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# Improvement of allocentric spatial memory resolution in children from 2 to 4 years of age

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**Abstract**

Allocentric spatial memory, the memory for locations coded in relation to objects comprising our environment, is a fundamental component of episodic memory and is dependent on the integrity of the hippocampal formation in adulthood. Previous research from different laboratories reported that basic allocentric spatial memory abilities are reliably observed in children after 2 years of age. Based on work performed in monkeys and rats, we had proposed that the functional maturation of direct entorhinal cortex projections to the CA1 field of the hippocampus might underlie the emergence of basic allocentric spatial memory. We also proposed that the protracted development of the dentate gyrus and its projections to the CA3 field of the hippocampus might underlie the development of high-resolution allocentric spatial memory capacities, based on the essential contribution of these structures to the process known as pattern separation. Here, we present an experiment designed to assess the development of spatial pattern separation capacities and its impact on allocentric spatial memory performance in children from 18 to 48 months of age. We found that: (1) allocentric spatial memory performance improved with age, (2) as compared to younger children, a greater number of children older than 36 months advanced to the final stage requiring the highest degree of spatial resolution, and (3) children that failed at different stages exhibited difficulties in discriminating locations that required higher spatial resolution abilities. These results are consistent with the hypothesis that improvements in human spatial memory performance might be linked to improvements in pattern separation capacities.

**Keywords**

capacity, episodic, hippocampus, memory, pattern separation



Allocentric spatial memory, the memory for locations coded in relation to the objects comprising our surrounding environment, is a fundamental component of episodic memory: the "where" component of the defining "what, where and when" of episodic memories (Tulving, 2002). An allocentric spatial representation of one's environment, which is also described as a viewpoint-independent representation, is distinct from an egocentric spatial representation where the locations of objects are coded in relation to one's own body, in a viewpoint-dependent manner (Nadel & Hardt, 2004). Allocentric spatial memory has been shown to be dependent on the integrity of the hippocampal formation (a brain structure described in more detail below) in adult rodents (Morris, Garrud, Rawlins, & O'Keefe, 1982; Morris, 2007; O'Keefe & Nadel, 1978), monkeys (Banta Lavenex, Amaral, & Lavenex, 2006), and humans (Abrahams, Pickering, Polkey, & Morris, 1997; Banta Lavenex, Colombo, Ribordy Lambert, & Lavenex, 2014; Holdstock et al., 2000; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). In contrast, egocentric spatial memory is sensitive to lesions of the parietal and parahippocampal cortices, but persists following lesion of the hippocampal formation (Eichenbaum, Stewart, & Morris, 1990; Rogers & Kesner, 2006; Weniger & Irle, 2006; Weniger, Ruhleder, Wolf, Lange, & Irle, 2009).

We previously reported the emergence of basic allocentric spatial memory abilities in children at 2 years of age (Ribordy, Jabès, Banta Lavenex, & Lavenex, 2013), when children were able to discriminate one goal location among four locations, 220 cm apart, in a 4 m × 4 m open-field arena closed off by curtains on three sides. This finding was consistent with previous findings from Newcombe and colleagues (Newcombe, Huttenlocher, Bullock Drummey, & Wiley, 1998; Sluzenski, Newcombe, & Satlow, 2004), who described the emergence of allocentric spatial capacities in children around 22 months of age. Furthermore, we found that by 3.5 years of age, children exhibited high-resolution allocentric spatial memory capacities allowing them to learn and remember three rewarded locations among 18 closely-apposed locations, 80 cm apart, in the same 4 m × 4 m open-field arena (Ribordy et al., 2013). Neuroanatomical data in monkeys suggests that the emergence of allocentric spatial memory capacities coincides with the development of particular hippocampal circuits (Jabès, Banta Lavenex, Amaral, & Lavenex, 2011; Lavenex & Banta Lavenex, 2013; Ribordy et al., 2013). The hippocampal formation, a serially- and parallely-organized memory structure, is at the apex of a hierarchy of associational networks, and acts to ultimately integrate much of the processing that takes place within the neocortex and a number of subcortical brain areas (Lavenex & Amaral, 2000). The predominant trisynaptic hippocampal pathway

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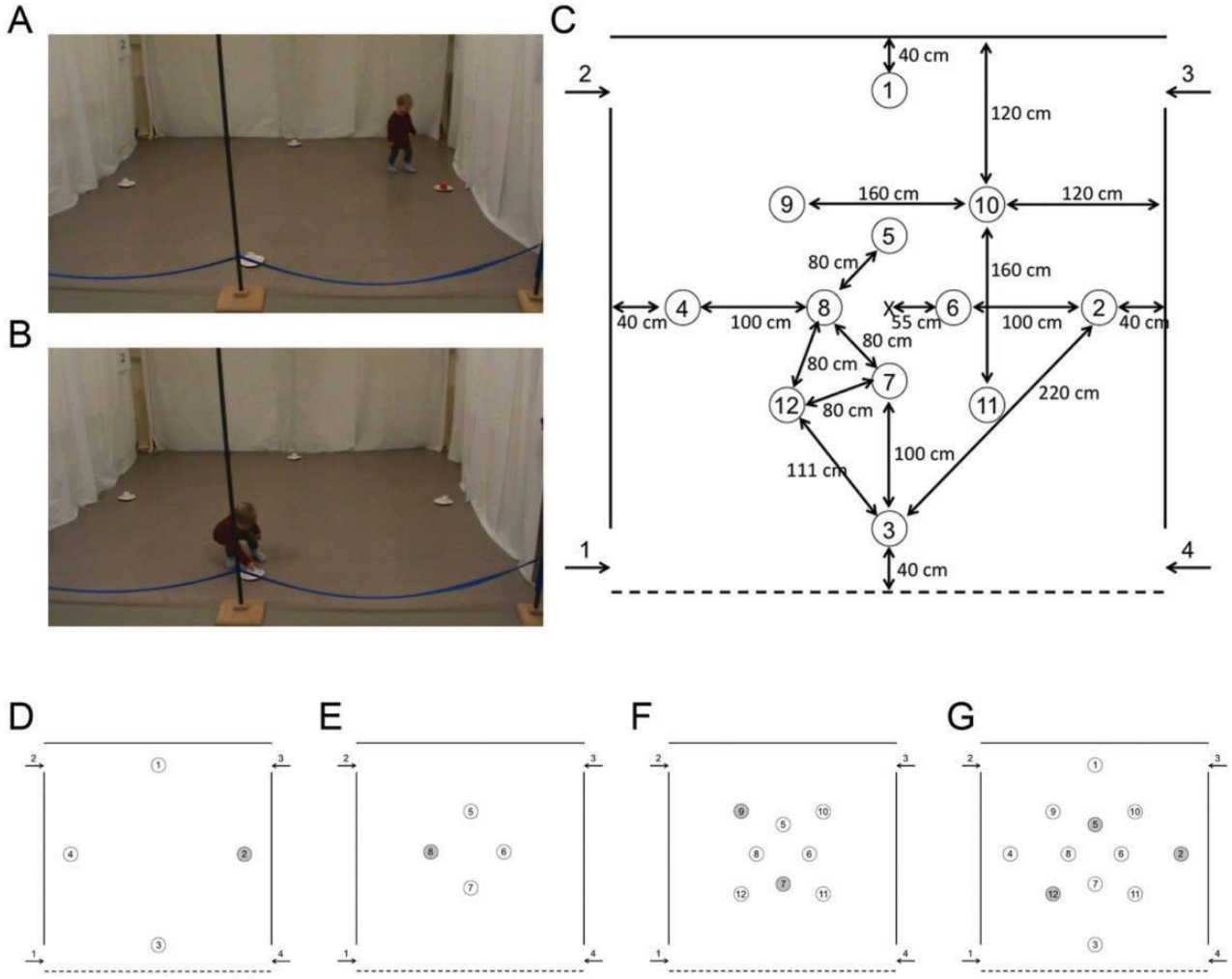


**Figure 1.** Experimental setup. A. Picture of a participant in the arena in the local cue (LC) condition of Stage 1. B. Picture of a participant in the arena in the allocentric spatial (AS) condition of Stage 1. C. Schematic representation of all 12 locations and their actual positions in the arena. D. Schematic representation of Stage 1, with 1 rewarded location (either 2 or 4) among 4 potential locations (1–4) on the *outer array*. E. Schematic representation of Stage 2, with 1 rewarded location (either 6 or 8) among 4 potential locations (5–8) on the *inner array*. F. Schematic representation of Stage 3, with two rewarded locations: location 7 on the *inner array*, and location 9 on the *middle array* (locations 9–12). G. Schematic representation of Stage 4, with three rewarded locations: location 2 on the *outer array*, location 5 on the *inner array*, and location 12 on the *middle array*.

