commentary on Pearce, 2009). *Quarterly Journal of Experimental Psychology (2006)*, *63*(9), 1683–1699. https://doi.org/10.1080/17470210903540771

Julian, L. J. (2011). Measures of Anxiety. *Arthritis Care*. https://doi.org/10.1002/acr.20561.Measures

Kaplan, R., Schuck, N. W., & Doeller, C. F. (2017). The Role of Mental Maps in Decision-Making. *Trends in Neurosciences*. https://doi.org/10.1016/j.tins.2017.03.002

Kato, Y., & Takeuchi, Y. (2003). Individual differences in wayfinding strategies. *Journal of Environmental Psychology*.

https://doi.org/10.1016/S0272-4944(03)00011-2

Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' (columba livia) encoding of geometric and geatural properties of a spatial environment. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.112.3.259

Kelly, J. W., & McNamara, T. P. (2010). Reference frames during the acquisition and development of spatial memories. *Cognition*. https://doi.org/10.1016/j.cognition.2010.06.002

Kennedy, H. J., Evans, M. G., Crawford, A. C., & Fettiplace, R. (2003). Fast adaptation of mechanoelectrical transducer channels in mammalian cochlear hair cells. *Nature Neuroscience*. https://doi.org/10.1038/nn1089

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion. *Psychological Science*. https://doi.org/10.1111/1467-9280.00058

Kleen, J. K., Sitomer, M. T., Killeen, P. R., & Conrad, C. D. (2006). Chronic stress impairs spatial memory and motivation for reward without disrupting motor ability and motivation to explore. *Behavioral Neuroscience*, *120*(4), 842–851. https://doi.org/10.1037/0735-7044.120.4.842

Konishi, K., Mckenzie, S., Etchamendy, N., Roy, S., & Bohbot, V. D. (2017). Hippocampus-dependent spatial learning is associated with higher global cognition among healthy older adults. *Neuropsychologia*, *106*(July 2016), 310–321. https://doi.org/10.1016/j.neuropsychologia.2017.09.025

Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behavior Processes*, *39*(2), 126–139. https://doi.org/10.1037/a0031199

Kosko, B. (1986). Fuzzy cognitive maps. *International Journal of Man-Machine Studies*. https://doi.org/10.1016/S0020-7373(86)80040-2

Kudielka, B. M., Hellhammer, D. H., & Kirschbaum, C. (2007). Ten years of research with the Trier Social Stress Test (TSST) - revisited. In *Social Neuroscience: Integrating Biological and Psychological Explanations of Social Behavior*.

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: A practical primer for t-tests and ANOVAs. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2013.00863

Lamers, M. H., & Lanen, M. (2021). Changing Between Virtual Reality and Real-World Adversely Affects Memory Recall Accuracy. *Frontiers in Virtual Reality*, *2*(March), 1–11. https://doi.org/10.3389/frvir.2021.602087

Laurance, H. E., Learmonth, A. E., Nadel, L., & Jacobs, W. J. (2003). Maturation of spatial navigation strategies: Convergent findings from computerized spatial environments and self-report. *Journal of Cognition and Development*, *4(2)*, *211*-.

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

Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddlers’ use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology*. https://doi.org/10.1006/jecp.2001.2635

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

Lee, S. A. (2017). The boundary-based view of spatial cognition : a synthesis. *Current Opinion in Behavioral Sciences*, *16*, 58–65. https://doi.org/10.1016/j.cobeha.2017.03.006

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

Lee, S. A., & Spelke, E. S. (2010a). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*. https://doi.org/10.1016/j.cogpsych.2010.04.002

Lee, S. A., & Spelke, E. S. (2010b). Two systems of spatial representation underlying navigation. *Experimental Brain Research*. https://doi.org/10.1007/s00221-010-2349-5

Lei, X., Mou, W., & Zhang, L. (2020). Developing global spatial representations through across-boundary navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*. https://doi.org/10.1037/xlm0000716

