

Children five-to-nine years old can use path integration to build a cognitive map without vision



Mathilde Bostelmann^a, Pierre Lavenex^a, Pamela Banta Lavenex^{a,b,*}

^a *Laboratory of Brain and Cognitive Development, Institute of Psychology, University of Lausanne, 1005 Lausanne, Switzerland*

^b *Faculty of Psychology, Swiss Distance University Institute, 3900 Brig, Switzerland*

ARTICLE INFO

Keywords:

Egocentric
Homing behavior
Allocentric
Cognitive map
Precision
Spatial resolution
Development

ABSTRACT

Although spatial navigation competence improves greatly from birth to adulthood, different spatial memory capacities emerge at different ages. Here, we characterized the capacity of 5–9-year-old children to use path integration to build egocentric and allocentric spatial representations to navigate in their environment, and compared their performance with that of young adults. First, blindfolded participants were tested on their ability to return to a starting point after being led on straight and two-legged paths. This egocentric homing task comprising angular and linear displacements allowed us to evaluate path integration capacities in absence of external landmarks. Second, we evaluated whether participants could use path integration, in absence of visual information, to create an allocentric spatial representation to navigate along novel paths between objects, and thus demonstrate the ability to build a cognitive map of their environment. Ninety percent of the 5–9-year-old children could use path integration to create an egocentric representation of their journey to return to a starting point, but they were overall less precise than adults. Sixty-four percent of 5–9-year-old children were capable of using path integration to build a cognitive map enabling them to take shortcuts, and task performance was not dependent on age. Imprecisions in novel paths made by the children who built a cognitive map could be explained by poorer integration of the experienced turns during the learning phase, as well as greater individual variability. In sum, these findings demonstrate that 5–9-year-old children can use path integration to build a cognitive map in absence of visual information.

1. Introduction

Although spatial competence improves greatly from birth to adulthood, different spatial capacities emerge at different ages during development (Lavenex & Banta Lavenex, 2013; Newcombe & Huttenlocher, 2000). Egocentric spatial capacities emerge first in the newborn, and dominate the child's spatial world for at least the first six months (Acredolo & Evans, 1980; Acredolo, 1978; Bremner, 1978). Between 8.5 and 12 months, infants become capable of using cues or landmarks to remember spatial locations (Acredolo & Evans, 1980; Bremner, 1978; Bushnell, McKenzie, Lawrence, & Connell, 1995), and can use landmarks that are close to a goal to recall that location (Lew, Bremner, & Lefkovitch, 2000). At the same time, infants demonstrate that they can also track their position relative to landmarks following simple positional changes that provoke changes in vestibular and optic flow inputs, such as translation along a straight line or rotational displacements (Cornell & Heth, 1979; Keating, McKenzie, & Day, 1986; Landau & Spelke, 1988; McKenzie, Day, & Ihlen, 1984). From 12 months of age, children can track their position relative to landmarks following more

* Corresponding author at: Faculty of Psychology, Swiss Distance University Institute, 3000 Brig, Switzerland.
E-mail address: pamela.banta@unidistance.ch (P. Banta Lavenex).

complex positional changes involving translation and rotation, i.e., when they move to a new location and change heading simultaneously (Acredolo & Evans, 1980; Acredolo, 1978; Acredolo, Adams, & Goodwyn, 1984; Bremner, Knowles, & Andreasen, 1994; Lew et al., 2000; Newcombe, Huttenlocher, Drummey, & Wiley, 1998). Finally, by 18 months of age, children can track the direction and the magnitude of their own rotational displacements in the absence of visual cues, a capacity fundamental to path integration (Rieser & Heiman, 1982; Rider & Rieser, 1988). The culmination of this early period of spatial competence improvement occurs around 20 months of age when the capacity to form viewpoint-independent, allocentric spatial representations of the environment begins to emerge in children, with reliable expression being observed in children 24 months of age and older (Newcombe et al., 1998; Ribordy Lambert, Lavenex, & Banta Lavenex, 2016; Ribordy, Jabès, Banta Lavenex, & Lavenex, 2013).

In a recent review, Newcombe (2019) provided an extensive description of empirical data supporting these incremental and hierarchical developmental profiles in children. Surprisingly, cognitive mapping abilities were described as emerging last and extremely tardily: “*In line with research on normative development, 12 years of age may be the time not only when cognitive maps become widely evident but also when the adult variation pattern stabilizes.*” (p. 6). It has also been reported that the integration of visual and self-motion information to support small-scale navigation may not be present in 4- to 8-year-old children (Nardini, Jones, Bedford, & Braddick, 2008), and that viewpoint-independent allocentric strategies are either lacking or rudimentary in children under 6 years of age (Nardini, Thomas, Knowland, Braddick, & Atkinson, 2009). However, these assessments contrast with experimental evidence showing that allocentric spatial processing emerges by two years of age in children (Newcombe et al., 1998; Ribordy et al., 2013), and that 3-year-old children benefit from external “room” landmarks to identify a toy’s location in an array of cups (Nardini, Burgess, Breckenridge, & Atkinson, 2006), as well as findings from previous studies describing the cognitive mapping abilities of children between 2.5 and 9 years of age (Landau, Gleitman, & Spelke, 1981; Landau, Spelke, & Gleitman, 1984; Morrongiello, Timney, Humphrey, Anderson, & Skory, 1995). Evaluation of the literature on the development of spatial capacities suggests that there may be two main reasons why the relevance of these previous findings has been overlooked. First, there may be some confusion about the concept of cognitive maps and its relation to the concept of allocentric spatial representations. Indeed, although the studies by Landau et al. (1981, 1984) and Morrongiello et al. (1995) clearly investigated cognitive mapping in children, and by inference the studies of Newcombe et al. (1998), Ribordy et al. (2013) and Ribordy Lambert, Lavenex, and Banta Lavenex (2015) also studied cognitive mapping, none of these publications used this term explicitly. Second, there may be some doubts concerning the validity and reliability of the results presented in the studies of Landau et al. (1981, 1984) and Morrongiello et al. (1995), which may have led some scholars to consider these results as insufficient evidence of cognitive mapping abilities in children. In this article, we will address both of these reasons, the former theoretically and the latter with empirical data, in an attempt to clarify the issue and establish a consistent age at which cognitive mapping abilities emerge in children.

1.1. Allocentric spatial representations are cognitive maps

Tolman (1948) first coined the term cognitive map and described it as “*a tentative map, indicating routes, paths and environmental relationships which finally determines what responses, if any, the animal will finally release*”. O’Keefe and Nadel (1978) concept of a cognitive map was consistent with Tolman’s definition, although they further proposed that cognitive maps possessed Euclidean properties, specifically exact directional and distance information. Recent views suggest that spatial cognitive maps represent the relationships between world elements such as objects, environmental landmarks and locations, which may support flexible behavior (Behrens et al., 2018); this view is consistent with Tolman’s conceptualization, and the one that we adopt here. Although the use of the term allocentric spatial representation is more recent, it is now well-accepted by experimental psychologists and neuroscientists alike that in the spatial domain, the terms allocentric representations and cognitive maps are synonymous (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Nadel & Hardt, 2004), and that both refer specifically to viewpoint-independent representations of the relations between different objects in the environment (Golledge, Klatzky, & Loomis, 1996; Langston et al., 2010; McNaughton et al., 2006; O’Keefe & Nadel, 1978; Ruddle & Lessels, 2006; Spiers & Barry, 2015; Wang, Chen, & Knierim, 2019; Wills, Cacucci, Burgess, & O’Keefe, 2010). Thus, animals that are capable of building allocentric spatial representations are capable of using these representations to navigate between objects in their environment in a flexible manner, and take novel, never before experienced routes or shortcuts, to navigate to a desired destination. Indeed, the ability to take novel routes has come to be regarded as hallmark evidence to infer the existence of cognitive maps.

It is also well-established that cognitive maps are subserved by a distributed network of neurons and neural systems in the medial temporal lobe that include head-direction cells, grid cells and place cells (Lavenex & Banta Lavenex, 2013; McNaughton et al., 2006; Newcombe, 2019; Taube, 2007; Wang et al., 2019). Moreover, anatomical and electrophysiological evidence in rats and monkeys (Jabès, Banta Lavenex, Amaral, & Lavenex, 2011; Langston et al., 2010; Lavenex, Banta Lavenex, & Amaral, 2004, 2007; Lavenex, Sugden, Davis, Gregg, & Banta Lavenex, 2011; Wills et al., 2010) and behavioral evidence in rats, monkeys and humans (Langston et al., 2010; Lavenex & Banta Lavenex, 2006, 2013; Newcombe et al., 1998; Ribordy et al., 2013; Wills et al., 2010) indicate that the spatial memory processes dependent on these neural systems emerge concomitantly with the functional maturation of different cell types and circuits in the medial temporal lobe.