treats afferent information coming from the cortex to the entorhinal cortex, to the dentate gyrus, to CA3, to CA1. However, parallel pathways send afferent information from the entorhinal cortex directly to CA3, CA1 and the subiculum (see Graphical Abstract and Figure 1 of Lavenex & Banta Lavenex, 2013). Evidence from lesion and neuroimaging studies suggests that discrete hippocampal substructures carry out discrete functions. For example, CA1 is proposed to act as a comparator, detecting mismatch between previously stored memory traces and currently perceived stimuli (Chen, Olsen, Preston, Glover, & Wagner, 2011; Duncan, Ketz, Inati, & Davachi, 2012). The dentate gyrus and CA3 are thought to subserve two complementary processes: pattern separation, the process of transforming neural representations that code our memories of related events, items or locations into more dissimilar, non-overlapping neural representations; and pattern completion which facilitates recall when a memory is cued by a noisy or incomplete set of cues (Bakker, Kirwan, Miller, & Stark, 2008; Gilbert, Kesner, & DeCoteau, 1998; Gold & Kesner, 2005; Leutgeb, Leutgeb, Moser, & Moser, 2007; Nakazawa et al., 2002; Neunuebel & Knierim, 2014). We previously proposed that the early functional maturation of direct projections from the entorhinal cortex to CA1 might underlie the emergence of basic allocentric spatial memory (Jabès et al., 2011; Lavenex & Banta Lavenex, 2013; Ribordy et al., 2013), allowing young children to learn and remember locations based on allocentric topological relations with environmental cues. We also proposed that the protracted development of the dentate gyrus and its projections to CA3 might underlie the emergence of more elaborate, high-resolution allocentric spatial memory capacities (Jabès et al., 2011; Lavenex & Banta Lavenex, 2013; Ribordy et al., 2013), based on the essential contribution of these structures to the process of pattern separation.

Although pattern separation is thought to be a common feature of many neuronal ensembles, it is believed to be an especially prominent and important feature of the dentate gyrus. Indeed, computational models and imaging studies in humans (Bakker et al., 2008; Treves & Rolls, 1994; Yassa et al., 2011; Yassa & Stark, 2011), as

well as lesion/inactivation studies in rodents (Gilbert & Kesner, 2006; Gilbert et al., 1998; Gilbert, Kesner, & Lee, 2001), highlight the role of the dentate gyrus and its projections to CA3, as being particularly important for pattern separation. In rodents, for example, although lesion of the dentate gyrus does not entirely disrupt allocentric spatial memory capacities (lesioned animals are still able to find one goal location in the Morris water maze; Brun et al., 2002; Nakashiba, Young, McHugh, Buhl, & Tonegawa, 2008), it does disrupt the animals' ability to distinguish closely-apposed locations in allocentric spatial memory tasks (Gilbert & Kesner, 2006; Gilbert et al., 1998, 2001).

Here, we present the results of a multi-stage study designed to assess the development of spatial pattern separation capacities and its impact on allocentric spatial memory performance in children from 18 to 48 months of age.

## Methods

### Participants

Participants were 59 children between 1.5 and 4 years of age (26 males: 19.7–47.1 months; 33 females: 17.9–48.3 months). Participants were tested one to four times (in one to four separate stages), dependent on their successful performance at each stage. Testing at each stage consisted of two sessions of approximately 45 minutes, which took place in general on 2 consecutive days, but may have been separated by up to 3 days depending on the participant's availability. Testing took place Monday through Saturday, between 8 a.m. and 6:30 p.m. Human subjects research was approved by the Intercantonal Ethics Committee for Jura, Neuchatel, Fribourg (protocol no. 10/2007), and the Ethical Commission for Clinical Research in Vaud (protocol no. 38/08), and was in accordance with the NIH guidelines for the use of human subjects in research. The parents of all participants gave informed written consent.

### Testing facility

We had testing facilities at two different sites in Switzerland; 9 children were tested in the canton of Vaud, and 50 in the canton of Fribourg. We found no differences in the behaviour or performance of the children tested in these two locations, and therefore data gathered at these two sites was grouped for analysis and presentation. The main features of the testing facilities were consistent between the two sites. Testing took place within large rectangular rooms (Vaud: 9 m × 6 m; Fribourg: 7 m × 6 m) containing many polarizing features such as doors, obscured windows, tables, chairs, wall posters (Ribordy et al., 2013). Within the room, we placed a 4 m × 4 m testing arena (Figure 1) that consisted of three walls made of suspended, opaque plastic curtains (2 m high). Whereas the curtain on the back wall was 4 m wide, the curtains on the side walls extended only 3 m, so that there was a 50 cm gap at the front and the back of the wall, thus creating four entry points through which participants passed in order to enter and exit the arena. The fourth (front) boundary of the arena was delineated by a rope attached to the two opposing sides of the arena, and suspended 30 cm off the ground. Exterior to the two side walls, the inter-trial waiting area was a corridor (1 m × 4 m) that contained two chairs with their backs to the arena, and various items including a trash can, occluded windows, doors, child-oriented posters, none of which could be viewed from within the arena. Importantly, from within the arena, and from the inter-trial waiting area, participants had access to distant visual cues in front of the arena.

The arena's floor was uniform and the testing arena was empty, except for symmetrically arranged white paper plates (18 cm in diameter; Figure 1C–G). An inverted opaque plastic cup (7.5 cm in diameter, 6.5 cm high) was placed on each plate. A reward was placed under the inverted cup at the goal location, for example location 2 or 4 for Stage 1 (Figure 1D), or locations 2, 5 and 12 for Stage 4 (Figure 1G). Participants had to lift or turn over the plastic cups to obtain the reward. Rewards were referred to as "treats" and were usually Smarties®, Goldfish® crackers, pieces of breakfast cereal or pretzels. Occasionally, small stickers served as rewards for children that were not interested in food rewards. All parents were queried with respect to alimentary allergies prior to any testing. All testing was videotaped with a video camera located in front of the testing arena.

### Testing procedure

*General description.* All testing involved a team of two experimenters. Experimenter 1 (E1) would stay with the child throughout testing and would enter the arena with the child, encourage the child to search for the hidden rewards, verbally praise the child when a reward was found, pick up cups that had been searched by the child and place them in a plastic bucket that she carried, direct the child to the correct exit at the end of the trial, and occupy the child during the inter-trial interval by reading or talking. Experimenter 2 (E2) was responsible for replacing the reward(s) between trials, recording the data, and announcing the entry and exit doors.

Before testing began, children were free to view the arena with the arranged plates (no cups present), from in front of the arena. E1 then showed the child a reward item on a paper plate that she held in her hand. While the child was watching, E1 would lower a white plastic cup over the treat to hide it. The child would then be asked "Where is the treat? Can you show me where it is?" When the child lifted the cup to expose the treat, they would be verbally praised and told that the treat was theirs to eat or keep in a bag for later. Once the child had been shown that treats could be found underneath the plastic cup, the child and E1 would go to the predetermined side of the arena where testing would begin. If the child was reluctant to go alone with E1, the child's accompanying parent would be asked to join E1 and the child. Once the child was behind the curtain and occupied, E2 would hide a treat in the predetermined rewarded location(s). For Stage 1, location 2 was the designated goal for half of the children and location 4 was the designated goal for the other half. Children completed two different types of trials: Local Cue trials and Allocentric Spatial trials. On Local Cue (LC) trials, a local cue, a red cup, covered the reward(s) (Figure 1A), whereas non-rewarded locations were covered with white cups. This condition allowed us to gauge children's motivation to participate, as well as to test each child's ability to find rewards at spatially fixed locations marked by a local cue. In this condition, children could find and remember the reward location either by associating the presence of the local cue with the reward, or by remembering the allocentric spatial location of the reward based on its relations to distal environmental objects (Lavenex & Schenk, 1995, 1997; Lavenex, Shiflett, Lee, & Jacobs, 1998). Although some may consider unlikely that children would use allocentric memory in the presence of the local cues, because both the local cue and the

absolute spatial position of the rewarded location are coherent, children may rely on either source of information to determine the reward location. Indeed, we have previously shown that both adults and children can learn and remember rewarded locations following a single experience in the local cue condition (Banta Lavenex & Lavenex, 2010; Ribordy et al., 2013), thus supporting the theory that allocentric information is continuously and automatically encoded during exploration and navigation (Andrade & Meudell, 1993; Ellis, 1991; Wang & Morris, 2010). On Allocentric Spatial (AS) trials, no local cues marked the reward location, as white cups covered all locations. In this case, children could not discriminate between rewarded and never-rewarded locations based on local features. Instead, children had to rely on an allocentric spatial representation of the environment to discriminate these locations, that is, they had to code the goal location in relation to distal environmental objects. Local cue and allocentric spatial trials alternated ($LC_1$, $AS_1$, $LC_2$, $AS_2$, ... , $LC_{10}$, $AS_{10}$). At each stage, each participant had a total of 20 trials (10 LC and 10 AS trials) distributed over two sessions. Detailed information regarding age-dependent verbal instructions and conditions ensuring task specificity were described previously (Ribordy et al., 2013).

