



PAPER

The role of landmarks and boundaries in the development of spatial memory

Jessie Bullens,¹ Marko Nardini,² Christian F. Doeller,³ Oliver Braddick,⁴ Albert Postma¹ and Neil Burgess³

1. Helmholtz Research Institute, Department of Experimental Psychology, Utrecht University, The Netherlands

2. Centre for Brain and Cognitive Development, Birkbeck College, University of London, UK

3. UCL Institute of Cognitive Neuroscience, UCL Institute of Neurology, University College London, UK

4. Department of Experimental Psychology, Oxford University, UK

Abstract

It has been suggested that learning an object's location relative to (1) intramaze landmarks and (2) local boundaries is supported by parallel striatal and hippocampal systems, both of which rely upon input from a third system for orientation. However, little is known about the developmental trajectories of these systems' contributions to spatial learning. The present study tested 5- and 7-year-old children and adults on a water maze-like task in which all three types of cue were available. Participants had to remember the location of an object hidden in a circular bounded environment containing a moveable intramaze landmark and surrounded by distal cues. Children performed less accurately than adults, and showed a different pattern of error. While adults relied most on the stable cue provided by the boundary, children relied on both landmark and boundary cues similarly, suggesting a developmental increase in the weighting given to boundary cues. Further, adults were most accurate in coding angular information (dependent on distal cues), whereas children were most accurate in coding distance, suggesting a developing ability to use distal cues to orient. These results indicate that children as young as 5 years use boundary, intramaze landmark, and distal visual cues in parallel, but that the basic accuracy and relative weighting of these cues changes during subsequent development.

Introduction

As we find our way during everyday tasks, our spatial navigation is guided by an interaction between perceived environmental information and memories of where things are and how we got to them in the past. Different categories of learning processes have been proposed to support mammalian navigation, with differential dependencies on different neural systems. A distinction is made between *place* learning and *response* learning (Packard & McGaugh, 1992, 1996; Tolman, Ritchie & Kalish, 1946; White & McDonald, 2002) or equivalently between *locale* and *taxon* navigation (O'Keefe & Nadel, 1978). *Place* or *locale* refers to knowledge of a location defined in terms of distance and direction to the configuration of surrounding environmental information, which can consist of landmarks and/or the geometry of the environment. The location of the self or of an object can be resolved flexibly, e.g. as when starting from a new position, and relies heavily on the hippocampal system (Cohen & Eichenbaum, 1993; Hartley, Maguire, Spiers & Burgess, 2003; Iaria, Petrides, Dagher, Pike & Bohbot, 2003;

O'Keefe & Nadel, 1978; Packard & McGaugh, 1996). By contrast, *response* or *taxon* refers to behaviour which is directly guided by sensory information (as when the target location is visible, or at the end of a marked path) or which inflexibly re-instantiates a previous sequence of movements, and relies on the striatal system (e.g. Hartley *et al.*, 2003; Iaria *et al.*, 2003; Packard & McGaugh, 1996).

Spatial tasks originally developed to study *place* and *response* learning systems (or *locale* and *taxon* navigation) in rodents were the cross maze paradigm (Tolman *et al.*, 1946), and the Morris water maze (Morris, 1981). The latter task has been widely used to specifically study *place* learning (e.g. Hamilton, Akers, Weisend & Sutherland, 2007; Hamilton, Akers, Johnson, Rice, Candelaria, Sutherland, Weisend & Redhead, 2008; Maurer & Derivaz, 2000; Morris, Garrud, Rawlins & O'Keefe, 1982; Pearce, Roberts & Good, 1998). The Morris water maze consists of a large circular pool in which rats are required to escape from the water by swimming to a platform hidden just under the surface. It has been shown that learning of the platform location depends on the hippocampus (Morris *et al.*, 1982). The

Address for correspondence: J. Bullens, Helmholtz Research Institute, Experimental Psychology, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands; e-mail: J.Bullens@uu.nl

animal remains oriented by the distal cues hung around the pool, while the response location is defined relative to the boundary of the pool (Hamilton *et al.*, 2007, 2008; Maurer & Derivaz, 2000). By contrast, learning to locate a platform whose location is paired with an intramaze landmark (both are moved together within the pool between trials) is not hippocampal dependent (Pearce *et al.*, 1998).

Orientation relative to distal cues is most likely maintained by the system of 'head-direction cells' found along Papez's circuit (Taube, 1998) which projects into both the hippocampal formation and the striatum, consistent with the performance deficits on this task after anterior thalamic lesions (Wilton, Baird, Muir, Honey & Aggleton, 2001). Location relative to environmental boundaries is most likely maintained by the 'place cells' found in the hippocampus (O'Keefe, 1976), which respond in locations defined by environmental boundaries (O'Keefe & Burgess, 1996) rather than intramaze landmarks (Cressant, Muller & Poucet, 1997).