Leising, K. J., Garlick, D., & Blaisdell, A. P. (2011). Overshadowing Between Landmarks on the Touchscreen and in ARENA With Pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*. https://doi.org/10.1037/a0023914

León, I., Tascón, L., & Cimadevilla, J. M. (2016). Age and gender-related differences in a spatial memory task in humans. *Behavioural Brain Research*, *306*, 8–12. https://doi.org/10.1016/j.bbr.2016.03.008

Leplow, B., Lehnung, M., Pohl, J., Herzog, A., Ferstl, R., & Mehdorn, M. (2003). Navigational place learning in children and young adults as assessed with a standardized locomotor search task. *British Journal of Psychology*, *94*(3), 299–317. https://doi.org/10.1348/000712603767876244

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers,

T. (2017). The aging navigational system. *Neuron*. https://doi.org/10.1016/j.neuron.2017.06.037

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. https://doi.org/10.1002/dev.21109

Lithfous, S., Dufour, A., & Després, O. (2013). Spatial navigation in normal aging and the prodromal stage of Alzheimer’s disease: Insights from imaging and behavioral studies. *Ageing Research Reviews*, *12*(1), 201–213. https://doi.org/10.1016/j.arr.2012.04.007

Lourenco, S. F., & Huttenlocher, J. (2007). Using geometry to specify location: Implications for spatial coding in children and nonhuman animals. *Psychological Research*, *71*(3), 252–264. https://doi.org/10.1007/s00426-006-0081-3

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences*, *97*(8), 4398–4403. https://doi.org/10.1073/pnas.070039597

Maguire, Eleanor A., Burgess, N., & O’Keefe, J. (1999). Human spatial navigation: Cognitive maps, sexual dimorphism, and neural substrates. *Current Opinion in Neurobiology*. https://doi.org/10.1016/S0959-4388(99)80023-3

Maguire, Eleanor A., Woollett, K., & Spiers, H. J. (2006). London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus*, *16*(12), 1091–1101. https://doi.org/10.1002/hipo.20233

Marchette, S. A., Ryan, J., & Epstein, R. A. (2017). Schematic representations of local environmental space guide goal-directed navigation. *Cognition*, *158*, 68–80. https://doi.org/10.1016/j.cognition.2016.10.005

McEwen, B. S., & Sapolsky, R. M. (1995). Stress and cognitive function. *Current Opinion in Neurobiology*, *5*(2), 205–216. https://doi.org/10.1016/0959-4388(95)80028-X

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

McGregor, Anthony, 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*. https://doi.org/10.1037/a0014536

McGregor, Anthony, 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. https://doi.org/10.1037/0097-7403.32.3.314

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the "cognitive map." *Nature Reviews Neuroscience*. https://doi.org/10.1038/nrn1932

Mehler, B., Reimer, B., Coughlin, J. F., & Dusek, J. A. (2009). Impact of incremental increases in cognitive workload on physiological arousal and performance in young adult drivers. *Transportation Research Record*. https://doi.org/10.3141/2138-02

Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., … Watzl, S. (2005). Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.0408550102

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. https://doi.org/10.1037/0097-7403.33.3.191

Mix, K. S., Levine, S. C., Cheng, Y. L., Young, C., Hambrick, D. Z., Ping, R., & Konstantopoulos, S. (2016). Separate but correlated: The latent structure of space and mathematics across development. *Journal of Experimental Psychology: General*. https://doi.org/10.1037/xge0000182

Moffat, S. D., Elkins, W., & Resnick, S. M. (2006). Age differences in the neural systems supporting human allocentric spatial navigation. *Neurobiology of Aging*, *27*(7), 965–972. https://doi.org/10.1016/j.neurobiolaging.2005.05.011

Moffat, S. D., Resnick, S. M., Graham, A., Jackson, B., Kitner-triolo, M., & Maci-, L. (2002). Effects of age on virtual environment place navigation and allocentric cognitive mapping. *Behavioral Neuroscience*, *116*(5), 851–859. https://doi.org/10.1037/0735-7044.116.5.851