*Four stages.* The goal and decoy locations were located at the corners of a matrix of up to three nested squares (Figure 1C), and children were tested on up to four successive stages. For Stage 1, there was one goal among four locations distributed in a large square pattern rotated 45 degrees relative to the orientation of the arena (Figure 1D); we refer to this array as the *outer array*. Adjacent corners were separated by 220 cm, opposite corners separated by 310 cm, and each corner located 40 cm from the nearest wall of the arena. For half of the participants, location 2 was rewarded, for the other half, location 4 was rewarded (locations 1 and 3 were never rewarded). For Stage 2, there was one goal among four locations distributed in a small square pattern rotated 45 degrees, the *inner array* (Figure 1E). For each participant, the location on the opposite side from the location that was rewarded in Stage 1 was rewarded (thus, for half of the participants, location 6 was rewarded, and for half, location 8). For Stage 3, there were two goals among eight locations distributed on two nested squares (maintaining a 1:3 ratio between rewarded and non-rewarded locations): the *inner array* with location 7 rewarded, and a *middle array*, which consisted of a mid-size square aligned with the arena's walls, on which location 9 was rewarded (Figure 1F). For Stage 4, rewarded locations were found on all three of the nested squares: location 2 on the *outer array*, location 5 on the *inner array*, and location 12 on the *middle array* (maintaining a 1:3 ratio between rewarded and non-rewarded locations, Figure 1G).

All participants were tested in Stage 1 ($n = 59$). In Stage 2, the potential goal locations were closer to each other than in Stage 1, and optimal performance was supposed to require increased spatial resolution abilities as compared to Stage 1. Therefore, only the participants that performed above chance level in Stage 1 (at least 5 errorless trials within the last 8 trials in the AS condition: unilateral paired $t$ test, $p < .05$) continued with testing on Stage 2. The same criterion was used at each consecutive stage, as the task design required increased spatial resolution abilities at each stage. However, some children who succeeded on Stage 1 were unable to participate in the rest of the experiment for reasons unrelated to their performance. For each stage, we report the number of participants, their sex and age (see also Supplementary Table 1). Usually 6 days (but no less than 2) elapsed between stages. At the beginning of each stage, E1 explained to the child that E2 chose (a) new location(s) to hide the treats that the child should discover and remember, because these new locations would now remain the same.

## Data analysis

For each stage, we first analysed the number of correct choices made before erring (CBE), as a proxy to estimate memory capacity (Banta Lavenex, Boujon, Ndarugendamwo, & Lavenex, 2015; Banta Lavenex et al., 2014), and calculated an average value per child for the last 8 trials in the AS condition (omitting the first 2 trials). We also determined the average of the total number of locations visited (TNV) in order to find the reward for the last 8 trials in the AS condition. These two measures provide different kinds of information about task performance and thus more specific clues about memory processes: CBE requires perfect memory performance in order to get the maximal score, whereas TNV allows us to discriminate between a child making one error before finding the reward(s), no matter when the child makes the error in the sequence of visits, and a child finding the reward(s) after making several errors. We did not include the first two trials in the AS condition, because performance during these initial trials is strongly influenced by the drive to explore the environment following a change in the task, and are thus not representative of the subjects' optimal performance.

## Statistics

First, we performed regression analyses on the number of correct choices before erring (CBE), and on the number of visits to find the reward (TNV), with the age of children (in months) as a predictor. Second, we split children into two groups: 45 children younger than 35.7 months of age (20 boys and 25 girls: average = 26.2 months, range 17.9–35.6 months) and 14 children older than 35.7 months of age (6 boys and 8 girls: average = 48.3 months, range: 35.8–48.3 months). This age corresponded to the age at which task performance reached a stable and maximum level in Stage 1, as well as to the median-split age of the children who performed above criterion in Stage 1 and were able to continue with Stage 2. Third, we analysed the types of locations chosen by children upon entering the arena: whether it was a rewarded location and the position of unrewarded choices in relation to the goal. For Stages 1 and 2, we analysed the first choice (since there was only one rewarded location) for each of the first four trials in the AS condition, that is only during the learning phase when children still made a sufficient number of errors for this analysis to be informative with respect to the type of information guiding their choices (children made too few errors thereafter). For Stage 3, we analysed the first choice and the first two choices (since there were two rewarded locations) for each of the last 8 trials in the AS condition (once performance was stable). In contrast to Stages 1 and 2, for Stage 3 we focused the data analysis on the trials following the initial exploration phase triggered by the change in configuration of rewarded locations (once children had explored and became familiar with the new configuration of locations in the arena). For Stage 4, we analysed the first choice and the first three choices (since there were three rewarded locations) for each of the last 8 trials in the AS condition, again once performance was stable and children had a chance to explore and become familiar with the new configuration of locations in the arena. For these analyses, we normalized the number of choices based on the

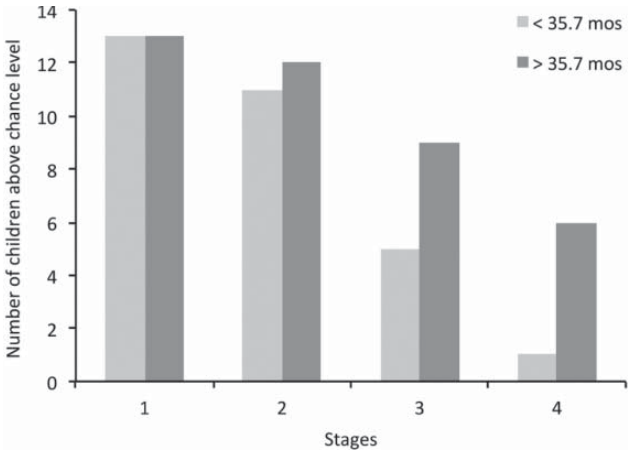


**Figure 2.** Numbers of children who performed above chance level at each experimental stage. Approximately the same number of younger (<35.7 months) and older (>35.7 months) children passed Stages 1 and 2, whereas fewer younger children who passed Stage 1 performed above chance level in Stage 4. See main text and Supplementary Table 1 for more information.

probability to make those choices. The number of choices of the rewarded location on any array was divided by one, and the number of choices of unrewarded locations on the same array (inner, middle or outer array) was divided by three. We performed analyses of variance (ANOVA) with age as a factor (younger versus older) and the types of choices as repeated measures. Significance level was set at $p < .05$ for all analyses. All statistical analyses were performed with SPSS 18.0 statistical software.

## Results

### *Overall performance*

The number of children performing the task above chance level decreased at each successive stage (Figure 2; note that this graph represents only the children who passed Stage 1 and were available to participate in the multi-stage study over several weeks, $n = 26$). Older (> 35.7 months) children successfully passed a greater number of stages than younger (< 35.7 months) children (Supplementary Table 1: > 35.7 months: 3.08 $\pm$ 0.29 stages; < 35.7 months: 2.31 $\pm$ 0.24 stages: one-tail $t$ test: $t_{(24)} = 23.151$, $p = .0251$). Eleven of 13 younger children (85%) and 12 of 13 older children (92%) passed Stage 2; five of 11 younger children (45%) and nine of 12 older children (75%) passed Stage 3 ($Chi^2$ analyses were not significant). At Stage 4, six older children performed above chance level (of 13 who started in Stage 1), whereas only one younger child did (of 13 who started in Stage 1; $Chi^2 = 4.887$, $p < .05$).

### *Stage 1*

Participants were 59 children between 1.5 and 4 years of age (26 males, range: 19.7–47.1 months; 33 females, range: 17.9–48.3 months). Although we previously showed that basic allocentric spatial memory abilities emerge around 24 months of age (Ribordy et al., 2013), here we found that allocentric spatial memory performance for one location among four locations further improves after 24 months of age. Specifically, we found that for children from 17.9 to 48.3 months of age, the number of correct choices made before an error increased with age (CBE $= -0.0009\ \text{age}^2 + 0.0811\ \text{age} - 0.8906$; $R^2 = 0.49657$; $p < .0001$; Figure 3A), and the total number of visited locations to find the reward decreased with age (TNV $= 0.002\ \text{age}^2 - 0.174\ \text{age} + 4.8185$; $R^2 = 0.48296$; $p < .0001$; Figure 3B). Nevertheless, in Stage 1, we observed a ceiling effect with a maximal performance being reached at about 36 months of age.