In sum, evidence for the use of allocentric spatial representations can be taken as evidence of the ability to build cognitive maps. To date, however, the ability of children to use allocentric spatial representations has mainly been assessed by testing their ability to use visual cues to learn and remember the location of one to several hidden rewards. Although this evidence should be sufficient for concluding that these children are capable of building cognitive maps, such experiments do not provide hallmark evidence for the ability to take shortcuts. In contrast, aside from the studies by Landau et al. (1981, 1984) and Morrongiello et al. (1995), whose results may be considered inconclusive, children’s ability to use path integration to build cognitive maps in the absence of visual information has been much less studied.

1.2. Path integration can be used to build cognitive maps

Path integration is the ability to use self-motion information generated by one's own body movement (i.e., idiothetic cues) to keep track of one's position in space (Etienne, Maurer, & Séguinot, 1996; Mittelstaedt, 1999; Mittelstaedt & Mittelstaedt, 1980), and is generally described as a mechanism that predominates when visual information is minimized or absent. For path integration, the estimation of both direction and distance is required. In absence of visual flow information, angular displacements (rotations) are estimated primarily based on vestibular information from the semi-circular canals, and linear displacements (translations) are estimated primarily based on proprioceptive information, but also from information pertaining to linear acceleration transmitted by the otolith organs found in the vestibular labyrinth of the inner ear (Etienne & Jeffery, 2004; Etienne et al., 1996; Taube, 2007). Efferent copies of motor commands complement vestibular and proprioceptive information in the estimation of both rotations and translations (Taube, 2007), and contribute to the coding of spatial location by hippocampal neurons (Foster, Castro, & McNaughton, 1989). As an individual moves along a path in their environment, information about rotations and translations must be integrated continuously in order to calculate their position with respect to the journey's starting point. Although path integration does enable an individual to return to a starting point, path integration should not be equated to "homing". Path integration is a neural computational process and homing is just one behavior supported by this process (Savelli & Knierim, 2019). Importantly, and contrary to navigational processes employing vision, path integration is an imprecise process in which error is accrued with every step (translational displacement) and every turn (rotational displacement), unless or until external cues can be used as landmarks to (re) calibrate the path integration system (Allen, 2004; Etienne & Jeffery, 2004; Etienne et al., 1996; Fujita, Klatzky, Loomis, & Golledge, 1993; Klatzky et al., 1990; Loomis et al., 1993; McNaughton et al., 1996). Thus, when using path integration, external sensory information from the environment such as familiar visual, tactile or olfactory stimuli must be provided at least occasionally in order to confirm or update the individual's position and correct for cumulated error (Etienne & Jeffery, 2004; McNaughton et al., 1996; Savelli & Knierim, 2019).

Path integration can be used to construct either egocentric or allocentric spatial representations of the environment (Alyan & McNaughton, 1999; Etienne et al., 1996, 1998; Jayakumar et al., 2019; McNaughton et al., 1996, 2006). Egocentric representations encode objects or goal locations in relation to the subject's body (e.g., on my left) or via a sequence of body-centered actions (e.g., turn right, walk ten steps, turn left). Egocentric representations constructed from path integration lack contextual spatial information that can place an individual in a particular place in relation to environmental landmarks. When moving, an individual's self-motion information is constantly and automatically encoded and updated. When the individual is ready to return home, a direct return trajectory can be derived which can support homing behavior even in the absence of specific contextual spatial information concerning the surrounding environment. Most often, studies of path integration have been limited to assessing performance on homing tasks in the absence of vision. In triangle completion tasks, for example, physiologically blind or blindfolded sighted participants are guided along a trajectory with two legs connected by an angle of a particular size, and then asked to return to the starting point using the most direct route. In this case, the memory representation that is created is the location of a fixed reference point in relation to one's body, and thus includes the direction and distance to this reference point (Loomis et al., 1993; Loomis, Klatzky, & Golledge, 2001). Humans and a wide variety of species, such as ants, rodents, dogs and hamsters demonstrate the ability to return to a starting point via the most direct path after being led or locomoting independently along a path that includes one or more turns (Corlett, Patla, & Williams, 1985; Fujita et al., 1993; Giovannini, Jacomuzzi, Bruno, Semenza, & Surian, 2009; Klatzky et al., 1990; Loomis et al., 1993; Mittelstaedt & Mittelstaedt, 1980; Muller & Wehner, 1988; Seguinot, Cattet, & Benhamou, 1998; Seguinot, Maurer, & Etienne, 1993; Smith, McKeith, & Howard, 2013).

Path integration also plays a fundamental role in the formation of allocentric spatial representations of the environment (McNaughton et al., 1996, 2006), which include the relative positions of objects and locations within the environment, as well as in coding the individual's position with respect to those environmental landmarks (Etienne & Jeffery, 2004; Jayakumar et al., 2019; Savelli & Knierim, 2019). Indeed, the same information about direction and distance traveled by an individual between different objects' locations contributes to the definition of the position of those objects in relation to each other, within a representation of the environment that is independent of the observer's position (Jayakumar et al., 2019; McNaughton et al., 1996). Importantly, path integration is not used only when external landmarks are unavailable; it is a continuously operating, automatic process that integrates with landmark processing (Savelli & Knierim, 2019; Tcheang, Bultthoff, & Burgess, 2011). In fact, whenever possible, both systems are used concurrently since they normally provide coherent, complementary information to help the individual orient, update its position and navigate (Jayakumar et al., 2019; Tcheang et al., 2011). Path integration is thus used to build allocentric representations of the relationships between external landmarks, while at the same time the external landmarks help to correct for cumulated error and calibrate the path integration system (McNaughton et al., 1996). In humans, behavioral studies have shown that both blindfolded and physiologically blind adults are capable of forming allocentric spatial representations of the explored environment (Giudice, 2018; Passini & Proulx, 1988). Altogether, these findings indicate that path integration contributes to building cognitive maps in humans.

1.3. Can children build cognitive maps without visual information?

Several studies have shown that 3–4-year-old children can use path integration in the presence or absence of vision to spatially update their position and keep track of locations and objects in their environment following self-movement (Rieser & Heiman, 1982; Rider & Rieser, 1988; Rieser & Rider, 1991; Bremner et al., 1994). In contrast, only two studies have investigated the capacities of blind or blindfolded children to build cognitive maps using path integration in the absence of vision (Landau et al., 1981, 1984; Morrongiello et al., 1995), and the theoretical implications of their results have sometimes been overlooked when considering how to

interpret the evidence from experiments designed to assess the spatial capacities of young children (Nardini et al., 2009; Negen, Heywood-Everett, Roome, & Nardini, 2018; Newcombe, 2019). This may be due to conceptual discrepancies, or to the assumption that such advanced spatial capacities cannot be present in young children who perform poorly in virtual environments or in real-world paradigms that dissociate or remove relevant spatial cues (Broadbent, Farran, & Tolmie, 2014; Buckley, Haselgrove, & Smith, 2015; Bullens, Klugkist, & Postma, 2011; Nardini et al., 2008). However, it may also be due to some weaknesses with these two previous studies that make assessing the validity and reliability of their data difficult.

Landau et al. (1981, 1984) tested a congenitally blind 2.5-year-old girl (Kelli), and five typically developing (TD) children (from 2 years and 10 months to 3 years and 9 months of age), as well as six TD adults. In their paradigm, Kelli and blindfolded TD participants were led along several paths connecting four different objects in a 2.44 m × 3.05 m room. Participants were then asked to walk novel, direct paths between the objects. A total of 12 “novel” path trials were administered: each of the three new paths (there and back) was repeated twice (thus, three novel paths, three repeated paths, and six reversed paths). To estimate performance on each trial, the experimenters recorded the subjects’ position 60 cm after they started along their path, and again at the end of their path. After 60 cm, Kelli was facing toward the correct goal location on 11 out of 12 trials. TD children exhibited similar performance with correct orientation on an average of 10 out of 12 trials. At the end of their path, participants were considered successful if their final position fell within a 40° segment originating at the starting location and containing the target. Kelli succeeded on 8 out of 12 trials, and TD children succeeded on an average of 7.4 out of 12 trials. However, individual results of the TD children were not provided, and thus we do not know about individual performance and variation at this age. Indeed, although a correct starting orientation on 10 of 12 trials sounds impressive, if the two “failed” trials were two of the three truly novel paths, and not the reversals or repeats of these paths, then these results may not provide sufficient support for the argument that children of this age can build cognitive maps in the absence of vision (Bennett, 1996). Moreover, given the small size of the experimental room, it is surprising that Kelli only succeeded at reaching the target on 8 of 12 trials, after heading in the correct direction on 11 trials. Finally, adults exhibited superior performance as compared to children, with their original orientation correct on an average of 11.5 out of 12 trials and their final position correct on an average of 10.8 out of 12 trials. In sum, because Kelli and the other children succeeded on approximately two-thirds of the paths, Landau et al. (1981) concluded that “*this blind child, and sighted controls, know about some of the metric properties of space, probably Euclidean properties.*” Although these findings are suggestive that children from 2.5 years of age can use path integration to build a cognitive map without vision, given the lack of detailed data concerning individual children’s trial-by-trial performance, these findings must be verified.