Morris, R. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods*, *11*(1), 47–60. https://doi.org/10.1016/0165-0270(84)90007-4

Morris, R. G. M., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature*. https://doi.org/10.1038/297681a0

Murias, K., Kwok, K., Castillejo, A. G., Liu, I., & Iaria, G. (2016). The effects of video game use on performance in a virtual navigation task. *Computers in Human Behavior*. https://doi.org/10.1016/j.chb.2016.01.020

Nardini, M., Burgess, N., Breckenridge, K., & Atkinson, J. (2006). Differential developmental trajectories for egocentric, environmental and intrinsic frames of reference in spatial memory. *Cognition*. https://doi.org/10.1016/j.cognition.2005.09.005

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of Cue Integration in Human Navigation. *Current Biology*. https://doi.org/10.1016/j.cub.2008.04.021

Nazareth, A., Weisberg, S. M., Margulis, K., & Newcombe, N. S. (2018). Charting the development of cognitive mapping. *Journal of Experimental Child Psychology*, *170*, 86–106. https://doi.org/10.1016/j.jecp.2018.01.009

Newcombe, N., Huttenlocher, J., Drummey, A. B., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development*. https://doi.org/10.1016/S0885-2014(98)90038-7

Newcombe, N. S. (2019). Navigation and the developing brain. *Journal of Experimental Biology*, *222*. https://doi.org/10.1242/jeb.186460

Newcombe, N. S., Ratliff, K. R., Shallcross, W. L., & Twyman, A. (2013). Is cognitive modularity necessary in an evolutionary account of development? In *Cognitive Biology*. https://doi.org/10.7551/mitpress/9780262012935.003.0094

Newman, M. C., & Kaszniak, A. W. (2000). Spatial Memory and Aging: Performance on a Human Analog of the Morris Water Maze. *Aging, Neuropsychology, and Cognition (Neuropsychology, Development and Cognition: Section B)*. https://doi.org/10.1076/1382-5585(200006)7:2;1-U;FT086

O’keefe, J., & Nadel, L. (1979). Précis of O’Keefe & Nadel’s The hippocampus as a cognitive map. *Behavioral and Brain Sciences*, *2*(4), 487–494. https://doi.org/10.1017/S0140525X00063949

Olejnik, S., & Algina, J. (2003). Generalized Eta and Omega Squared Statistics: Measures of Effect Size for Some Common Research Designs. *Psychological Methods*. https://doi.org/10.1037/1082-989X.8.4.434

Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory*, *65*(1), 65–72. https://doi.org/10.1006/nlme.1996.0007

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. *J Exp Psychol Anim Behav Process*, *30*(2), 135–147. https://doi.org/Doi 10.1037/0097-7403.30.2.135

Pearce, John M. (2013). *Animal learning and cognition: an introduction*. *Psychology Press*.

Pearce, John M. (2009). The 36th Sir Frederick Bartlett lecture: an associative analysis of spatial learning. *Quarterly Journal of Experimental Psychology (2006)*, *62*(9), 1665–1684. https://doi.org/10.1080/17470210902805589

Peer, M., Brunec, I. K., Newcombe, N. S., & Epstein, R. A. (2021). Structuring Knowledge with Cognitive Maps and Cognitive Graphs. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2020.10.004

Piaget, J. I., & Inhelder, B. (2013). *The Child’s Conception of Space* (eBook Publ). London (Original work published 1948): Routledge. https://doi.org/10.4324/9781315006239

Porter, B. E. (2011). *Handbook of Traffic Psychology*. *Handbook of Traffic Psychology*. https://doi.org/10.1016/C2009-0-01975-8

R Development Core Team. (2016). R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing Vienna Austria*. https://doi.org/10.1038/sj.hdy.6800737