In order to characterize the factors that might contribute to this gradual improvement in memory performance and determine what might be guiding their choices when they did not respond correctly, we analysed the errors made by children in their first choice upon entering the arena. We analysed the children's choices in the first four trials in the AS condition of Stage 1, that is, during the early learning phase. Of the 59 children included in the study, only 44 children were included in this analysis: nine children did not make any errors (four younger and five older children), and six younger children were excluded because they failed the task in the LC condition. Therefore, the group of younger children comprised 35 children (15 boys and 20 girls: average age: 26.4 months, range: 18.0–35.2 months); the group of older children comprised 9 children (6 boys and 3 girls: average age: 43.7 months, range: 39.3–48.3 months).

When they did not choose the goal location as their first choice upon entering the arena, both groups of children made the same types of errors, Figure 3D; age: $F(1, 42) = 0.52$, $p = .48$; choices: $F(2, 84) = 26.85$, $p = .0001$; interaction: $F(2, 42) = 1.53$, $p = .22$. Both younger and older children chose more often the location that was directly in front of them when entering the arena (Adjacent front: location 3 if entering from door 1 or 4; location 1 if entering from door 2 or 3; Figure 3C) than both the location opposite to the goal (location 4 if location 2 was rewarded, or location 2 if location 4 was rewarded; $p = .0001$), as well as the location adjacent to the goal that required crossing the arena (location 1 if entering from door 1 or 4; location 3 if entering from door 2 or 3; $p = .0001$). They also chose the location opposite to the goal more than the location adjacent to the goal that required crossing the arena (i.e., location 1 or 3, depending on the entrance; $p = .003$). We found the same pattern of results when considering only the children performing at least 5 errorless trials in the last 8 AS trials, who therefore continued on to Stage 2, or the children that failed to perform 5 errorless trials in the last 8 AS trials, who therefore did not continue on to Stage 2 (data not shown).

### *Stage 2*

Since Stage 2 was supposed to require higher spatial resolution abilities, we only tested participants who performed above chance level in Stage 1. Thus, for Stage 2, only 13 younger children (9 girls, 4 boys: average age: 29.09 months, range: 21.2–35.6 months) and 13 older children (7 girls, 6 boys: average age: 42.76 months, range: 35.8–48.3 months) participated. Following this selection procedure, and in contrast to what was observed for Stage 1 which included all participants, the number of correct choices made before an error did not increase with age in Stage 2, Figure 4A; CBE $= 0.668 + 0.005 \times \text{age}$; $R^2 = 0.040$; $p = .328$. Similarly, the total number of visits to find the reward did not decrease with age in Stage 2, Figure 4B; TNV $= 1.672 - 0.012 \times \text{age}$; $R^2 = 0.084$, $p = .151$.

We also analysed the children's choices for the first four trials in the AS condition (Figure 4D). When they did not choose the goal location as their first choice upon entering the arena, children did not choose significantly more any particular type of unrewarded

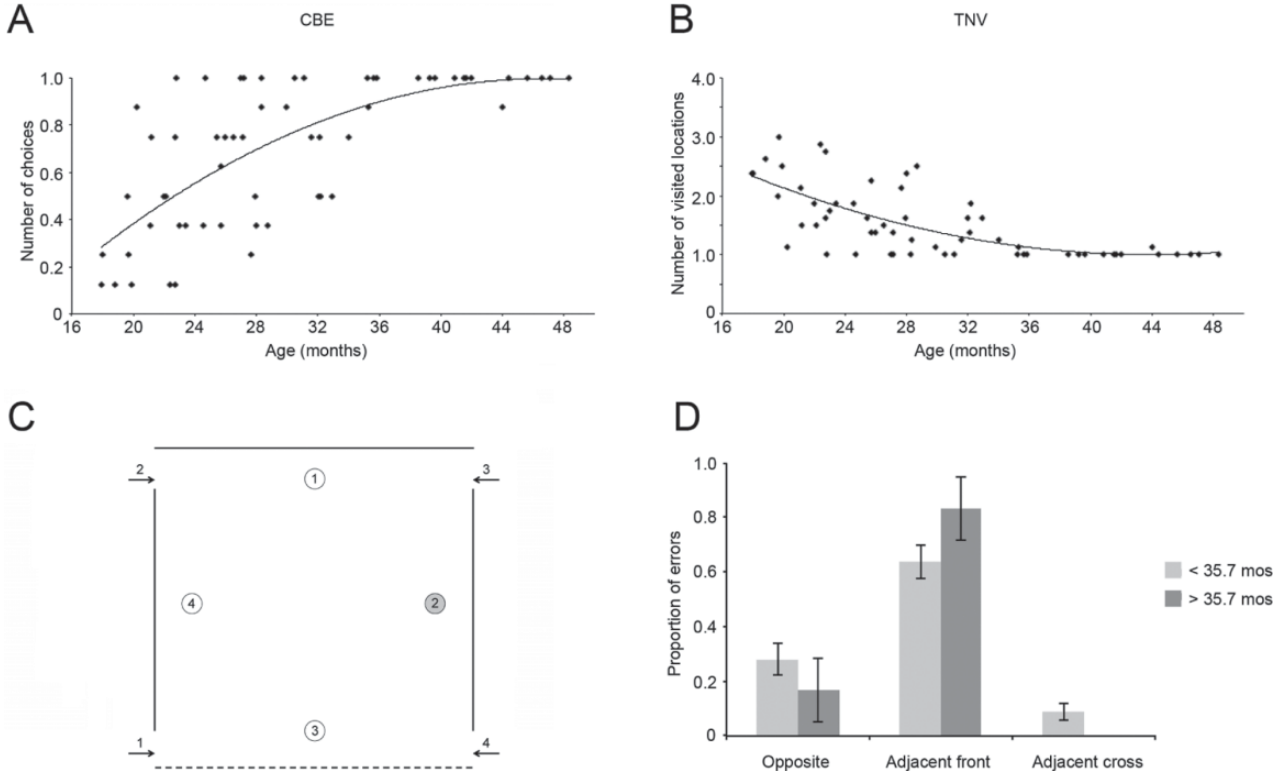


**Figure 3.** Results for children who participated in Stage 1 ($n = 59$), with one rewarded location among four potential locations. A. Number of correct choices made before making an error (CBE): CBE $= -0.0009\ \text{age}^2 + 0.0811\ \text{age} - 0.8906$; $R^2 = 0.49657$; $p < .0001$. B. Total number of visits to find the reward (TNV): TNV $= 0.002\ \text{age}^2 - 0.174\ \text{age} + 4.8185$; $R^2 = 0.48296$; $p < .0001$. C. Schematic representation of the testing arena. D. Types of visited locations when children (younger <35.7 months; older >35.7 months) made an error in the first four trials in the AS condition. Opposite: opposite to goal location (i.e., location 2 or 4); Adjacent front: Adjacent to goal location (i.e., location 1 or 3) and in front of entry door; Adjacent cross: adjacent to goal location (i.e., location 1 or 3) but across the arena from the entry door.

locations; age: $F(1, 11) = 0.408$, $p = .536$; choices: $F(2, 22) = 0.645$, $p = .160$; interaction: $F(2, 22) = 0.645$, $p = .534$.

## *Stage 3*

For Stage 3, 11 younger children (8 girls, 3 boys: average age: 28.6 months, range: 21.2–35.3 months) and 12 older children (7 girls, 5 boys: average age: 42.7 months, range: 35.8–48.3 months) participated. The number of correct choices made before an error increased with age, Figure 5A; CBE $= 0.012 + 0.037 \times$ age; $R^2 = 0.219$; $p = .025$. Accordingly, the total number of visits to find the reward decreased with age, Figure 5B; TNV $= 6.683 - 0.094 \times$ age; $R^2 = 0.222$; $p = .023$. Younger children made fewer correct choices before erring than older children, Figure 5A; Mann-Whitney U $= 28.00$, $p = .019$; they also visited more locations to find the reward than older children, Figure 5B; Mann-Whitney U $= 25.50$, $p = .012$.

*First choice.* In order to determine what might contribute to this differential performance, we analysed the first location children visited upon entering the arena, in the last eight trials in the AS condition, once task performance was stable. The two groups of children did not differ in their choice of the first visited location, Figure 5C; age: $F(1, 21) = 2.89$, $p = .104$; locations: $F(3, 63) = 33.84$, $p = .0001$; interaction: $F(3, 63) = 2.24$, $p = .093$. Children chose more often the rewarded location on the middle array (location 9) than the rewarded location on the inner array (location 7); they also chose the two rewarded locations more often than the unrewarded locations, Figure 5C; regardless of whether these locations were located on the inner or middle array; all $p < .05$. Interestingly, younger children chose the rewarded location on the inner array less often than older children did ($p = .039$).