Morrongiello et al. (1995) replicated Landau et al.’s study with a larger sample of TD children from 4.5 to 9 years of age. In contrast to Landau et al. (1984), Morrongiello et al. (1995) were unable to test 12 children younger than 4.5 years of age because they refused to wear the opaque goggles that blocked vision for the duration of the task and/or refused to walk alone while wearing the goggles or other blindfolds. They used a similar sized room (3.6 m × 4.8 m), but because the repetition of novel trials may enable learning and thus may not be used as evidence demonstrating the ability to make novel shortcuts, Morrongiello et al. (1995) only tested each of the three novel paths once. They also included more measures of performance, including the participants’ average distance from the target location, at both the beginning and the end of the novel paths taken. Based on all measures, 5- and 7-year-olds were farther from the target than 9-year-olds, suggesting an improvement in spatial performance from 4 to 9 years of age. Thus, whereas Landau et al. (1984) concluded that children from 2 years of age were indeed capable of creating an Euclidean representation of space, Morrongiello et al. (1995) concluded that the capacity to produce novel paths is not fully mature in 5-year-old children, but rather continues to improve until at least 9 years of age. However, without an adult comparison group, it is not possible to know whether the 9-year-old children exhibited fully-developed path integration capacities. Moreover, for all three novel paths the scores for the initial turn, the closest position to the target, and the final position relative to the target were averaged across all participants within each age group to yield a single estimate of performance for each age group. This procedure may have masked individual differences and obscured important information about potential errors or biases in the representation of the specific relations between environmental objects, both within and across age groups. Finally, even though Morrongiello et al. (1995) provided more specific measures of performance to test children’s ability to represent the Euclidean properties of space, they did not answer the question as to how many children were capable of building a cognitive map and at what age that capacity may emerge.

In sum, the lack of trial-by-trial data for individual children in these two studies makes their results difficult to scrutinize and assess by the independent reader, thus possibly explaining why these studies may sometimes be overlooked. Moreover, from the data reported it is not possible to determine whether children’s inaccuracies in novel path construction were due to: (1) errors in the topological representation of the relationships between objects, which would suggest that basic low-resolution allocentric spatial capacities are not yet capable of being formed in absence of vision, or (2) imprecisions in the Euclidean coding of angle and distance information, which would suggest that although basic allocentric spatial capacities are present, these capacities are still continuing to mature with respect to their precision and resolution (Ribordy Lambert et al., 2015, 2016).

1.4. Aim of this study

The aim of this study was to characterize the capacity of 5–9-year-old children to use path integration to home and to build cognitive maps supporting navigation in their environment. To assess the level of maturation of these capacities in young children, we also tested young adults on the same tasks. First, blindfolded participants were tested on their ability to return to a starting point after being led on straight and two-legged paths. Performance on this homing task that involved only simple angular and linear displacements allowed us to evaluate children’s path integration capacities in absence of external landmarks and the necessity to build a cognitive map. Second, we evaluated whether participants could use path integration, in absence of visual information, to

build a cognitive map. Similar to the studies by Landau et al. (1981, 1984) and Morrongiello et al. (1995), participants in our study had to navigate between four different objects placed in an $8\text{ m} \times 8\text{ m}$ room. After an initial phase where blindfolded participants learned some of the spatial relations between objects by walking between those objects, participants were then asked to walk directly to specific objects using three novel paths (shortcuts), and then to reverse that route. In order to provide an accurate description of each participant's capacity to encode the spatial relations between the different objects, each path was analyzed and reported separately for each participant. Accuracy measures (angles and distances) as well as dispersion measures (variability of the angles taken) were calculated to describe the participants' performance. By assessing the data from both the homing and the cognitive mapping tasks, we were able to determine: (1) whether 5–9-year-old children can build a cognitive map in the absence of vision, and if so, what percentage of children do so and at what age; (2) whether children who can build cognitive maps exhibit imprecisions in Euclidean coding, as compared to adults; and (3) whether imprecisions in Euclidean coding are due to a poor integration of the experienced angles and distances in an allocentric representation, or a poor ability to reproduce the correct turn angles and walk straight for the correct distance when blindfolded.

2. Methods

2.1. Participants

Twenty-eight typically developing children (15 girls; average age: 6.9 years, SD: 1.4 years, min: 4.8 years, max: 9.7 years) and twenty-three typically developed young adults (12 women; average age: 22.2 years, SD: 2.7 years, min: 19.3 years, max: 30.3 years) participated in both the homing and cognitive mapping tasks (Experiments 1 and 2, respectively). Children were recruited via personal connections, and via email postings on social networks and to the university community. Children were reported by their parents to have been typically developing, and were neither born prematurely, nor had any suspected or diagnosed neurological conditions or learning disabilities. Adults were undergraduate students enrolled in the Bachelor of Psychology at the University of Lausanne and received course credit for their participation.

The two experiments took place on separate days, which were anywhere from one day to a few months apart. Participants were assessed on the homing task during their first visit and on the cognitive mapping task during their second visit. Each experiment lasted about 45 min and took place Mondays through Saturdays, between 8:00 A.M. and 6:30 P.M. Human subjects research was approved by the Cantonal Ethics Commission for Human Research (Vaud, Switzerland; protocol no. 60/14), and was in accordance with the code of ethics of the World Medical Association (Declaration of Helsinki) for experiments involving human subjects in research. Adult participants or children's parents gave informed written consent.

2.2. Testing facilities and general procedures

Testing took place within an $8\text{ m} \times 8\text{ m}$ room (Fig. 1). During the homing task (Fig. 1A and B), the room was devoid of any objects. Construction tape that was undetectable when it was walked on was placed on the floor, 1.5 m from each of the walls that constituted the four corners of the room. At the corner closest to the entry door, the tape was arranged to represent a house, which was designated as "home", i.e., the position to which participants were instructed to always return on each trial. In the other three corners of the room, the tape formed a small "x" surrounded by a square that served as a visual landmark for the experimenter when guiding the participants. Participants were filmed with a camera placed in the far corner of the room opposite the corner containing the home. During the cognitive mapping task (Fig. 1C), the testing room contained four real-sized pieces of furniture. Each object was placed against the center of a wall: a bench (0°), a shelf (90°), a chair (180°) and a table (270°). Participants were filmed with a camera placed in the corner of the room between the bench and the table.

In both tasks, children were rewarded with small food rewards (e.g., Smarties®, Goldfish® crackers, gummy bears, pieces of

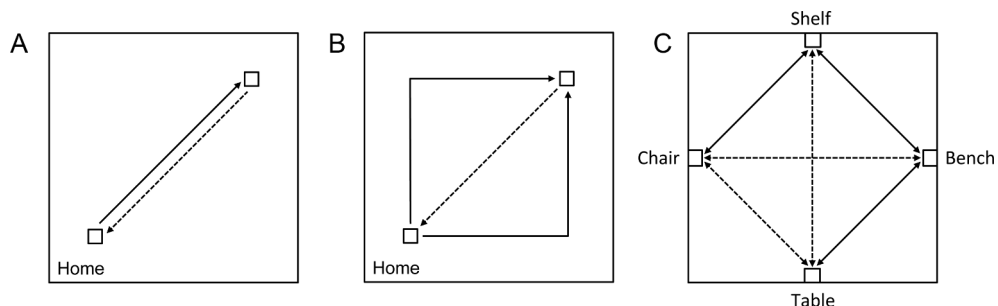


Fig. 1. Schematic representation of the experimental design carried out in an $8\text{ m} \times 8\text{ m}$ testing room; dashed lines indicate direct paths that participants were verbally requested to make. (A) Homing task, straight paths: 7 m straight line guided trajectory, 7 m return path. (B) Homing task, angled paths: 10 m angular guided trajectory with a right or left turn ($5\text{ m} + 5\text{ m}$), and 7 m return path. (C) Allocentric task: Guided routes (solid) and novel routes (dashed) between four objects. The paths between the bench and the chair, and between the table and the shelf were 7 m long; the other paths were 5 m long.

breakfast cereal or pretzels, etc.). One reward was given for each completed trial (a walked trajectory) and was not based on performance accuracy. Children's parents were queried with respect to alimentary allergies, and children were asked whether there were any treats that they did not like.