Following these studies, Doeller and Burgess (2008) investigated the role of boundaries and landmarks, and their related neural structures (Doeller, King & Burgess, 2008), in human spatial learning. They dissociated participants' ability to learn locations relative to a local boundary (boundary-related learning) and to a local landmark (landmark-related learning) within a single virtual reality (VR) task (Doeller & Burgess, 2008), which was also used in an fMRI study (Doeller *et al.*, 2008). The VR environment comprised a circular-bounded arena, containing an intramaze landmark and surrounded by distal landmarks. The distal landmarks provided information about the participant's orientation. Participants saw the locations of different objects hidden around the virtual arena. They were then moved to a different location and facing direction within the arena and asked to navigate to each hidden object's place. Representing locations relative to either (i) the boundary of the arena and distal landmarks, or (ii) the internal landmark and distal landmarks, would suffice to relocate the objects. To separate these two kinds of coding, the internal landmark and the boundary were moved relative to each other between test blocks. Unbeknownst to participants, some of the hidden objects were associated with the landmark, and thus moved with it between test blocks (keeping a fixed distance and direction relative to the landmark), while other objects were associated with the boundary, and so kept a fixed distance and direction relative to the boundary. This study was thus able to determine the extent to which the participants relied on either cue (when movement of the landmark brought them into conflict), and the extent to which they learnt over the course of the study that the boundary was reliable for finding one subset of objects, whereas the landmark was reliable for finding the other.

Note that in this paradigm, both types of learning depend on also orienting correctly with respect to the

distal landmarks. Thus as the object is not directly placed at the internal landmark, the correct angle from it also needs to be known. Therefore, simple '*response learning*' is not sufficient to relocate any of the objects given the participant's new starting locations on each trial. The results demonstrated that navigation based on the boundary and distal orienting cues was distinguished from navigation based on the local landmark and distal orienting cues by operating via different learning rules (Doeller & Burgess, 2008), and, as shown in the fMRI experiment, by producing differential activation of the hippocampal and striatal systems (Doeller *et al.*, 2008). Furthermore, it was shown that the learning systems do not compete (cf. Poldrack, Clark, Paré-Blagoev, Shohamy, Creso Moyana, Myers & Gluck, 2001), but that they independently influence behaviour at similar rates, and that they act in parallel during learning. In the present study we adapted this task with the aim of examining the developmental trajectories of these two systems in children.

Given that studies using (adaptations of) the Morris water maze provided evidence for specific brain-behaviour relationships in animals (Pearce *et al.*, 1998) and adult humans (Doeller *et al.*, 2008) when tested on the same task, inferences might be made about the ontogeny of the neural systems involved in learning behaviour in children (Overman, Bachevalier, Miller & Moore, 1996a). That is, children's ability to learn locations relative to environmental boundaries and intramaze landmarks might provide some insight into the relative developmental time-courses for the functional maturation of the hippocampal and striatal systems involved in human wayfinding. Similarly, previous developmental studies, which used paradigms related to the Morris water maze to study (local and distal) landmark use in children at primary school age, showed that *place learning* and *response learning* can be dissociated in terms of their developmental trajectories, with spontaneous *response learning* being present early in life (at least at the age of 5 years) and *place learning* developing up until the age of 7 to 10 years (Lehning, Leplow, Friege, Herzog & Ferstl, 1998; Lehning, Leplow, Ekroll, Herzog, Mehdorn & Ferstl, 2003; Leplow, Lehning, Pohl, Herzog, Ferstl & Mehdorn, 2003; Overman, Pate, Moore & Peuster, 1996b) which can possibly be related to a late maturation of the hippocampus (Newcombe & Huttenlocher, 2000; Overman *et al.*, 1996b). However, accurate representations of locations within the testing room also appear to be present at younger ages (Nardini, Burgess, Breckenridge & Atkinson, 2006).

The present study aimed to provide a parametric measure of accuracy for boundary-related and landmark-related learning, so that their interaction and development could be studied. To do this we adapted the paradigm of Doeller and colleagues (2008) testing children's and adults' recall for locations in a (real life) circular environment containing an

experimentally controlled landmark and surrounded by distal orientation cues. The design was the same in that the landmark moved relative to the boundary between test blocks so that landmark and boundary cues were placed in conflict. Participants had to learn the location of two objects, of which one was associated with the landmark and the other with the boundary.

Method

Participants

Twenty-nine children and 16 adult students participated in the study which was conducted at the Visual Development Unit at Oxford University. The children comprised two age groups: 5-year-olds ($n = 13$, number of girls = 6; mean age = 5.5, $SD = 0.16$ years) and 7-year-olds ($n = 13$, number of girls = 8; mean age = 7.4, $SD = 0.32$ years). Three additional children were excluded from the analysis because of interruptions in the testing which could have interfered with learning. All children came from a database of volunteers recruited in Oxford, and parents gave consent for their child's participation in the study. Adult students (mean age = 20.0, $SD = 1.70$ years) were recruited through advertisements at Oxford University. They received course credit or payment for participation and gave written consent. All children and adults reported being healthy, had normal or corrected to normal vision and were unaware of the rationale of the study.