In order to characterize the behaviour of children who passed Stage 3 ($n = 14$; 9 older and 5 younger children) and those who did not ($n = 9$; 3 older and 6 younger children), we grouped the children based on whether they passed or failed, rather than according to their age. For the first choice, the two groups of children did not choose the two rewarded locations with similar frequency, Figure 5E; Pass/Fail: $F(1, 21) = 20.842$, $p < .001$; locations: $F(3, 63) = 33.134$, $p < .001$; interaction: $F(3, 63) = 7.385$, $p < .001$. Whereas children who passed chose the two rewarded locations (on the middle and inner arrays) equally and more often than the unrewarded locations (location 9 = location 7 > Other middle = Other inner; all $p < .05$), children who failed chose the rewarded location on the middle array more than all other locations but they did not choose the rewarded location on the inner array more than unrewarded locations (location 9 > location 7 = Other middle = Other inner; all $p < .05$).

*First two choices.* In contrast to what was observed for the first choice, younger and older children differed in the types of locations visited in their first two choices upon entering the arena, Figure 5D;

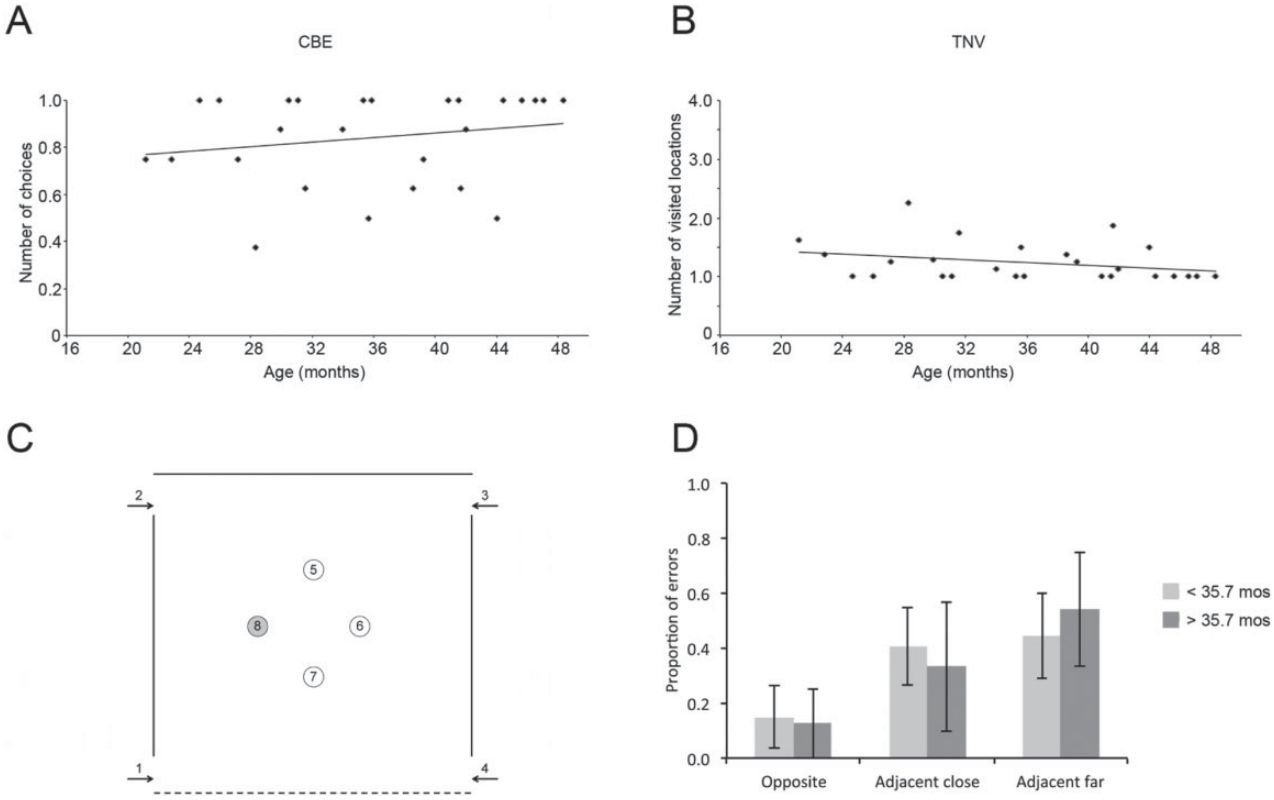


**Figure 4.** Results for children who participated in Stage 2, with one rewarded location among four closely-apposed potential locations. A. Number of correct choices made before making an error (CBE): CBE = 0.668 + 0.005 × age; $R^2 = 0.040$; $p = .328$. B. Total number of visits to find the reward (TNV): TNV = 1.672 − 0.012 × age; $R^2 = 0.084$, $p = .151$. C. Schematic representation of the testing arena. D. Types of visited locations when children made an error in the first four trials in the AS condition. Opposite: opposite to goal location (i.e., location 6 or 8); Adjacent close: adjacent to the rewarded location and closest to the entry door (i.e., location 5 or 7, depending on the entry point); Adjacent far: adjacent to the rewarded location and farther from the entry door (i.e., location 5 or 7, depending on the entry point).

age: $F(1, 21) = 3.825$, $p = .064$; locations: $F(3, 63) = 61.88$, $p = .0001$; interaction: $F(3, 63) = 4.80$, $p = .005$). Overall, children chose more often the rewarded locations than the unrewarded locations (regardless of whether these locations were located on the inner or middle arrays; all $p < .0001$). However, in contrast to older children's choices that did not differ between rewarded locations on the inner and middle arrays ($p = .089$), younger children chose more often the rewarded location on the middle array than the location on the inner array ($p = .015$). In addition, younger children chose the goal location on the inner array less often than older children did ($p = .009$).

Considering the first two choices of children who either passed or failed Stage 3, we found that the two groups of children did not choose the two rewarded locations with similar frequency, Figure 5F; Pass/Fail: $F(1, 21) = 80.929$, p < .001; locations: $F(3, 63) = 122.890$, $p < .001$; interaction: $F(3, 63) = 45.660$, $p < .001$. Whereas children who passed chose the two rewarded locations (on the middle and inner arrays) similarly and more often than the unrewarded locations (location 9 = location 7 > Other middle = Other inner; all $p < .05$), children who failed chose the rewarded location on the middle array more than unrewarded locations but did not choose the rewarded location on the inner array more than unrewarded locations (location 9 > other mid = other inner; all $p < .05$).

In sum, overall task performance in Stage 3 correlated with age in children from 21.2 to 48.3 months. In addition, choice analyses revealed that even though younger children discriminated rewarded locations from unrewarded locations, they were less efficient than older children at discriminating rewarded location on the inner array, although in Stage 2 these younger children showed that they were capable of discriminating the location on the inner array in absence of decoy locations surrounding it.

## *Stage 4*

For Stage 4, five younger children (3 girls, 2 boys: average age: 31.1 months, range: 24.7–35.3 months) and nine older children (6 girls, 3 boys: average age: 42.3 months, range: 35.8–48.3 months) participated. For Stage 4, the correlation between the number of correct choices made before an error and age failed to reach significance, Figure 6A; CBE = −0.048 + 0.057 × age; $R^2 = 0.218$; $p = .092$. In contrast, the number of visits to find the reward decreased significantly with age, Figure 6B; TNV = 9.853 − 0.137 × age; $R^2 = 0.360$, $p = .023$.