Radvansky, G. A., Tamplin, A. K., & Krawietz, S. A. (2010). Walking through doorways causes forgetting: Environmental integration. *Psychonomic Bulletin & Review*, *17*(6), 900–904. https://doi.org/10.3758/PBR.17.6.900

Redhead, E. S., & Hamilton, D. A. (2007). Interaction between locale and taxon strategies in human spatial learning. *Learning and Motivation*. https://doi.org/10.1016/j.lmot.2006.11.003

Redhead, E. S., & Hamilton, D. A. (2009). Evidence of blocking with geometric cues in a virtual watermaze. *Learning and Motivation*, *40*(1), 15–34. https://doi.org/10.1016/j.lmot.2008.06.002

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning. *Classical Conditioning II Current Research and Theory*. https://doi.org/10.1101/gr.110528.110

Restle, F. (1957). Discrimination of cues in mazes: A resolution of the "place-vs.-response" question. *Psychological Review*. https://doi.org/10.1037/h0040678

Rock, I. (1957). The role of repetition in associative learning. *The American Journal of Psychology*. https://doi.org/10.2307/1419320

Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*. https://doi.org/10.1016/j.neurobiolaging.2010.07.021

Roediger, H. L., & Arnold, K. M. (2012). The one-trial learning controversy and its aftermath: remembering Rock (1957). *The American Journal of Psychology*. https://doi.org/10.5406/amerjpsyc.125.2.0127

Rondi-Reig, L., Petit, G. H., Tobin, C., Tonegawa, S., Mariani, J., & Berthoz, A. (2006). Impaired sequential egocentric and allocentric memories in forebrain-specific-NMDA receptor knock-out mice during a new task dissociating strategies of navigation. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.3408-05.2006

Rstudio Team. (2019). RStudio: Integrated development for R. RStudio, Inc., Boston MA. *RStudio*. https://doi.org/10.1007/978-3-642-20966-6

Şahin, M., & Aybek, E. (2019). Jamovi: An Easy to Use Statistical Software for the Social Scientists. *International Journal of Assessment Tools in Education*. https://doi.org/10.21449/ijate.661803

Schwabe, L., Joëls, M., Roozendaal, B., Wolf, O. T., & Oitzl, M. S. (2012). Stress effects on memory: An update and integration. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2011.07.002

Sheline, Y. I., Wang, P. W., Gado, M. H., Csernansky, J. G., & Vannier, M. W. (1996). Hippocampal atrophy in recurrent major depression. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.93.9.3908

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*. https://doi.org/10.1016/S0010-0277(02)00110-5

Spelke, E. S., & Lee, S. A. (2012). Core systems of geometry in animal minds. *Philospohical Transactions of The Royal Society*, *367*, 2784–2793. https://doi.org/10.1098/rstb.2012.0210

Spiers, H. J., & Barry, C. (2015). Neural systems supporting navigation. *Current Opinion in Behavioral Sciences*, *1*, 47–55. https://doi.org/10.1016/j.cobeha.2014.08.005

Stahlman, W. D., & Blaisdell, A. P. (2009). Blocking of spatial control by landmarks in rats. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2009.02.007

Stern, R. M., Hu, S., LeBlanc, R., & Koch, K. L. (1993). Chinese hyper-susceptibility to vection-induced motion sickness. *Aviation Space and Environmental Medicine*.

Sturzl, W., & Zeil, J. (2007). Depth, contrast and view-based homing in outdoor scenes. *Biological Cybernetics*, *96*(5), 519–531. https://doi.org/10.1007/s00422-007-0147-3

Swanson, L. W. (2003). Brain Architecture: Understanding the Basic Plan. *Saudi Med J*.

Takeuchi, Y. (1992). Sense of direction and its relationship with geographical orientation, personality traits and mental ability. *Japanese Journal of Educational Psychology*. https://doi.org/10.5926/jjep1953.40.1_47

Thinus-Blanc, C. (1996). *Animal spatial cognition: Behavioural and brain approach*. World Scientific Publishing Company.