Apparatus and stimuli

The circular arena in which the children and adults were tested was formed by an empty circular swimming pool of diameter 366 cm and walls of height 91 cm (see Figure 1). This pool was placed in a rectangular testing room (4.9 m \times 6.7 m) whose walls were covered with black ceiling-to-floor curtains. The testing room was dark except for a projection light placed directly above the centre of the pool. Owing to the black curtains and low light, the shape of the surrounding room was not

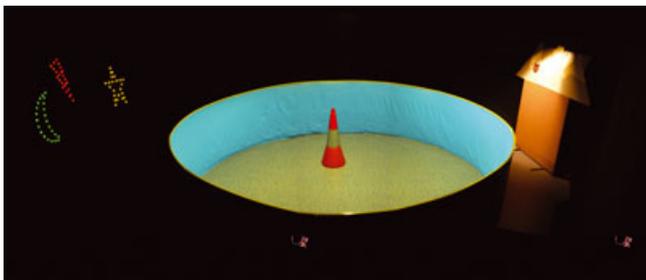


Figure 1 Experimental set-up showing the circular arena with the intramaze landmark (traffic cone), the boundary (circular wall of the pool) and the extramaze orientation cues (three differently coloured lights and the mountains cut from cardboard paper).

discernible, so it was not possible to use the geometry of the room as a cue. The floor of the pool was covered with blue linoleum in which 88 32 cm \times 32 cm 'doors' (hiding locations) were cut. Participants searched for laminated 21.5 cm \times 21.5 cm pictures of a frog and a ladybird, which could be hidden under different 'doors' in the floor. Due to the material used, the cuts of the doors were not visible; therefore participants could not use a counting strategy to code location. The landmark inside the pool consisted of a traffic cone (height 70 cm, diameter 25 cm), which was round with no cues as to its orientation. The distance between the landmark-related object and the landmark was 86 cm. The more distant cues surrounding the arena were LED arrays measuring 30 cm \times 15 cm which formed an array of a 'moon', a 'lightning bolt' and a 'star', and were placed at distance 110 cm and heights of 1.60 m, 1.83 m and 1.63 m, respectively, on one side of the room, and an array of mountains cut from cardboard paper (168 cm \times 69.4 cm) placed at distance 110 cm and height 110 cm on the other side of the room. The distal cues, which were deliberately made very different and distinctive to aid orientation, were similar in total width and were located at an absolute distance of 2.93 m from the centre of the pool. A light, not visible from inside the pool, was projected at the mountains.

Design

Participants had to remember the locations of two objects (frog and ladybird pictures) of which one remained at a location fixed relative to the boundary of the pool, while the other remained at a location fixed relative to the intramaze landmark (traffic cone). That is, between test blocks the landmark and the boundary were moved relative to each other, and the landmark-related object moved with the landmark between test blocks (keeping a fixed distance and direction relative to the landmark), while the boundary-related object kept a fixed distance and direction relative to the boundary (see Figure 2a). At the beginning of the experiment, each object was shown in its correct position, which was the same for all participants, starting with the landmark in the upper right corner and the two objects at equal distance from the landmark and the boundary. These distances were equal in the first block so that there was initially no reason to associate either object more strongly with either cue (see Figure 2a). For the second and third test blocks, the landmark and landmark-related object were moved to a predefined location in quasi random order (Figure 2b). The assignment of either object location as boundary-related or landmark-related, as well as the assignment of the 'frog' or 'ladybird' as a boundary- or landmark-related object, and the order of movement of the intramaze landmark (traffic cone) was randomized between participants. The relationship between the possible locations for the boundary-related object and the distal cues (lights and

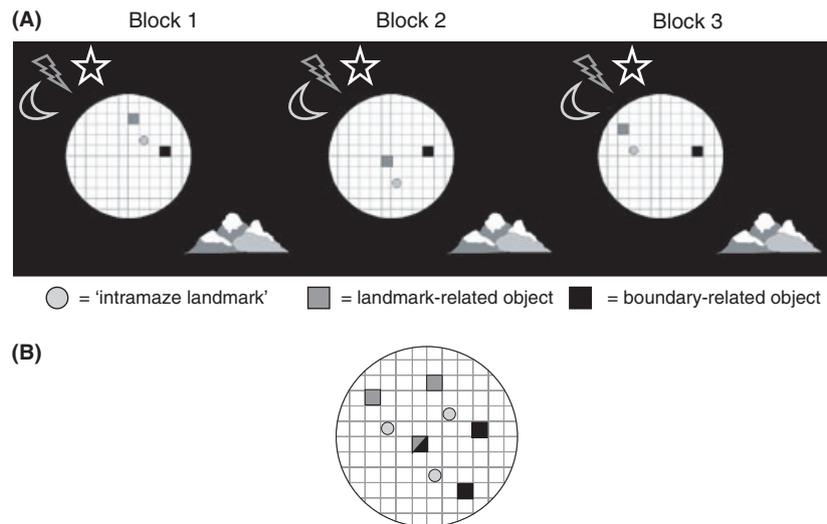


Figure 2 (A) *Experimental design: Participants learned two object locations over three blocks with the landmark (light grey circle) and the boundary moving relative to each other at the start of each block. One of the objects was associated with the landmark (dark grey square) and the other object was associated with the boundary (black square). The distal cues are presented as how they were actually positioned during the experiment.* (B) *Experimental design: Locations of the landmark (light grey circle) and the possible locations of the landmark-related and the boundary-related objects (dark grey and black squares). The assignment of either object location as boundary-related or landmark-related, as well as the assignment of the 'frog' or 'ladybird' as boundary-related or landmark-related, was randomized between subjects. All participants started the experiment with the landmark in the upper right corner and the two objects at equal distance from the landmark and boundary, as shown in Figure 2a (Block 1).*

mountains) can be seen in Figure 2a. The experiment comprised three test blocks of four trials, in which each trial consisted of the retrieval of both the boundary-related object and the landmark-related objects, thus 24 responses in total.