Visual information was eliminated with a "sleeping mask" blindfold individually adjusted to the subject's head and face at the start of each trial for the homing task, and before entering the room for the allocentric task. A black scarf was tied around the mask and the participant's head to ensure that they could not see any light. Two experimenters tested children. Experimenter 1 (E1) would guide the child, and Experimenter 2 (E2) recorded the data. For adults, E1 was responsible for both guiding the participants and recording the data. For children and adults, E1 walked next to or behind the participant, close enough to provide non-specific verbal encouragement (e.g., "You're doing great!", regardless of performance) and to assure their security when they were walking independently (e.g., to prevent them from walking into walls or objects), but far enough so as not to interfere with the participant's movements.

2.3. Specific testing procedures

2.3.1. Homing task

Participants were tested on their ability to return to a starting point ("home") after being led along a predetermined route. Before beginning, participants were told that they would be guided along some paths while blindfolded, and that it was their job to try to return to the starting point as precisely as possible at the end of each guided route. Participants were instructed that once they thought that they were at the home position they were to stop walking and remain stationary. Each participant performed a total of 20 trials without vision. Half of the trials consisted of a linear route of 7 m (Fig. 1A), and the other half of the trials consisted of a 10 m route with a 90° left or right turn in the middle (Fig. 1B). The trials were given in the following order: Straight path Session 1: 5 × 7 m linear route, guided by the left arm; Two-legged path Session 1: 5 × 10 m route with a 90° right turn at the halfway point, guided by the left arm; Straight path Session 2: 5 × 7 m linear route, guided by the right arm; Two-legged path Session 2: 5 × 10 m route with a 90° left turn at the halfway point, guided by the right arm. At the end of each guided route, and while still facing in the direction of the outbound travel, E1 released the participant's arm and instructed them to "go home" (i.e., to the starting point). Although participants had been instructed to stop walking once they estimated that they had arrived at home, if participants were approaching a wall and did not show signs of stopping, E1 gently placed a hand on the participant to stop them. Once participants were stationary, they could take off the blindfold, look where they were positioned in the room, and then return to the starting position (home) in order to prepare for the next trial. To ensure that all participants understood the task, prior to the beginning of each session they experienced a practice trial during which they were led through the guided part of the path without the blindfold, their arm released at the end of the guided path, and then asked to "go home". All trials began from the same starting point. A trial was terminated when a participant stopped alone or when the experimenter stopped the participant just before a wall.

2.3.2. Cognitive mapping task

Participants were tested on their ability to take novel paths (shortcuts) to navigate to previously visited locations marked by four large objects placed in the 8 m × 8 m room (Fig. 1C). Prior to entering the room, participants were told that they were going to be blindfolded, and that they would then explore our laboratory's living room. Participants were never told the goal of the experiment, or that they would have to remember the position of the objects in the room or navigate to those objects using novel routes. Although all participants were familiar with the empty room from having participated in the homing task, they were blindfolded prior to entering the room for the cognitive mapping task, and thus never saw the objects or their positions in the room. Once blindfolded, participants were led into the room and were guided to the bench where they were asked to sit down. Importantly, although the bench was located on the far-right wall relative to the entry door, some participants may not have had explicit knowledge of its position in the room; it could just as easily be perceived as being on the far wall opposite the door.

2.3.2.1. Learning phase. Participants were taught the routes between (1) the bench and the shelf, (2) the shelf and the chair, and (3) the bench and the table, always in this same order for each participant (solid lines in Fig. 1C; Supplementary Material 1). Accordingly, at the beginning of each trial, participants were positioned so that they were either sitting straight on the bench or chair, or so that their back was touching the shelf or the table, and their feet pointing straight forward. For each route to be learned, children were guided by the arm round-trip between the two objects twice by E1, then asked to make the round-trip alone one time, then guided through two more round-trips, and finally asked to make two more round-trips alone. For each route to be learned, adults were guided by the arm round-trip between the two objects twice by E1, then asked to make the round-trip alone twice. Each time participants reached an object by themselves or guided by E1, E1 named the object and participants were asked to touch the object or sit on it, for the chair and the bench.

In non-guided learning trials, if a participant came within 30 cm of the target object, E1 would gently take her/his arm and guide her/him into contact with the object, so that the participant would not startle or injure her/himself colliding with the object, thus terminating the trial. If the participant was in the correct quadrant of the room (tape markings on the floor outlined this zone), but not within 30 cm of the target object, the participant was allowed to continue walking until s/he came within 30 cm of a wall, at which point E1 gently stopped the participant and guided her/him to the target object. If a participant began walking in the wrong direction and after travelling 4 m was not in the correct quadrant, E1 would gently stop her/him and guide her/him back to the starting object, and then begin escorting the participant through the next two guided trials. This behavior was demonstrated only by a few children and only during their first one or two non-guided trial(s) of certain routes.

2.3.2.2. Testing phase. Participants ended the learning phase sitting on the bench, and immediately began the testing phase from this position. Participants were asked to walk alone and directly to objects, which would require them to take novel paths or shortcuts to these objects. First, E1 asked participants to walk directly from the bench to the chair (i.e., “now, go alone directly to the chair”). Once sitting in the chair, they were asked to walk directly to the table. Once their back was to the table, they were asked to walk directly to the shelf. Then, the participants were instructed to perform the three reverse routes: from the shelf to the table (i.e., “now, go alone directly to the table”), from the table to the chair, and from the chair to the bench. In the testing phase, each trial and data collection terminated when a participant either: (1) came within 30 cm of the target, at which point E1 gently guided the participant to the object, or (2) came within 30 cm of a wall, at which point E1 gently stopped the participant and guided her/him to the target object.

2.4. Data collection

Participants' movements and trajectories were recorded with the Noldus TrackLab system (Wageningen, The Netherlands). Participants wore a vest on which a radio frequency-emitting Ultra-Wide Band tag was affixed to each shoulder. The system collected the X and Y coordinates of each tag at a frequency of 4.75 Hz. The smoothed averaged X and Y coordinates of the two tags were computed to plot the location of the participant's head on a 2D representation of the room. Each trajectory was then transferred to the ImageJ program (NIH, USA), and retraced to measure the distance and angle information for the different parts of each individual trajectory.

We used several measures to quantify participants' performance on each trial: (1) The initial heading, defined as the angular difference between the ideal path and the participant's path one meter after starting their journey. (2) The final heading, defined as the angular difference between the ideal path and the participant's path after the participant either stopped alone (homing task), reached the target object (cognitive mapping task), or was stopped by E1 (homing and cognitive mapping tasks). (3) The distance to target, defined as the shortest distance between the participant's final position and home (homing task) or the target object (cognitive mapping task). For the homing task, the five trials of each session in absence of vision were averaged to obtain one single value for each of these measures (1–3) for each participant. For the cognitive mapping task, the six novel paths were analyzed separately.

We also provided an overall measure of task performance: (4) “Pass” or “Fail”. For the homing task, we estimated whether subjects passed or failed by determining whether their average end location was within the quadrant of the room that included the outbound journey's starting point (home), as defined by the two perpendicular bisectors of the room's walls. In the cognitive mapping task, we estimated whether subjects passed or failed each of the three novel paths and the three reverse paths. To be considered as passing, the end point of the participant's trajectory had to be within the same quadrant as the target object, as defined by the two diagonals bisecting the room. This defined the area of the room in which participants were closer to the target object than any other object. We did not use a more restrictive criterion, e.g., within an arbitrary distance to the target, because we did not expect (Loomis et al., 1993), nor did we find, that either adults or children could exhibit perfect performance and always come within contact-distance of the object at the end of their trajectory. Indeed, path integration is an imprecise mechanism, in which error is accrued with every step and every turn (Etienne & Jeffery, 2004). Path integration appears only capable of guiding an individual to a general area, but not necessarily to an exact location. Our data confirm this, showing that not all adults reached the goal objects precisely.

2.5. Data analysis

For angular measures of direction, we used circular statistics computed in Excel following the formulas described in Zar (1999). We performed one-sample tests for the mean angle (Zar, 1999; p.620) to determine whether each group's average initial or final heading followed a mean heading that deviated from zero° (0° was considered as the perfect angle). We considered a 99% confidence interval to define a significant departure from the ideal direction. Age group comparisons were performed with the two-sample Watson-Williams tests for angular measures (Zar, 1999; p.625).