Thomas, K. G. F., Laurance, H. E., Nadel, L., & Jacobs, W. J. (2010). Stress-induced impairment of spatial navigation in females. *South African Journal of Psychology*, *40*(1), 32–43. https://doi.org/10.1177/008124631004000104

Thomas, M. S. C., Annaz, D., Ansari, D., Scerif, G., Jarrold, C., & Karmiloff-Smith, A. (2009). Using developmental trajectories to understand developmental disorders. *Journal of Speech, Language, and Hearing Research*. https://doi.org/10.1044/1092-4388(2009/07-0144)

Thorndyke, P. W., & Goldin, S. E. (1983). Spatial Learning and Reasoning Skill. In *Spatial Orientation*. https://doi.org/10.1007/978-1-4615-9325-6_9

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. II. Place learning versus response learning. *Journal of Experimental Psychology*. https://doi.org/10.1037/h0060262

Tolman, Edward C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*(4), 189–208. https://doi.org/10.1037/h0061626

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. https://doi.org/10.1007/s10071-003-0182-y

Tosto, M. G., Hanscombe, K. B., Haworth, C. M. A., Davis, O. S. P., Petrill, S. A., Dale, P. S., … Kovas, Y. (2014). Why do spatial abilities predict mathematical performance? *Developmental Science*. https://doi.org/10.1111/desc.12138

Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: catalyzing children’s use of landmarks. *Developmental Psychology*. https://doi.org/10.1037/0012-1649.43.6.1523

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

van Gerven, D. J. H., Ferguson, T., & Skelton, R. W. (2016). Acute stress switches spatial navigation strategy from egocentric to allocentric in a virtual Morris water maze. *Neurobiology of Learning and Memory*, *132*, 29–39. https://doi.org/10.1016/j.nlm.2016.05.003

Van Mier, H. I., & Jiao, H. (2020). Influence of action video gaming on spatial representation in the haptic modality. *Experimental Brain Research*. https://doi.org/10.1007/s00221-020-05931-7

Vanderwolf, C. H., & Cain, D. P. (1994). The behavioral neurobiology of learning and memory: A conceptual reorientation. *Brain Research Reviews*. https://doi.org/10.1016/0165-0173(94)90015-9

Wall, P. L., Botly, L. C. P., Black, C. K., & Shettleworth, S. J. (2004). The geometric module in the rat: Independence of shape and feature learning in a food finding task. *Learning and Behavior*. https://doi.org/10.3758/bf03196028

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(02)01961-7

Wasserstein, R. L., & Lazar, N. A. (2016). The ASA's Statement on p-Values: Context, Process, and Purpose. *American Statistician*. https://doi.org/10.1080/00031305.2016.1154108

Web, I. (2010). Introduction to Mendeley. *Mendeley Desktop*.

Weisberg, S. M., Newcombe, N. S., & Chatterjee, A. (2019). Everyday taxi drivers: Do better navigators have larger hippocampi? *Cortex*. https://doi.org/10.1016/j.cortex.2018.12.024

Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: Understanding individual differences in navigation. *Journal of Experimental Psychology: Learning Memory and Cognition*, *40*(3), 669–682. https://doi.org/10.1037/a0035261

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

Wills, T. J., & Cacucci, F. (2014). The development of the hippocampal neural representation of space. *Current Opinion in Neurobiology*, *24*(1), 111–119. https://doi.org/10.1016/j.conb.2013.09.006

Wystrach, A., & Beugnon, G. (2009). Ants learn geometry and features. *Current Biology*. https://doi.org/10.1016/j.cub.2008.11.054

Young, C. J., Levine, S. C., & Mix, K. S. (2018). The connection between spatial and mathematical ability across development. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2018.00755

Young, S. D., Adelstein, B. D., & Ellis, S. R. (2007). Demand characteristics in assessing motion sickness in a virtual environment: or does taking a motion sickness questionnaire make you sick? *IEEE Transactions on Visualization and Computer Graphics*. https://doi.org/10.1109/TVCG.2007.1041