Procedure

Participant and experimenter entered the arena using the pool ladder, which was then moved out of sight. Participants were encouraged to take a good look around and to name everything they saw. The experimenter made sure that the intramaze landmark (traffic cone) as well as each of the distal cues was pointed out. Next, participants were told that the experimenter had a 'secret', namely that two pictures were hidden underneath the linoleum in the pool. Then the locations of both pictures were shown to participants who were told to remember both locations very well, since they would be asked to find them again. After that, participants were taken to the centre of the pool and asked to close their eyes. To disorient participants (so that they had to use visual cues to find the pictures), they were first rotated several times while the experimenter moved around in different directions in order not to provide a directional cue herself. Then, the participants were taken along a wandering path, still with eyes closed, to one of four positions on the north, east, south or west side of the pool, facing the pool wall. After participants had reached this starting point, they were asked to count to 20 out loud still with eyes closed. During this period the experimenter, if necessary (i.e. on the first trial of a

new test block), covertly moved the landmark and the picture related to it to their new position. Subsequently, participants were asked to open their eyes and turn around. They were provided with a copy of one of the hidden pictures and told to place it on top of the linoleum where they thought the original picture was located. Then feedback was provided: The experimenter showed participants the correct location of the hidden picture. This procedure was repeated for the second picture. The order in which the two pictures were retrieved varied randomly from trial to trial. Then the participant proceeded to the next trial, starting with the disorientation procedure in the centre of the pool. Throughout testing, the experimenter stayed in the pool with the child, but moved around in order to avoid becoming a stable landmark herself.

Results

In this section we will discuss participants' overall performance on the task, the extent to which their errors can be explained by reliance on the incorrect cue and how participants had used the landmark and/or boundary cues in order to locate the objects, thereby differentiating between distance and angular scores. Table 1 summarises the significant results that will be discussed below.

Overall performance

The first analysis focused on participants' overall accuracy at relocating the objects. Performance was

Table 1 Summary of significant results in the different ANOVAs

Overall performance: Group (3) × Type of Object (2) × Block (3) × Trial (4)	
Factors	
Group	$F(2, 39) = 103.86, p < .0001$
Group × Type of Object	$F(2, 39) = 5.12, p < .05$
Trial	$F(3, 117) = 7.27, p < .0001$
Group × Trial	$F(6, 117) = 4.81, p < .0001$
Group × Block × Type of Object	$F(4, 78) = 2.88, p < .05$
Group × Type of Object × Trial	$F(6, 117) = 5.41, p < .0001$
Block × Trial	$F(6, 234) = 2.76, p < .05$
Type of Object × Block × Trial	$F(6, 234) = 2.66, p < .05$
Group × Type of Object × Block × Trial	$F(12, 234) = 2.37, p < .01$
Performance relative to the incorrect cue: Group (3) × Type of Object (2) × Block (2) × Trial (4)	
Factors	
Type of Object	$F(1, 39) = 7.82, p < .01$
Group × Type of Object	$F(2, 39) = 6.58, p < .01$
Group × Block	$F(2, 39) = 4.10, p < .05$
Trial	$F(3, 117) = 10.53, p < .0001$
Group × Trial	$F(6, 117) = 6.72, p < .0001$
Type of Object × Trial	$F(3, 117) = 17.98, p < .0001$
Group × Type of Object × Trial	$F(6, 117) = 7.94, p < .0001$
Cue use: distance and angle: Group (3) × Block (3) × Cue Type (2) × Measure (2)	
Factors	
Group	$F(2, 39) = 89.77, p < .0001$
Block	$F(2, 78) = 8.47, p < .0001$
Block × Measure	$F(2, 78) = 7.92, p < .01$
Group × Measure	$F(2, 39) = 5.70, p < .01$

calculated based on the distance (error) between a subject's response and the target object's true location. Since the raw distance (cm) does not give an equivalent measure of performance for objects near the edge and those near the centre of the arena (with the latter ones, on average, getting smaller errors if responding was at chance, i.e. uniformly randomly distributed in the pool), we transformed raw distance to a standardized performance score. This score is equivalent across locations in that it is scaled against the level of performance that would be expected by chance. Distances were transformed into standardized performance scores with the formula: performance score = $100 \times (\text{chance distance} - \text{error distance}) / \text{chance distance}$ (see Nardini *et al.*, 2006). Chance distance was calculated as the average of the distances from each of the 88 possible response locations to the correct location. Following this transformation, a score of 0 indicates chance performance, while a score of 100 indicates a correct search. A score below 0 indicates an error greater than that expected by chance.

Figure 3a plots performance by age group, object type, and block (1–3), for each block's four individual trials (left) and collapsed over the whole block (right). The two child groups made large errors, but tended to attain

above-chance performance throughout. Adults' performance was close to ceiling, with the exception of the landmark-related object on the first trials of blocks 2 and 3; these were the trials immediately after the landmark and landmark-related object had moved relative to the boundary.