*First choice.* Younger and older children did not differ in their first choice upon entering the arena, Figure 6C; age: $F(1, 12) = 2.640$, $p = .130$; locations: $F(5, 60) = 14.897$, $p = .0001$, interaction: $F(5, 60) = 0.218$, $p = .953$. All children were more likely to visit the rewarded location on the outer array (location 2), than either the rewarded locations on the middle array (location 12) or the inner array (location 5). In addition, children were more likely to visit the

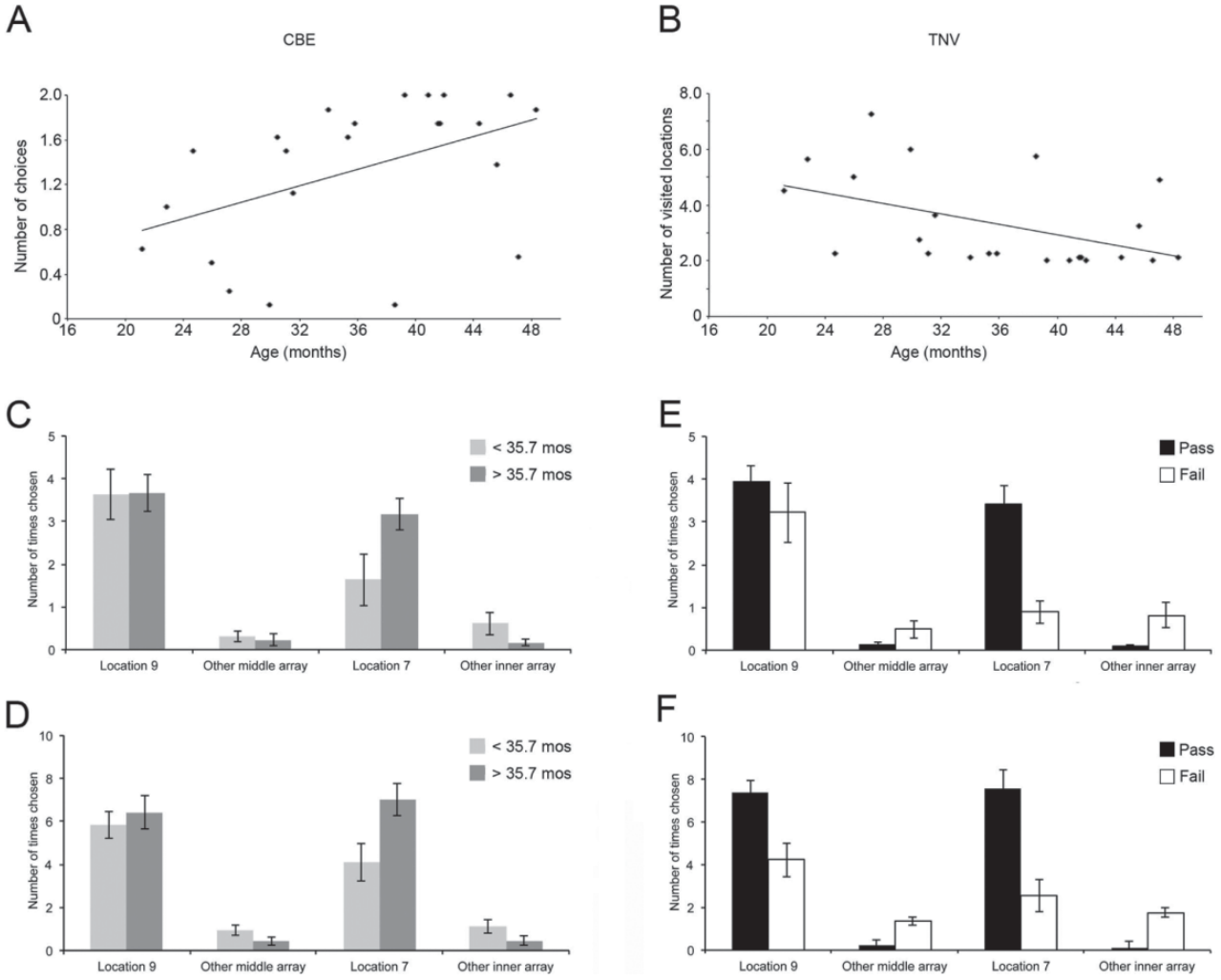


**Figure 5.** Results for children who participated in Stage 3, with two rewarded locations among eight potential locations. A. Number of correct choices made before making an error (CBE): CBE = 0.012 + 0.037 × age; $R^2 = 0.219$; $p = .025$. B. Total number of visits to find the reward (TNV): TNV = 6.683 − 0.094 × age; $R^2 = 0.222$; $p = .023$. C. First location visited by younger and older children in the last eight trials in the AS condition. D. First two locations visited by younger and older children in the last eight trials in the AS condition. E. First location visited by children that passed and children that failed Stage 3. F. First two locations visited by children that passed and children that failed Stage 3.



rewarded locations on the outer and middle arrays, locations 2 and 12, respectively, than unrewarded locations (all $p < .05$).

Considering the first choice of children who either passed (6 older and 1 younger children) or failed (3 older and 4 younger children) Stage 4, we found that children that passed chose more rewarded locations than children that failed, Figure 6E; Pass/Fail: $F(1, 12) = 5.194$, $p = .042$; locations: $F(5, 60) = 17.222$, $p < .001$; interaction: $F(5, 60) = 0.742$, $p = .595$. Overall, children chose the rewarded location on the outer array more than the rewarded locations on the middle and inner arrays as well as unrewarded locations (all $p < .05$).

*First three choices.* Younger and older children did not differ in their first three choices upon entering the arena, Figure 6D; age: $F(1, 12) = 2.35$, $p = .152$; locations: $F(5, 60) = 61.43$, $p = .0001$; interaction: $F(5, 60) = 1.43$, $p = .224$. Children were more likely to visit rewarded locations than unrewarded locations (all $p < 0.5$). In addition, they chose the rewarded location on the outer array (location 2) more often than the rewarded location on the inner array (location 5; $p = .020$).

Considering the first three choices of children who either passed or failed Stage 4, we found that the two groups of children did not choose the three rewarded locations with similar frequency, Figure 6F; Pass/Fail: $F(1, 12) = 32.56$, $p < .001$; locations: $F(5, 60) = 105.96$, $p < .001$; interaction: $F(5, 60) = 7.97$, $p < .001$). Whereas children who passed and children who failed chose the rewarded location on the outer array similarly ($p = .241$), children who failed chose the rewarded location on the middle array less than children who passed ($p = .007$); children who failed also chose the rewarded location on the inner array less than children who passed ($p = .003$).

In sum, in Stage 4, only the total number of visits (TNV), an overall measure of task performance, exhibited a statistically significant correlation with age. The first choice upon entering the arena indicated that all children chose preferentially the rewarded location on the outer array as compared to the rewarded locations on the middle and inner arrays. In addition, for the first three choices,