To quantify the variability for individual participants, we computed the angular deviation for each participant ($r = \sqrt{\sin(\alpha)^2 + \cos(\alpha)^2}$, where α is the average angle for each subject within a session), and then calculated the average angular deviation for each group. Statistical analyses of the angular deviation and the distance to target were performed with the SPSS 25.0 software. We used General Linear Model analyses with age groups as a between-subject factor and test sessions or trials as repeated measures to analyze the distance to target, and the individual variability (r) of initial and final headings. We used independent samples t-tests to compare age groups within one session or trial. We used Pearson's r correlations to evaluate the relations between children's age and performance.

3. Results

3.1. Homing task: Straight outbound paths

3.1.1. “Pass” or “Fail”

Fig. 2 shows the average end locations of adults and children who were asked to return to “home” after being led blindfolded on a straight 7 m path, thus ideally requiring a 180° turn and a 7 m straight walk to return to the starting point. For Session 1, 22/23 adults (Fig. 2A; participant A56 failed) and 26/28 children (Fig. 2B; participants C36 and C167 failed) had an average end location in the quadrant of the room where the home was located and were thus considered to have passed the homing task. For Session 2, 23/23

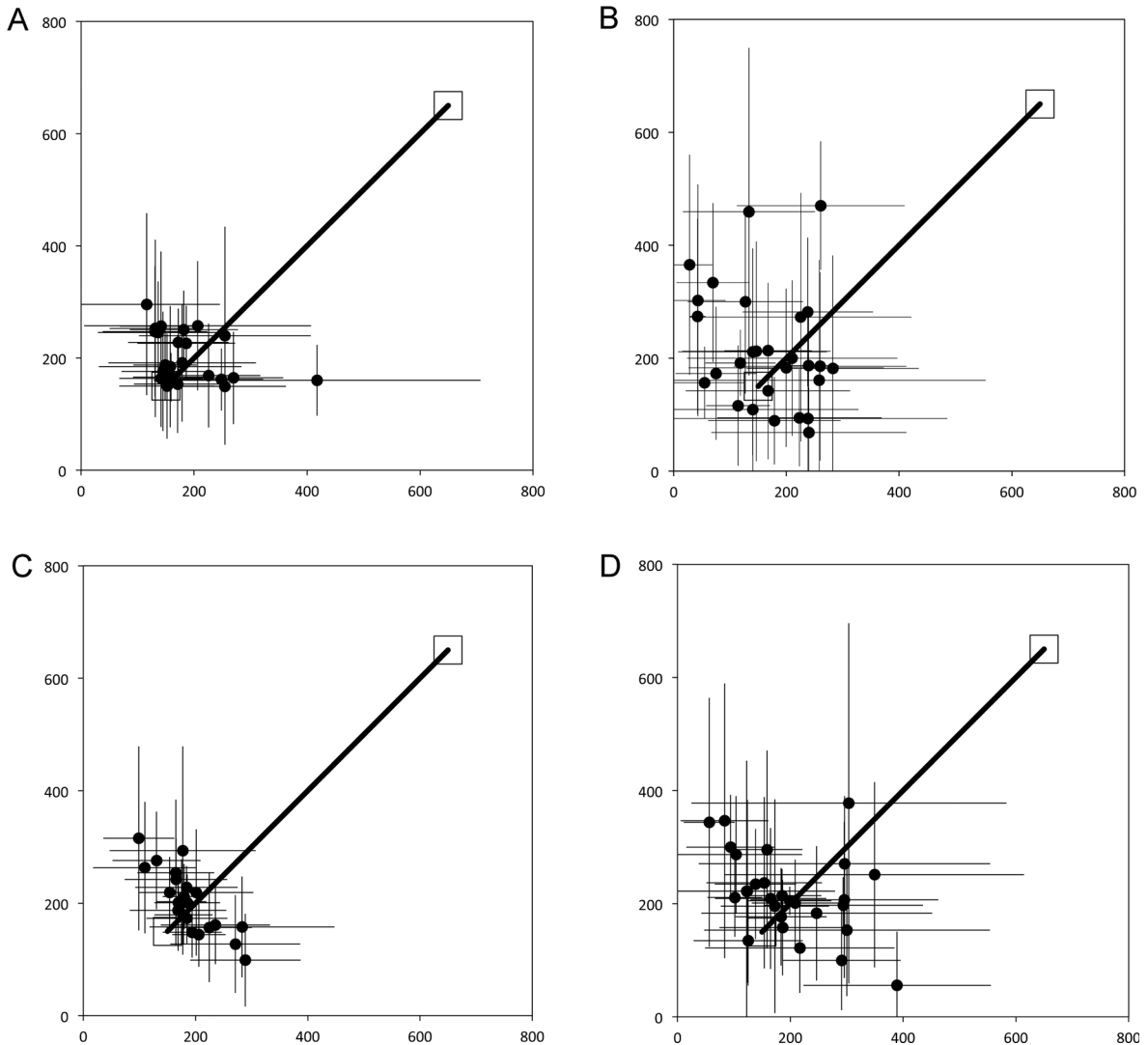


Fig. 2. Average end location of individual participants' return paths, following a straight 7 m outward path in the homing task. The horizontal and vertical error bars represent the standard deviation for each individual across one session. The solid line indicates the outward straight path. The top right square indicates the starting point of the return path. The bottom left square indicates "home". (A) Adults, Session 1. (B) Children, Session 1. (C) Adults, Session 2. (D) Children, Session 2. Room size: 800 cm × 800 cm.

adults (Fig. 2C) and 28/28 children (Fig. 2D) had an average end location in the quadrant of the room where the home was located and were thus considered to have passed the task.

3.1.2. Average distance from home

There were differences between age groups ($F_{(1,49)} = 17.461$, $p < 0.001$) and sessions ($F_{(1,49)} = 4.538$, $p = 0.038$), but no interaction between age groups and sessions ($F_{(1,49)} = 0.090$, $p = 0.766$). In both sessions, children's average distance between their end location and home was greater than the adults' (Session 1: adults: 145 ± 12 cm, children: 202 ± 13 cm, $t_{(49)} = 3.140$, $p = 0.003$; Session 2: adults: 120 ± 9 cm, children: 184 ± 13 cm, $t_{(49)} = 3.768$, $p < 0.001$). The average distance from home was shorter in Session 2 than in Session 1 when both groups were considered together, but the difference between sessions was not significant when each group was considered separately (adults: $t_{(22)} = 1.646$, $p = 0.114$; children: $t_{(27)} = 1.359$, $p = 0.185$). For children, the average distance between the participant's end location and home did not correlate with age (Session 1: Pearson's $r = -0.060$, $n = 28$, $p = 0.760$; Session 2: Pearson's $r = -0.198$, $n = 28$, $p = 0.313$). It is important to note, however, that children often did not stop on their own and E1 stopped children more often than adults because they were approaching a wall (out of 10 trials; adults: 0.68 ± 0.14 trials; children: 3.96 ± 0.49 trials; $t_{(48)} = 5.735$, $p < 0.001$).

3.1.3. Initial heading

Following a straight 7 m outward path, neither the adults' nor the children's group average initial heading, after turning and walking one meter, differed from the ideal heading; the children's group average initial heading did not differ from that of adults (Supplementary Material 2). In contrast, children's angular deviation was greater than adults' in both sessions, showing that children's initial heading was more variable than that of adults. Accordingly, the within-subject variability in initial heading was higher in children than in adults ($F_{(1,49)} = 4.885$, $p = 0.032$); it did not differ between Sessions 1 and 2 ($F_{(1,49)} = 1.731$, $p = 0.194$) and there was no interaction between groups and sessions ($F_{(1,49)} = 0.974$, $p = 0.328$).

3.1.4. Final heading

Following a straight 7 m outward path, neither the adults' nor the children's group average final heading differed from the ideal heading; the children's group average final heading did not differ from that of adults (Supplementary Material 3). In contrast, children's angular deviation was greater than adults' in both Sessions 1 and 2, showing that children's final heading was overall more variable than that of adults (as was observed for the initial heading). Accordingly, the within-subject variability in final heading was higher in children than in adults ($F_{(1,49)} = 7.631$, $p = 0.008$); it did not differ between Sessions 1 and 2 ($F_{(1,49)} = 0.057$, $p = 0.813$) and there was no interaction between groups and sessions ($F_{(1,49)} = 1.751$, $p = 0.192$).