These standardized performance scores were subjected to a repeated measure ANOVA with Group (1–3) as between-subjects factor and Type of Object (landmark-related or boundary-related), Block (1–3) and Trial (1–4) as the within-subjects factors. The analysis revealed a significant effect of age group ($F(2, 39) = 103.86, p < .0001$). Despite the fact that all age groups significantly performed above chance level on the task: 5-year-olds, $t(12) = 6.71, p < .0001$; 7-year-olds, $t(12) = 5.67, p < .0001$, and adults, $t(15) = 66.48, p < .0001$, post-hoc comparisons (Bonferonni corrected) showed that both child groups (5-year-olds = 22.7% and 7-year-olds = 29.1%) differed markedly from the adults (83.7%) on overall performance score ($ps < .0001$); however, the child groups did not differ significantly from each other ($p = .31$). Additionally, the children differed markedly from the adults on most (or a combination) of the above-mentioned factors; Group × Type of Object, $F(2, 39) = 5.12, p < .05$; Group × Trial, $F(6, 117) = 4.81, p < .0001$; Group × Block × Type of Object, $F(4, 78) = 2.88, p < .05$; Group × Type of Object × Trial, $F(6, 117) = 5.41, p < .0001$; Group × Type of Object × Block × Trial, $F(12, 234) = 2.37, p < .01$. Most importantly, post-hoc paired-samples *t*-tests (alpha adjusted) showed that, for the second and the third test blocks the adults performed significantly better on the boundary-related object than on the landmark-related object, $t(15) = -6.74, p < .0001$. The 5- and 7-year-olds, on the other hand, showed no difference in performance on the two object types: 5-year-olds, $t(12) = -1.75, p = .11$, and 7-year-olds, $t(12) = .63, p = .54$. The result showing that adults performed worse on the landmark-related object suggests that they relied more on the boundary than on the intramaze landmark. By contrast there was no such significant difference in the child groups.

Performance relative to the incorrect cue

To check the extent to which errors were explained by reliance on the 'wrong' cue for a given object, standardized performance scores (standardized in the same way as described for the overall performance scores), which again consisted of distance errors, were calculated relative to the search place predicted by the landmark (for the boundary object) and by the boundary (for the landmark object). This analysis was carried out for blocks 2 and 3 (since in block 1, both cues predicted the same locations). Figure 3b plots these scores. While there seems to be no strong indication of the child groups searching with respect to the wrong cue, it is clear that adults' large errors in locating the landmark-related

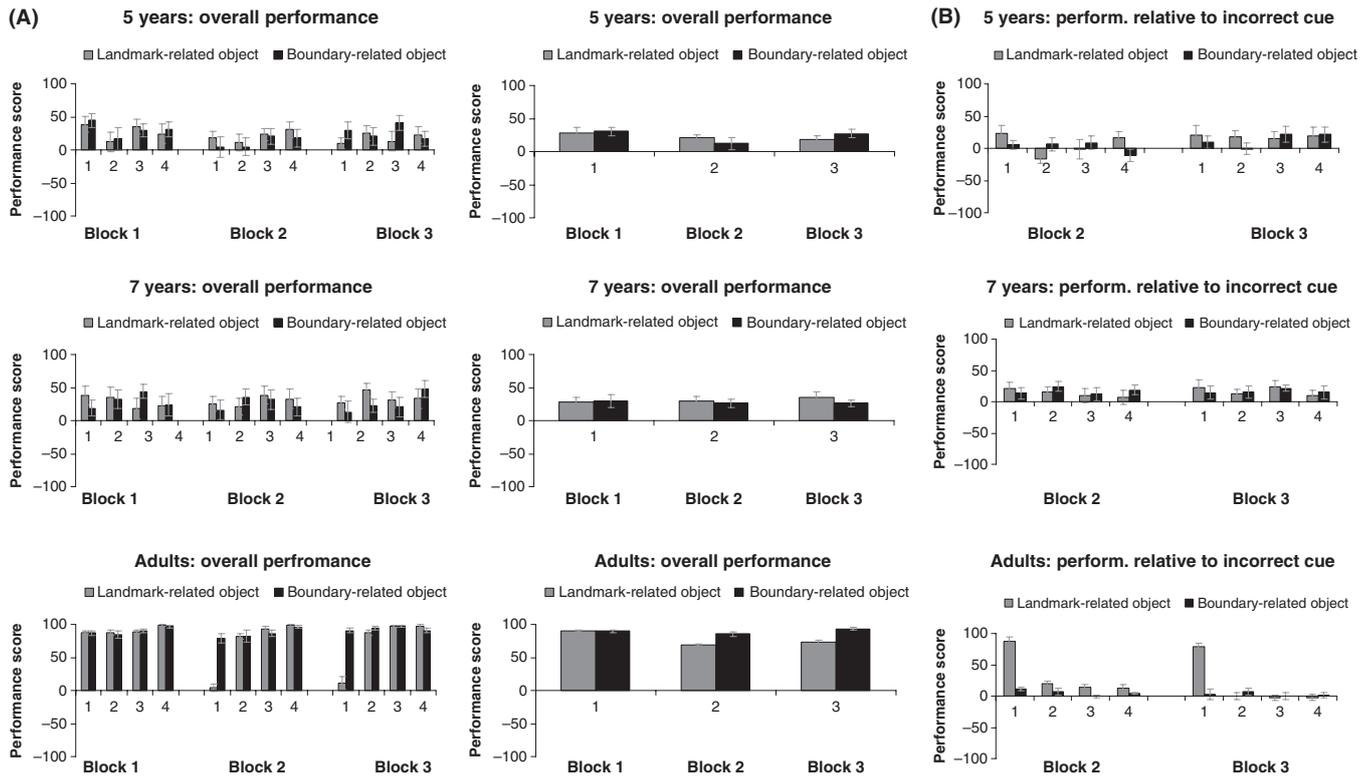


Figure 3 (A) Standardized performance scores based on distance of the response location to the correct location for all three age groups, shown by block and object type for the four trials in each block (left) and collapsed by block (right). (B) Standardized performance scores based on distance of the response location to the location predicted by the use of the incorrect cue for all three age groups, shown by block and object type for the four trials in each of blocks 2 and 3.

object after the landmark and object moved (Figure 3a) are explained by searches close to the place predicted by the boundary (Figure 3b), i.e. the object's location within the arena before it and the landmark moved.