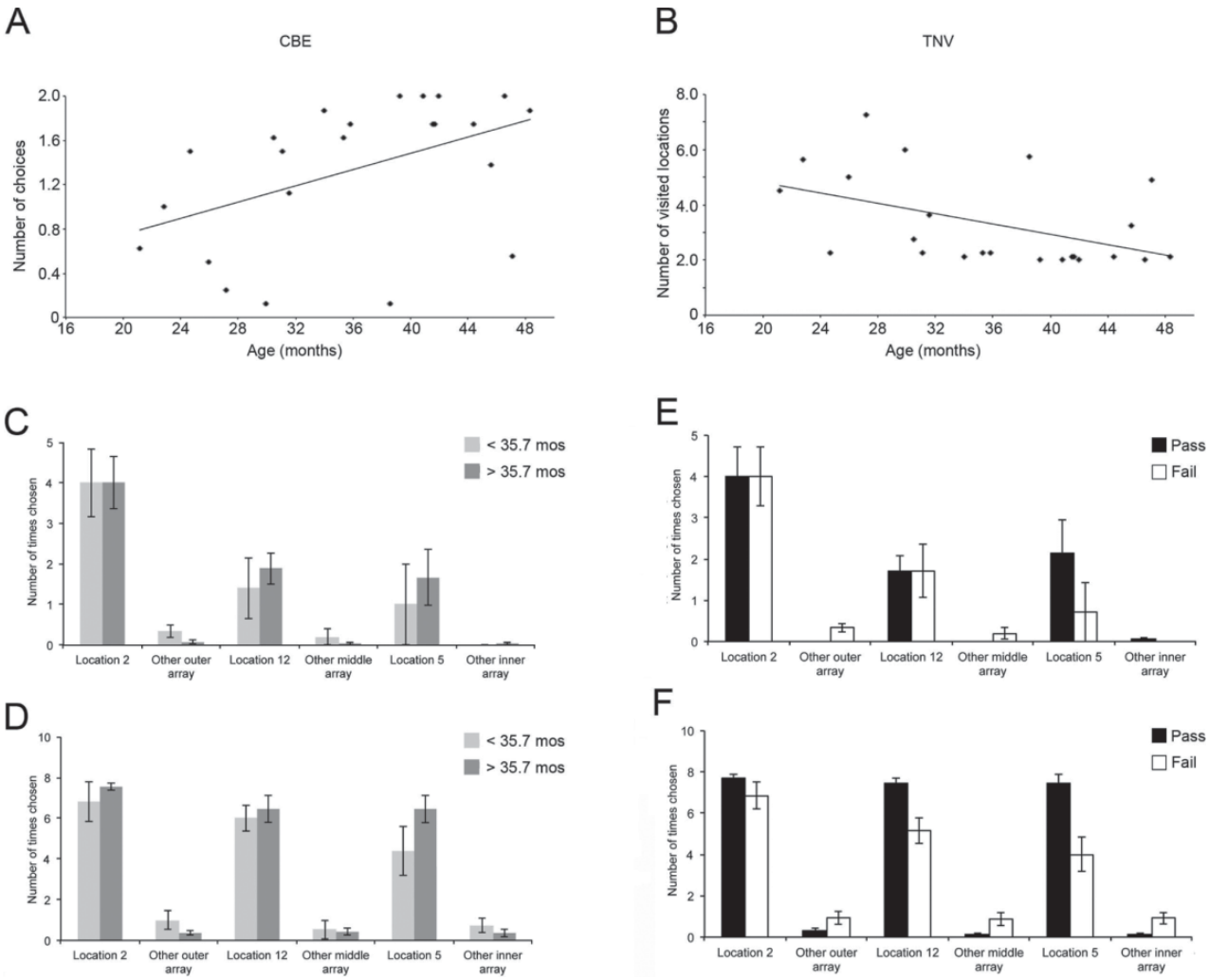


**Figure 6.** Results for children who participated in Stage 4, with three rewarded locations among 12 potential locations. A. Number of correct choices made before making an error (CBE): CBE = − 0.048 + 0.057 × age; $R^2 = 0.218$; $p = .092$. B. Total number of visits to find the reward (TNV): TNV = 9.853 − 0.137 × age; $R^2 = 0.360$, $p = .023$. C. First location visited by younger and older children in the last eight trials in the AS condition. D. First three locations visited by younger and older children in the last eight trials in the AS condition. E. First location visited by children that passed and children that failed Stage 4. F. First three locations visited by children that passed and children that failed Stage 4.

children who passed Stage 4, irrelevant of age, were able to discriminate the rewarded locations on the inner, middle and outer arrays equally well, $F(5, 30) = 267.828$, $p < .001$; location 2 = location 12 = location 5 > unrewarded locations; all $p < .05$), whereas the children who did not pass Stage 4 discriminated the location on the outer array significantly better than they discriminated the rewarded locations on the inner array, $F(5, 30) = 19.654$, $p < .001$; location 2 > location 5; rewarded locations > unrewarded locations; all $p < .05$).

## Discussion

### *Stage 1*

We previously reported that basic allocentric spatial memory abilities are reliably observed in children after 24 months of age (Ribordy et al., 2013). Here, we found that the youngest child to perform above statistically-defined chance level was 22.8 months of age, thus confirming our previous findings (Ribordy et al., 2013) and those of Newcombe and colleagues (Newcombe et al., 1998; Sluzenski et al., 2004). In addition, based on two different measures of memory performance (CBE: the number of correct choices before erring; TNV: the total number of visited locations to find the reward), we found that basic allocentric memory abilities improved from 18 to 36 months of age; performance reached ceiling level at about 36 months of age in this task.

When children made errors, they tended to open the first cup they encountered when entering the arena. This was true for children who succeeded in the task, as well as for children who failed. Could these errors be due to the fact that children failed to inhibit their response to unrewarded cups, despite the fact that they knew which cup was rewarded? If so, the maturation of inhibitory processes, rather than developmental changes in the ability to form spatial memories, might explain these results. However, in both this study and our previous study (Ribordy, 2013), we found that when a local cue marked the goal location(s), children older than 20 months were capable of choosing the rewarded location at above chance level, and thus were capable of inhibiting their

responses to unrewarded cups. Corroborating evidence comes from experiments by Newcombe and colleagues (Newcombe et al., 1998; Sluzenski et al., 2004), which similarly revealed the emergence of basic allocentric spatial abilities at around 22 months of age. In their task, children had to find the location of an object buried in sand. Since no visible decoy locations could trigger the children's response, their behavioural results were not subject to the influence of the maturation of behavioural inhibition processes. Thus, in our task, children who opened the unrewarded cup directly in front of the entry door during the first four AS trials are likely responding to a cup = reward association that they established before they developed the understanding that it is absolute location that predicts the presence of a reward. Altogether, these four studies (Newcombe et al., 1998; Ribordy et al., 2013; Sluzenski et al., 2004; the present study) indicate that: (1) basic allocentric spatial memory abilities are reliably observed after 24 months of age; (2) basic, low-resolution spatial memory performance continues to improve until at least 36 months of age; and (3) improvement in spatial memory performance after 24 months of age is unlikely to be due to the maturation of behavioural inhibition processes.

## *Stage 2*

Our previous findings that children younger than 43 months of age could not learn and remember three rewarded locations among 18 closely-apposed locations, 80 cm apart (Ribordy et al., 2013), led us to hypothesize that young children failed because they did not exhibit high-resolution allocentric spatial memory capacities allowing them to distinguish these closely-apposed spatial locations. For the current experiment, we therefore hypothesized that only older children might be able to perform above chance level in Stage 2, when children were asked to discriminate one goal among four closely-apposed locations, 80 cm apart, placed at the centre of the arena.

In contrast to our hypothesis, our results did not demonstrate a difference in the performance of younger (< 35.7 months) and older (> 35.7 months) children in Stage 2 with four closely-apposed locations: only 2 younger children (of 13) and 1 older child (of 13) did not perform above chance level (i.e., at least 5 errorless trials on the 8 last trials in the AS condition). Importantly, however, younger children made twice as many errors as older children on the first four trials in the AS condition (during the learning phase), and when children made an error, they almost always chose a location that was adjacent to the rewarded location (17 of 20 errors) rather than the location that was opposite to the rewarded location (3 of 20 errors; Figure 2D). Furthermore, there was no difference between children's choices for the adjacent location that was closest to their point of entry into the arena and the adjacent location that was farthest from their point of entry, demonstrating that children often ''passed by'' two other locations (either an adjacent and the opposite location or an adjacent and the rewarded location) in order to choose the adjacent location farthest from their point of entry. This finding provides further evidence against the influence of poor behavioural inhibition on task performance.

Although it seemed logical to predict that immature spatial pattern separation abilities would preclude younger children from being able to discriminate four closely-apposed locations, this is not what was observed in Stage 2. However, it is still possible that children who exhibited relatively poor spatial pattern separation abilities in Stages 3 and 4 still managed to solve the task in Stage 2 by relying on a topographic representation of the environment (Poucet, 1993). Using this type of coding, individuals can define locations in an allocentric manner relative to distal objects in their environment, but without the precise metric information provided by distance and angular (a.k.a. directional or bearing) estimations that are necessary to code locations in high resolution. Thus, a location in our arena might be defined as ''on the door side'' or ''on the cabinet side.'' However, in our experimental design, with four symmetrically arranged locations and entry points that lead children to enter equidistant from the two closest locations and equidistant from the two farthest locations, what is defined as ''on the door side'' may become ambiguous (both during encoding and recall), thus leading children to make errors to adjacent, but not opposite, locations. Accordingly, a basic allocentric representation of the environment might have been sufficient to support spatial memory performance in Stage 2.

## *Stage 3*

In Stage 3, participants were required to learn and remember the location of two goals among eight locations (maintaining the 1:3 ratio of rewarded to unrewarded locations). Both CBE and TNV correlated with age, and older children performed overall better than younger children. Although topographic coding may enable children to encode the rewarded location on the middle array, it will not be adequate to distinguish rewarded locations on the inner array from closely-apposed, surrounding decoy locations on the inner and middle arrays. Accordingly, whereas older children chose rewarded locations on the middle and inner arrays with similar frequency, younger children chose locations on the inner array less frequently than older children, and less frequently than they chose locations on the middle array. These results suggest that younger children had difficulty discriminating the locations on the inner array in Stage 3 (even though they demonstrated that they could discriminate the same locations with a high degree of accuracy in Stage 2), presumably because discriminating the rewarded location on the inner array from surrounding decoy locations required children to form high-resolution allocentric spatial representations.

## *Stage 4*

In Stage 4, participants were required to learn and remember the location of three goals among 12 locations (maintaining a 1:3 ratio of rewarded to non-rewarded locations). TNV correlated with age, but CBE did not. In the end, six older children (one male, five females: 39.3–48.3 months old) passed Stage 4, whereas only one younger child (male: 30.5 months old) did.