3.1.5. Heading correlations

Children's average of the unsigned angle after one meter correlated negatively with age in Session 1 (Pearson's $r = -0.507$, $n = 28$, $p = 0.006$) and Session 2 (Pearson's $r = -0.377$, $n = 28$, $p = 0.048$), indicating a decrease in angular error with age. Interestingly, however, although children's initial heading correlated with their final heading in Session 1 (Pearson's $r = 0.731$, $n = 28$, $p < 0.001$) and Session 2 (Pearson's $r = 0.858$, $n = 28$, $p < 0.001$), the average of the unsigned final heading angle did not correlate with children's age in Session 1 (Pearson's $r = -0.069$, $n = 28$, $p = 0.729$), and the correlation just failed to reach the predefined level of statistical significance in Session 2 (Pearson's $r = -0.350$, $n = 28$, $p = 0.068$).

3.2. Homing task: two-legged angled paths

3.2.1. "Pass" or "Fail"

Fig. 3 shows the average end locations of adults and children who were asked to return "home" after being led blindfolded on a two-legged path of 10 m, with a 90° right turn after 5 m (Session 1) or a 90° left turn after 5 m (Session 2), thus ideally requiring a 135° right (Session 1) or 135° left (Session 2) turn at the end of the guided path, and a 7 m straight walk to return home. Although participants could also turn "the long way around" requiring an ideal turn of 225° to the left (Session 1) or to the right (Session 2), in Session 1 only three children turned left one time each, and in Session 2 only two children turned right one time and one child turned right two times (for a total of only seven "long way" turns, out of 280 turns). No adult turned left in Session 1, and only one adult turned right one time in Session 2.

For Session 1, 23/23 adults (Fig. 3A) and 26/28 children (Fig. 3B; participants C52 and C53 failed) had an average end location in the quadrant of the room where the home was located and were thus considered to have passed. For Session 2, 23/23 adults (Fig. 3C) and 25/28 children (Fig. 3D; participants C36, C39 and C50 failed) had an average end location in the quadrant of the room where the home was located and were thus considered to have passed the task.

3.2.2. Average distance from home

There were differences between groups ($F_{(1,49)} = 15.281$, $p < 0.001$), but no difference between sessions ($F_{(1,49)} = 0.062$, $p = 0.804$), and no interaction between groups and sessions ($F_{(1,49)} = 0.552$, $p = 0.461$). In both sessions, children's average distance between their end location and home was greater than the adults' (Session 1: adults, 138 ± 8 cm, children, 191 ± 14 cm, $t_{(49)} = 3.056$, $p = 0.004$; Session 2: adults, 132 ± 10 cm, children, 203 ± 19 cm, $t_{(40.896)} = 3.268$, $p = 0.002$). Children's average distance between their end location and home did not correlate with age in Session 1 (Pearson's $r = -0.138$, $n = 28$, $p = 0.483$). In contrast, the average distance between the children's end location and home correlated negatively with age in Session 2 (Pearson's $r = -0.610$, $n = 28$, $p = 0.001$). These results were linked to both an improvement of the performance of older children and a worsening of the performance of younger children in Session 2. As was the case for straight outbound paths, E1 stopped children more often than adults because they were approaching a wall (out of 10 trials; adults: 0.55 ± 0.17 trials; children: 4.14 ± 0.51 trials; $t_{(48)} = 6.082$, $p < 0.001$).

3.2.3. Initial heading

Following a two-legged 10 m angled outward path, the adults' group average heading after turning and walking one meter toward home did not differ from the ideal heading (Supplementary Material 4). In contrast, the children's group average initial heading differed from the ideal heading in both Sessions 1 and 2. Moreover, for both sessions, children's average initial heading differed from the adults'. The observed angular deviation was also greater for children. Accordingly, the within-subject variability in the initial heading was higher in children than in adults ($F_{(1,49)} = 9.623$, $p = 0.003$); it did not differ between sessions ($F_{(1,49)} = 1.037$, $p = 0.313$) and there was no interaction between groups and sessions ($F_{(1,49)} = 0.331$, $p = 0.568$). Altogether, these data indicate that children had more difficulty integrating the 90° turn in the middle of the guided path, as compared to adults, and as compared to the straight path with no turn to be integrated, thus deriving a less accurate and less precise turn angle than the one needed to return home. Importantly, children's initial headings following both the paths with the 90° left turn and the 90° right turn revealed that children tended to under-rotate their initial rotation to start the return path.

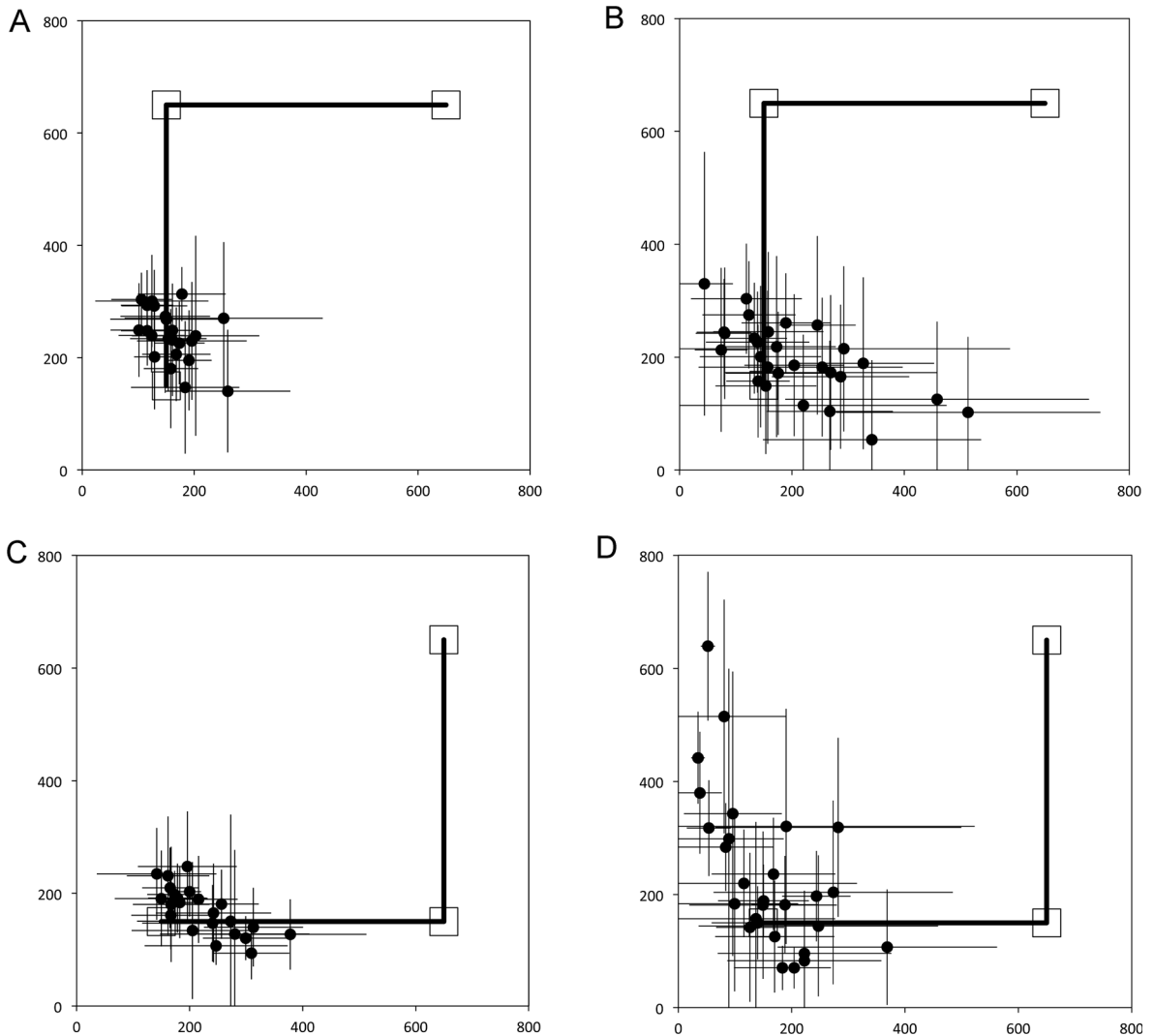


Fig. 3. Average end location of individual participants' return paths, following a two-legged 10 m angled outward journey in the homing task. The horizontal and vertical error bars represent the standard deviation for each individual across one session. The solid line indicates the outward angled path. The top right square indicates the starting point of the return path. The bottom left square indicates "home". (A) Adults, Session 1. (B) Children, Session 1. (C) Adults, Session 2. (D) Children, Session 2. Room size: 800 cm × 800 cm.