These scores relative to the location predicted by the use of the incorrect cue were subjected to a repeated measure ANOVA with Group (1–3) as between-subjects factor and Type of Object (landmark-related or boundary-related), Block (1–2) and Trial (1–4) as the within-subjects factors. The analysis did not show a main effect for Group, $F(2, 39) = 1.47$, $p > .05$. However, the factor Group did interact with the other factors; Group \times Type of Object, $F(2, 39) = 6.58$, $p < .01$; Group \times Block, $F(2, 39) = 4.10$, $p < .05$; Group \times Trial, $F(6, 117) = 6.72$, $p < .0001$, and there was also a three-way interaction of Group \times Type of Object \times Trial, $F(6, 117) = 7.94$, $p < .0001$. This latter interaction showed that when the configuration of the maze changed, the adults, but not child participants, tended to relocate both objects relative to the boundary, thereby ignoring the landmark.

Cue use: distance and angle

To gain more insight into how participants used the landmark and/or boundary cues in localizing the objects, distance and angular accuracy was examined separately

relative to both cues. To calculate a distance performance score, the distance between a participant's response and the boundary or landmark was compared with the correct distance between the hidden object and the boundary or landmark, scaled against the discrepancy between these that would be expected by chance (as before) – see Figure 4. To calculate an angular performance score, the angle of a response from the boundary or landmark was compared with the actual angle of the hidden object from the boundary or landmark, scaled against the discrepancy between these that would be expected by chance (see Figure 4). Note that this measure does *not* reflect the relative influence of either cue on the participant's response. When an error occurs, e.g. responding in the location predicted by the boundary for a landmark-related object, these four measures separately reveal the extent to which the incorrect location nonetheless maintains the correct angle or distance to landmark or boundary.

Figure 5 plots these standardised distance and angle performance scores by age, block and cue type. The scores were subjected to a repeated measure ANOVA with Group (1–3) as between-subjects factor and Block (1–3), Cue Type (landmark or boundary) and Measure (distance or angle) as the within-subject factors. The significant results of this ANOVA are presented in Table 1. The most important finding from this analysis was a two-way

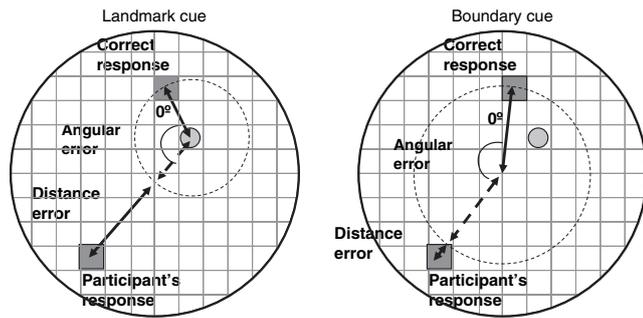


Figure 4 Measures of distance error and angular error relative to the landmark and boundary cues. To calculate the distance performance score, the distance between a participant's response and the boundary or landmark was compared with the correct distance between the hidden object and the boundary or landmark, scaled against the discrepancy between these that would be expected by chance. Likewise, to calculate the angular performance score, the angle between a participant's response and the boundary or landmark was compared with the correct angle between the hidden object and the boundary or landmark. These distance and angular performance scores were converted to standardized scores by taking into account the differences between correct and measured distances and angles that would be expected by chance.

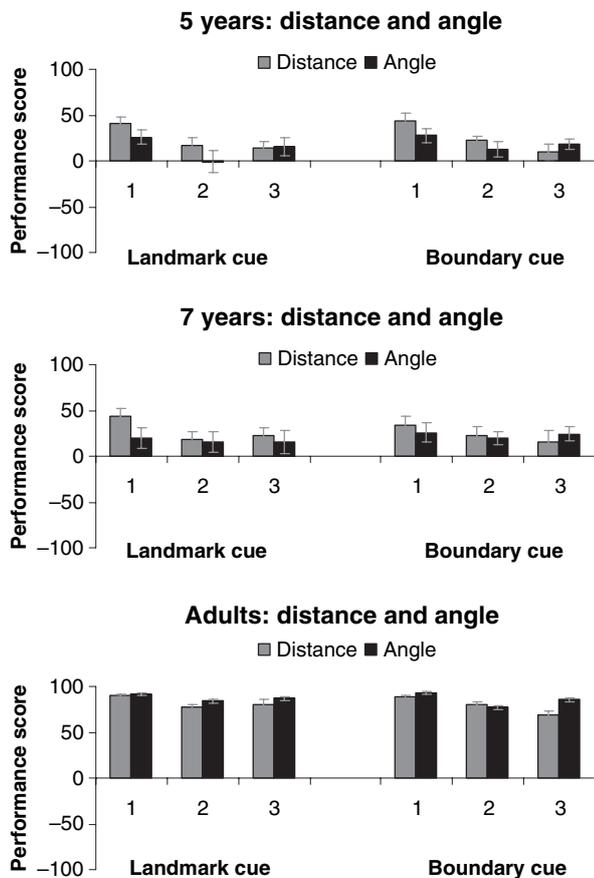


Figure 5 Standardised scores for distance and angular performance relative to the landmark and boundary, shown for both objects combined, across the three blocks, see Figure 4.