As for Stage 3, topographic coding was insufficient to enable children to discriminate locations on the inner array. In Stage 4, however, locations on the middle array were also surrounded by locations on the outer array, making it more difficult to use topographic coding, and thus requiring high-resolution spatial representation abilities in order to discriminate these locations. In contrast, topographic coding may enable children to discriminate rewarded locations from unrewarded locations on the outer array. Our analyses revealed that children of all ages chose the rewarded location on the outer array more often than the rewarded location on the inner array, suggesting that the location on the inner array

was more difficult to discriminate. Moreover, when we combined children who failed, regardless of age, and compared their performance to that of children who passed, we found that indeed, as predicted, children who failed chose the goal locations on the inner and middle arrays less often than children who passed, even though these children had previously discriminated these locations in Stages 2 and 3 in absence of surrounding decoy locations. Importantly, five of the seven children who passed Stage 4 were older than 42 months of age (the other two were 30.5 and 39.3 months), the age at which children had demonstrated high-resolution allocentric capacities necessary to learn and remember three goals among 18 locations in our previous study (Ribordy et al., 2013).

Altogether, our results suggest that a gradual improvement of spatial pattern separation abilities in children from 24 to 48 months of age might underlie the improvement in allocentric spatial memory performance. Although topographic allocentric coding remains available in order to solve basic allocentric tasks, as children age, they might become more competent at using angular and distance information to compute the precise coordinates of locations in allocentric terms (see further discussion below).

## *Memory load*

Since the number of rewarded locations increased from 1 to 2 to 3 across stages, while nevertheless maintaining a reward to decoy ratio of 1:3, it is possible that increasing memory load could negatively influence children's performance. However, the fact that in Stage 3, for example, with two rewarded locations to be learned over 20 trials, younger children showed that they had more difficulty in demonstrating where, specifically, the reward was located on the inner array, and not simply that there was a second rewarded location, argues against a major influence of memory load on performance. Indeed, if memory load were at the root of the problem, then children should not show a preference for the goal located on either the middle or inner array; instead, they should remember (or forget) different locations within the arena with equal frequency. In contrast, children had greater difficulty discriminating the goal on the inner array than the goal on the middle array. This suggests that, in this task, spatial resolution abilities might underlie spatial memory performance.

## *Spatial memory in previous studies*

Although our model linking the development of specific hippocampal circuits to the emergence of distinct allocentric spatial memory capacities is novel (Jabès et al., 2011; Lavenex & Banta Lavenex, 2013), the idea that there are distinct, yet integrated topological and high-resolution spatial encoding systems is not. Huttenlocher and colleagues previously described spatial processing as consisting of a system composed of a categorical spatial system and a fine-grained spatial system (Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Newcombe, & Sandberg, 1994). Poucet also described distinct neurobiological systems for coding topological versus metric (distances and angles) aspects of space (Poucet, 1993; Poucet & Benhamou, 1997). However, we specifically propose that a basic allocentric representation of space, which can be subserved by the CA1 field of the hippocampus without any major inputs from the dentate gyrus and CA3, encodes the topological or categorical relations between objects in the environment. In contrast, the functional maturation of the dentate gyrus and its projections to CA3 is required in order to process and incorporate the metric (fine-grained) information necessary to elaborate a high-resolution allocentric representation of space.

Accordingly, previous studies have shown that children's precision in the encoding of spatial location improves with age. Acredolo and colleagues found that 8-year-old children showed greater precision in remembering where an item had been dropped than 3- and 4-year-old children; they explained children's improvements in terms of an increasing ability to use metric information to code locations (Acredolo, Pick, & Olsen, 1975). In an experiment asking children to reconstruct a model town on the floor of either a room that had objects and landmarks in very close proximity (a classroom with the furniture moved to the sides of the room) or a room with very distal objects and landmarks (a gymnasium), Herman and Siegel found that performance of 5-year-olds was significantly improved when landmarks were in close proximity, whereas the performance of 7- and 10-year-olds was unaffected by the proximity of objects and landmarks (Herman & Siegel, 1978). Error that is inherent in the metric coding of locations comes from both distance and bearing estimation. Distance errors, for example, increase nearly linearly with the distance to the object being used as a landmark (Wiest & Bell, 1985); thus, the closer the landmarks, the more accurate the calculation. Accordingly, the results of Herman and Siegel (Herman & Siegel, 1978) are consistent with the hypothesis that the spatial resolution of 7- and 10-year-olds is higher than that of 5-year-olds. Finally, in a study testing the predictive value of the Dynamic Field Theory for spatial working memory in an egocentric A-not-B task, Schutte and colleagues found that A-not-B biases in a sandbox task depend both on the distance of target separation and on the age of the child being tested (Schutte, Spencer, & Schöner, 2003). When the targets A and B were separated by at least 15 cm in the sandbox, 2- and 4-year-olds made A-not-B-type errors, whereas 6-year-olds did not. However, when the A and B target locations were separated by only five cm, 6-year-olds made A-not-B-type errors, whereas 11-year-olds and adults did not. These findings are consistent with an improvement in spatial pattern separation and spatial resolution with age. However, our experiment differs from that of Spencer and colleagues in a fundamental way: Our task was an allocentric spatial memory task, whereas theirs was an egocentric spatial memory task (Schutte et al., 2003). Since we proposed that improvements in spatial pattern separation, brought about by the maturation of the dentate gyrus and its projection to CA3, underlie improvements in allocentric spatial memory performance, is it possible that they might also subserve the improvements in what may be described as an egocentric spatial working memory task?

Pattern separation, the orthogonalization of neural information, is a general property of neural ensembles (Hunsaker & Kesner, 2013). Thus, it is possible that brain regions responsible for processing egocentric spatial information, such as the posterior parietal cortex or the parahippocampal cortex, also perform pattern separation on egocentrically coded spatial information and that such processes improve with age. However, an alternative explanation is also possible. Although the A-not-B task presumably assesses ''where'' in an egocentric frame of reference, it does not preclude reliance on an allocentric representation of space to code the location of the targets in relation to the objects comprising the surrounding environment. In the Schutte et al.'s (2003) task, in order to accurately find the buried object, participants

must correctly judge locations that are not necessarily centred around their own body. A high-resolution, allocentric spatial representation coding the locations of the hidden objects based on both topological relations and metric information derived from the environment might improve task performance. Accordingly, improvements in spatial pattern separation in an allocentric frame of reference might also contribute to the improvements in a spatial memory task that can be solved with relatively less precision in an egocentric reference frame alone.

## *Episodic memory*

Infantile amnesia is the term used to describe the phenomenon that as adults we have no memories for the events or episodes of the first 2 to 3 years of our life. The period of infantile amnesia is followed by a period referred to as childhood amnesia from 3 to 7 years of age, where although as adults we have memories from that time, we have fewer memories than would be predicted based on simple forgetting alone (for a review, see Bauer, 2007). Interestingly, the offset of infantile amnesia around 2 years of age corresponds with the time when basic allocentric spatial memory emerges in children (Newcombe et al., 1998; Ribordy et al., 2013; Sluzenski et al., 2004). We have previously proposed that the emergence of basic allocentric spatial memory, as well as the offset of infantile amnesia, are subserved by the maturation of the direct projections from the entorhinal cortex to CA1 (Jabès et al., 2011; Lavenex & Banta Lavenex, 2013) which may enable the relational representation of multiple items that is necessary for both allocentric spatial and episodic memory. We also proposed that improvements in allocentric spatial memory after two years of age were linked to the protracted maturation of the dentate gyrus (Jabès et al., 2011; Lavenex & Banta Lavenex, 2013; Ribordy et al., 2013), to which significant numbers of postnatally-born neurons are added daily for the first several years of life (Jabès, Banta Lavenex, Amaral, & Lavenex, 2010).

Here, we further suggest that the progressive functional maturation of the dentate gyrus might similarly underlie improvements in episodic memory performance in children from 3 to 7 years of age, and eventually the offset of childhood amnesia. Improved coding of episodic memories requires pattern separation in order to make individual memories as distinct from one another as possible. Moreover, recalling memories at later time points likely requires a process known as pattern completion in order to recall multiple elements of an event, a process thought to be subserved by CA3 (Hunsaker & Kesner, 2013). Accordingly, the balance between highly plastic, immature neurons and less plastic, mature neurons born earlier during development, might not be optimally tuned to contribute to the separate encoding of distinct episodes until late postnatal development (Jabès et al., 2011). Constant remodelling of the dentate gyrus to CA3 pathway due to high rates of postnatal neurogenesis likely disrupt both pattern separation processes, as well as the maintenance of established memory traces (Jabès et al., 2010). A recent study carried out in rodents supports this view by showing that increasing rates of neurogenesis in the dentate gyrus of adult animals can induce forgetting, whereas reducing neurogenesis in immature rodents can reduce forgetting (Akers et al., 2014). Altogether, these results provide further credence to the hypothesis that the differential maturation of distinct hippocampal circuits contributes to the ontogeny of distinct memory processes in humans.


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### Supplemental material

Supplementary Table 1 is available online at http://jbd.sagepub.com/supplemental

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