3.2.4. Final heading

Following a two-legged 10 m outward journey, the children's group average final heading did not differ from the ideal heading in either Session 1 or 2, but it differed from the adult's group average final heading in Session 2 (Supplementary Material 5; the difference just failed to reach the predefined level of statistical significance in Session 1). The adults' average final heading did not differ from the ideal heading in Session 1, but it was different from the ideal heading in Session 2, despite the rather small deviation from the ideal path. Children's angular deviation was greater than the adults' angular deviation in Session 1, but the difference failed to reach the predefined level of statistical significance in Session 2. Accordingly, the within-subject variability in final heading was higher in children than in adults ($F_{(1,49)} = 8.535$, $p = 0.005$); it did not differ between sessions ($F_{(1,49)} = 0.112$, $p = 0.739$) and there was no interaction between groups and sessions ($F_{(1,49)} = 0.389$, $p = 0.536$). Altogether, the final heading indicates that on average both adults and children walked in the direction of their starting point (home) after a two-legged 10 m path with a 90° angle, but the children's performance was overall more variable than the adults'.

3.2.5. Headings correlations

Children's average of the unsigned angles after one meter did not correlate with age in either Session 1 (Pearson's $r = -0.165$, $n = 28$, $p = 0.402$) or Session 2 (Pearson's $r = -0.253$, $n = 28$, $p = 0.193$). Children's initial heading correlated with their final heading in Session 1 (Pearson's $r = 0.794$, $n = 28$, $p < 0.001$) and in Session 2 (Pearson's $r = 0.865$, $n = 28$, $p < 0.001$). The average of the unsigned final heading angle did not correlate with children's age in Session 1 (Pearson's $r = 0.025$, $n = 28$,

$p = 0.900$) or Session 2 (Pearson's $r = -0.369$, $n = 28$, $p = 0.053$), at the predefined level of statistical significance.

3.3. Homing task: Results summary

Altogether, the results from the homing task show that both children and adults can succeed in returning to the area where the starting point of a walking journey was located after being led blindfolded on straight or two-legged outward paths, but on average, children end up significantly farther from home than adults. Moreover, and in contrast to adults, when children must integrate a turn (as in the two-legged path), their initial heading (after turning and walking one meter) is less accurate (compared to adults and to the ideal heading) and more variable (compared to adults) than when they must simply turn 180° after walking a straight outward path. Importantly, this relatively poorer performance appears to be at least partially due to the children's diminished capacity to integrate the 90° turn in the middle of the two-legged path, rather than solely due to their capacity to turn accurately, since the ideal 180° turn needed to return home following the straight path is greater than the ideal 135° angle needed to return home following the two-legged path (i.e., turning error is cumulative, and larger angular displacements should incur larger errors (Loomis et al., 1993)). Knowing that children as young as 4.8 years of age were capable of using path integration to build an egocentric spatial representation supporting homing behavior, we next evaluated whether these same children were capable of using path integration to build an allocentric spatial representation to take shortcuts, the hallmark of cognitive mapping abilities.

3.4. Cognitive mapping task

3.4.1. "Pass" or "Fail"

After having been blindfolded and guided along three selected paths between four different objects located in an $8\text{ m} \times 8\text{ m}$ room (Fig. 1; Supplementary Material 1), participants were asked to make six direct never-traveled trajectories between these objects, the first three being entirely novel paths and the last three being their reverse paths. Figs. 4 and 5 show the individual end location, for each adult and each child, for each trajectory. Between 91% and 100% of the adults exhibited passing performance by ending in the quadrant that contained the target object on each trial (Bench to Chair: 21/23; Chair to Table: 23/23; Table to Shelf: 23/23; Shelf to Table: 23/23; Table to Chair: 23/23; Chair to Bench: 22/23). Between 57% and 86% of the children exhibited passing performance by ending in the quadrant that contained the target object on each trial (Table 1; Bench to Chair: 16/28; Chair to Table: 20/28; Table to Shelf: 22/28; Shelf to Table: 23/28; Table to Chair: 24/28; Chair to Bench: 22/28).

We considered that a reasonably stringent criterion to define overall successful performance in the cognitive mapping task would require participants to succeed on at least four of the six novel paths, including the two paths with a 45° angle (i.e., Chair to Table, and Table to Chair). We reasoned that successful performance on the two paths with a 45° angle was necessary in order to claim the existence of a cognitive map, since successful performance on all of the other novel routes could be achieved by adopting a strategy of simply walking straight from the object at the beginning of the path, and that such a strategy might be adopted by participants who had not constructed a cognitive map of the spatial relationships between the four objects' locations. Indeed, as shown below in the paragraph on initial heading, our data confirmed this. When applying these criteria, 23/23 adults (100%) and 18/28 children (64%; Table 1) were able to travel to the target objects using novel paths, therefore demonstrating that they had built a cognitive map using path integration and could use this map to successfully navigate between the four objects without vision.

Importantly, the ability of children to construct a cognitive map did not correlate with age, between 4.8 and 9.7 years of age (Pearson's $r = 0.090$, $n = 28$, $p = 0.650$). Indeed, one of the three youngest children (a 4.8-year-old girl) reached the passing criterion, whereas the oldest child (a 9.7-year-old boy) did not. Moreover, the same proportion of younger children (< 7 years of age: 9/14) and older children (≥ 7 years of age: 9/14) reached the passing criterion for the cognitive mapping task.

3.4.2. Average distance from the target

There were differences between groups in the distance between the target object and the participant's end location in the novel path trials ($F_{(1,49)} = 17.019$, $p < 0.001$), no difference between paths ($F_{(3,592,175,990)} = 2.068$, $p = 0.094$; Greenhouse-Geisser correction) and no interaction between groups and paths ($F_{(3,592,175,990)} = 0.896$, $p = 0.459$). The distance between the end location and the target object was greater for children than for adults for all six paths, except for the path between the table and the chair for which the difference just failed to reach the predefined level of statistical significance. We also compared the adults' performance with that of the 18 children who passed the cognitive mapping task. There were no differences between the adult group and the group of children who passed the cognitive mapping task, except for the first path: Bench to Chair (adults: 105 ± 21 cm; vs all children: 264 ± 36 cm, $t_{(42,729)} = 3.841$, $p < 0.001$; adults vs passing children: 203 ± 35 cm, $t_{(28,842)} = 2.431$, $p = 0.022$); Chair to Table (adults: 95 ± 15 cm; vs all children: 212 ± 37 cm, $t_{(35,675)} = 2.933$, $p = 0.006$; adults vs passing children: 98 ± 17 cm, $t_{(37,079)} = 0.149$, $p = 0.882$); Table to Shelf (adults: 81 ± 13 cm; vs all children: 175 ± 30 cm, $t_{(36,805)} = 2.878$, $p = 0.007$; adults vs passing children: 131 ± 27 cm, $t_{(24,854)} = 1.648$, $p = 0.112$); Shelf to Table (adults: 78 ± 12 cm; vs all children: 169 ± 27 cm, $t_{(37,465)} = 3.105$, $p = 0.004$; adults vs passing children: 146 ± 34 cm, $t_{(21,273)} = 1.877$, $p = 0.074$); Table to Chair (adults: 78 ± 16 cm; vs all children: 163 ± 41 cm, $t_{(35,224)} = 1.904$, $p = 0.065$; adults vs passing children: 59 ± 12 cm, $t_{(37,800)} = 0.926$, $p = 0.360$); Chair to Bench (adults: 103 ± 17 cm; vs all children: 172 ± 27 cm, $t_{(43,868)} = 2.188$, $p = 0.034$; adults vs passing children: 120 ± 26 cm, $t_{(29,741)} = 0.564$, $p = 0.577$). Importantly, the average distance between the end location and the target object did not correlate with children's age across the six novel paths (Pearson's $r = -0.243$, $n = 28$, $p = 0.212$). The only path for which there was a negative correlation between the distance to target and children's age was the path from the shelf to the table (Pearson's $r = -0.506$, $n = 28$, $p = 0.006$). For all the other paths, the correlations were not statistically significant (all Pearson's