interaction between Measure and Group, $F(2, 39) = 5.70$, $p < .01$, which indicated that the relative amount of error in angle vs. distance changed with age. A post-hoc analysis with adjusted alpha found that overall the children performed significantly better on the distance measure than the angular measure, $t(25) = 2.42$, $p < .05$, whereas the adults performed significantly better on the angular measure in comparison with the distance measure, $t(15) = -5.71$, $p < .0001$. No effects were found for the factor Cue Type ($ps > 0.05$).

Discussion

In the present study, children aged 5 and 7 years and adult students were tested in a real life object location memory task in which they were required to find two hidden objects. One of the objects was related to an intramaze landmark which moved between test blocks and the other object was related to the circular boundary of the environment. Both landmark and boundary cues were useful only in conjunction with the orientation provided by the stable distal landmarks surrounding the maze. Participants' performance on either object type indicated their ability to code the object's location relative to either the intramaze landmark or the boundary of the environment.

Overall, although adults performed markedly better than children, all age groups were significantly above chance (Figure 3a). However, adults tended to be less successful at finding the landmark-related object than the boundary-related object – they relied more on the boundary than on the landmark, and so searched incorrectly after the landmark and landmark-related object moved. These incorrect searches were close to the place predicted by the boundary (Figure 3b). There was no significant difference in children's performance with the two object types. This suggests that children's weighting of boundary vs. landmark information was different to adults'; they did not rely so strongly on the boundary, but seemed to rely similarly weakly on both cues. This is consistent with other suggestions that the weighting of spatial cues changes in development (Newcombe & Huttenlocher, 2006; Learmonth, Newcombe, Sheridan & Jones, 2008).

Differential weighting could be adaptive if it reflected developmental changes in the underlying reliabilities of the different information sources (Cheng, Shettleworth, Huttenlocher & Rieser, 2007). Thus if development in the accuracy of using two kinds of spatial information sources were uneven, it could be adaptive to weight one source more at an early age, and the other source more at a later age. The present results could therefore correspond to an adaptive reweighting (see also Newcombe & Ratliff, 2007). Alternatively, children's apparently even weighting in the present study, compared with adults' uneven weighting, could indicate a failure to integrate the different sources of information at all (see

Nardini, Jones, Bedford & Braddick, 2008). To settle this question, future research should isolate boundary and landmark cues to determine developmental changes in their accuracy individually, and manipulate the reliability of each cue for finding the target. Reliability can be manipulated by varying the proximity of the hidden object to the landmark or boundary, or by varying the size of the landmark and/or the height of the boundary. In addition, the configuration of boundaries and/or landmarks can be manipulated to reveal their influence on responding (e.g. Hartley, Trinkler & Burgess, 2004; Maurer & Derivaz, 2000; Nardini *et al.*, 2006). One issue to consider is the potential effect of the different heights of the children and adults. We note that all children were taller than the pool wall so that their view of the distal landmarks was not obscured, and that both types of cue (landmark and boundary) would appear taller to the children than to the adults. Nonetheless, it is still possible that the extra relative height of the pool wall for the children might have contributed to their diminished use of the distal landmarks, or have otherwise affected the salience or apparent reliability of the different information sources (see also Newcombe & Ratliff, 2007), and thus affected their relative influence (Nardini *et al.*, 2008).

The fact that the adults seemed to have focused solely on the boundary and distal cues for orientation, thereby neglecting the intramaze landmark, has some echoes in the animal literature. When the location of a food reward was paired with distinct landmarks, rats ignored the landmarks when their locations were varied relative to the background, whereas they used the combination of landmarks and background when they remained fixed relative to each other (Biegler & Morris, 1993). Nonetheless, the study by Pearce *et al.* (1998), using the Morris water maze paradigm, demonstrated that rats can associate a goal location with an intramaze landmark that moves relative to the background cues. A similar result was found in the VR study (Doeller *et al.*, 2008) in which adults showed a similarly strong influence of both cues. Our finding that adults neglect the intramaze landmark might be taken as a sign that, although it has been previously shown that testing in virtual and real environments led to similar results (Péruch & Wilson, 2004), in our experiment, adults experienced the real boundary and distal cues as relatively more stable than in the VR environment. This might relate to the process of walking through the surrounding building before starting the experiment, or the fact that the distal orientation cues provided motion parallax indicating that the boundary was fixed, while in the VR experiment, the distal cues were rendered at infinity and so did not contribute to judgments of the location of either boundary or landmark. In line with the suggestion to systematically vary the salience of the cues to investigate its effects on developmental patterns in the differential weighting of cues, future studies

could attempt to strengthen the association of the object location to the landmark by hiding the object closer to it, or by increasing the size of the landmark, as both manipulations were found to increase the influence of the landmark on response location in the VR studies.

Although the performance of the children was much worse than that of the adults, it was better than chance, indicating an ability to use the distal orientation cues in addition to the landmark or boundary. Previous studies have indicated that when distal and proximal landmarks conflict, children do not select the distal landmarks until school age (Lehning *et al.*, 1998; Lehning *et al.*, 2003; Leplow *et al.*, 2003). However, when there is no conflict, children as young as 3 years can use distal natural landmarks to reorient (Smith, Gilchrist, Cater, Ikram, Nott & Hood, 2008), and may rely on them preferentially when in conflict with unstable local landmarks (Nardini *et al.*, 2006). In the present study, children's above-chance scores on the main measure and on the angular measure indicate that they did use the distal cues to some degree to determine orientation. This finding is consistent with the extensive literature on children's ability to reorient in an enclosed environment, which shows that, when tested in a large enough testing room (8 by 12 feet – 2.4 m by 3.6 m) children aged 18 months are already able to, in combination with geometric information provided by the room, use landmark information to reorient (Learmonth, Newcombe & Huttenlocher, 2001; Cheng & Newcombe, 2005). Interestingly, 3- to 6-year-olds' use of landmark information depends on ease of movement and distance of the landmark (distant landmarks being used more reliably) (Learmonth *et al.*, 2008). In the present study, children were able to freely move around in the pool, and the distance of the distal cues to the centre of the search space was larger (2.93 m vs. 1.83 m) than in reorientation studies using the 8 by 12 feet room. Both these factors would be expected to facilitate landmark use.

In addition to the above-described results, an overall difference between adults and children was found in the way they used distance and angular information to relocate both object types. Children were more accurate on distance, whereas adults were better on angle than on distance. Since judging angle required the use of the distal cues, this indicates that the developmental change was in better use of the distal cues for orientation. Thus, although children of 5 and 7 years old seem to have used some combination of distance and angle information (the latter dependent on distal cues), they did not yet combine these to attain adult-like accuracy. They also relied relatively more on coding distance to the landmark and boundary cues. We might speculate that children's difficulties in using distal cues for orientation relate to their difficulties in using category information along the dimension of angle (Huttenlocher, Newcombe & Sandberg, 1994; Sandberg & Huttenlocher, 1996).

Relating back to the neural correlates associated with boundary- and landmark-related learning, as discussed in the Introduction, the above-chance performance of all age groups is consistent with evidence that, in rats, the hippocampus is functionally mature very early in life (Martin & Berthoz, 2002), and 18-month-old to 3-year-old children are able to locate objects relative to the experimental room (Nardini *et al.*, 2006; Newcombe & Huttenlocher, 2000). The absence of a bias towards use of the boundary in the 5-year-old children tested here might also indicate that striatal dependent representations (i.e. response learning or landmark-related learning) are equally mature at this age (Overman *et al.*, 1996a, 1996b). However, the low overall level of performance in these children rules out firm conclusions regarding the relative development of these two systems, and the finding that the children erred more in the direction of the responses than in the distance from the two types of cue may simply indicate poor use of the distal orientation cues. It is possible that the process of disorientation between trials was more disruptive for children than adults. Thus the adults may have been better at reorienting themselves relative to the distal cues at the start of each trial, possibly reflecting the developmentally delayed influence of distal cues in conflict situations referred to above. The orientation of the place cell representations in rats becomes decoupled from distal cues when the rat is disoriented before each trial (Knierim, Kudrimoti & McNaughton, 1995) or when the distal cues appear to be unstable relative to the rats' internal sense of direction (Rotenberg & Muller, 1997; Jeffery & O'Keefe, 1999). As mentioned earlier in the discussion, inability to combine different sources of information (in this case conflicting path integrative and visual cues) up to 8 years has been recently reported in both spatial (Nardini *et al.*, 2008) and non-spatial situations (Gori, Del Viva, Sandini & Burr, 2008).

In conclusion, we found evidence for differential object location learning patterns in children aged 5 to 7 years and in adults. While orienting in a maze, children seem to have used both landmark and boundary cues in order to relocate different object types, and were relatively more accurate in coding the distances than angles to these cues. Adults, on the other hand, relied more on the stable environmental cues, and were more accurate in coding angular information provided by distal (extramaze) landmarks than distance information. In addition to the 5- and 7-year-old children tested here, future studies may test older children to assess the point in development at which the adult pattern of behaviour emerges. That is, in line with place learning continuing to develop well into the school years (Lehning *et al.*, 1998, 2003; Leplow *et al.*, 2003; Newcombe, Lloyd & Ratliff, 2007), it would be interesting to provide a more thorough evaluation of the developmental trajectory for landmark- and boundary-related learning. Furthermore, future research should systematically vary the salience of the

cues to investigate its effects on developmental patterns in the differential weighting of cues, and determine in more detail how the ability to combine angular and distance information for boundary and landmark cues develops. Lastly, developmental imaging studies using virtual reality could provide insight into the maturation of specific neural structures associated with the different types of learning.

Acknowledgements

This work was supported by an EU NEST Fp6grant (No. 12959 – Wayfinding) and the Medical Research Council, UK. We would like to thank the children who participated in our study and Lisa Beeren for her help with the analyses.

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Received: 1 May 2008

Accepted: 27 November 2008