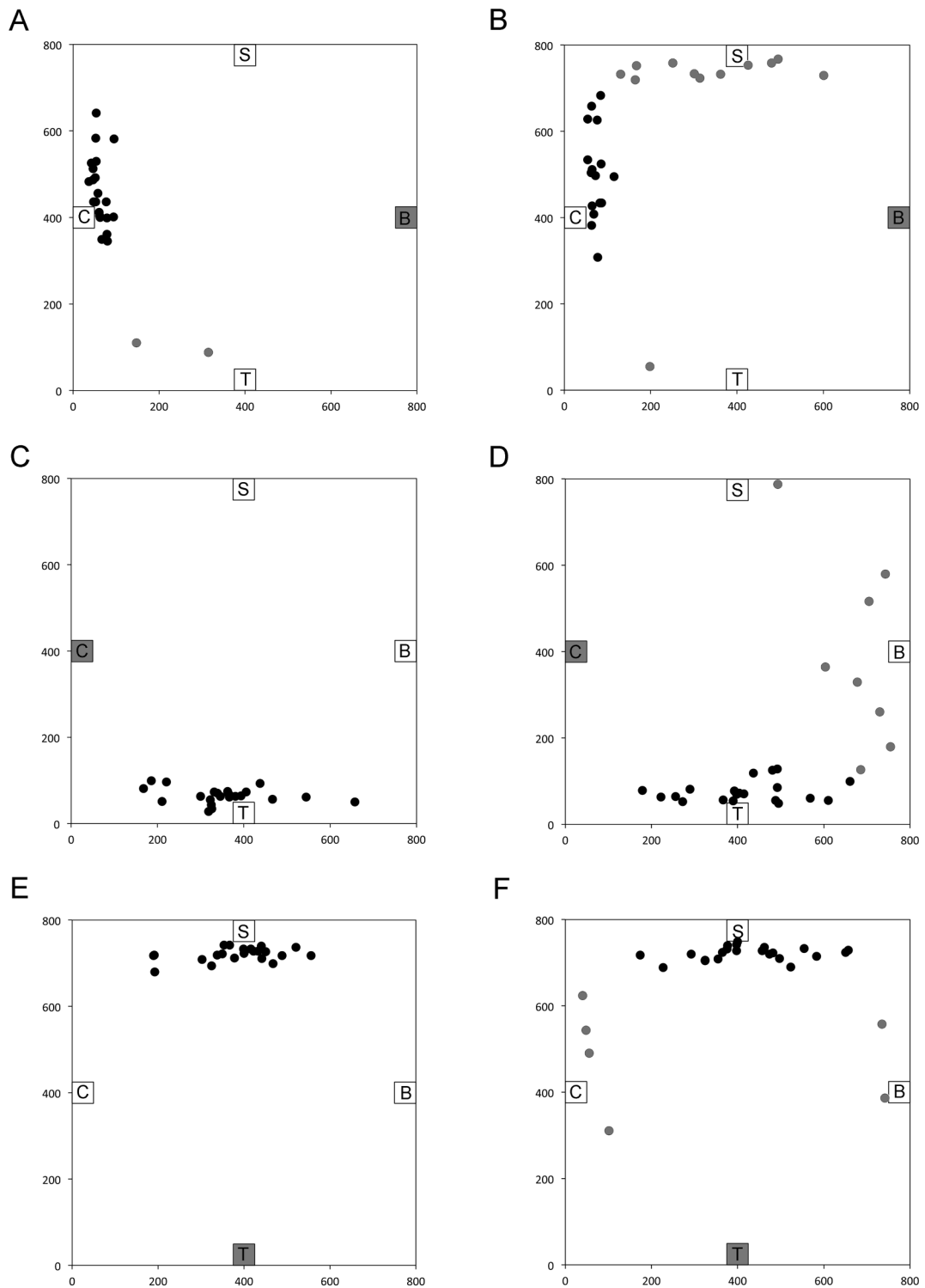


Fig. 4. End location of participants in the novel path trials of the cognitive mapping task. The shaded grey boxes represent the starting location. (A) Bench to Chair, adults: 21/23 ended in the quadrant of the room where the target object was located (black dot: in the correct quadrant; grey dot: in an incorrect quadrant). (B) Bench to Chair, children: 16/28 in the correct quadrant. (C) Chair to Table, adults: 23/23 in the correct quadrant. (D) Chair to Table, children: 20/28 in the correct quadrant. (E) Table to Shelf, adults: 23/23 adults in the correct quadrant. (F) Table to Shelf, children: 22/28 children in the correct quadrant. Room size: 800 cm × 800 cm.

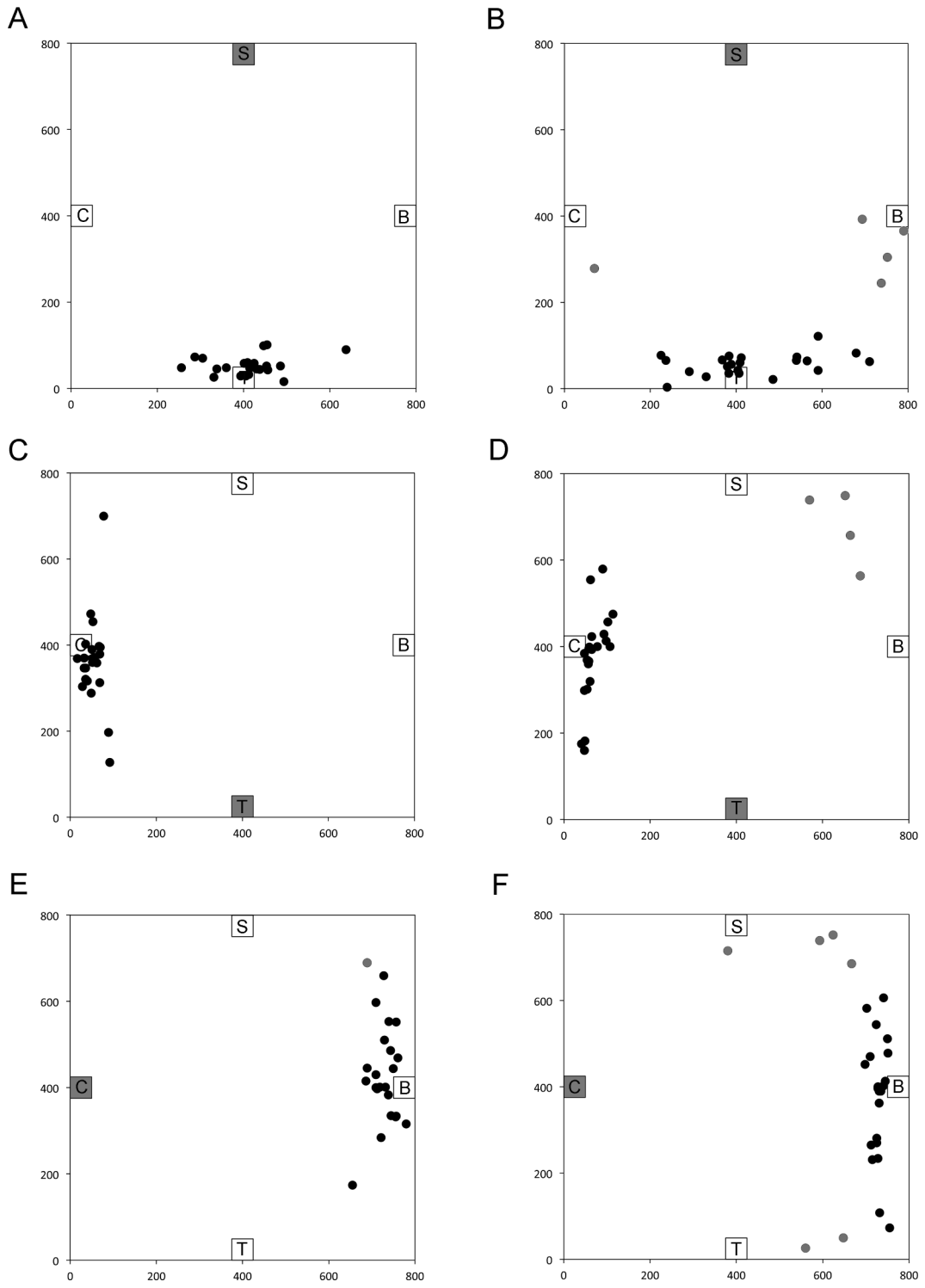


Fig. 5. End location of participants in the novel reverse path trials of the cognitive mapping task. The shaded grey boxes represent the starting location. (A) Shelf to Table, adults: 23/23 ended in the quadrant of the room where the target object was located (black dot: in the correct quadrant; grey dot: in an incorrect quadrant). (B) Shelf to Table, children: 23/28 in the correct quadrant. (C) Table to Chair, adults: 23/23 in the correct quadrant. (D) Table to Chair, children: 24/28 children in the correct quadrant. (E) Chair to Bench, adults: 22/23 in the correct quadrant. (F) Chair to Bench, children: 22/28 in the correct quadrant. Room size: 800 cm × 800 cm.

Table 1

Children's individual performance for the never traveled trajectories of the cognitive mapping task.

Subject	Gender	Age	Criterion	B-C	C-T	T-S	S-T	T-C	C-B
C39 ^{sa2}	F	4.83	Pass	1	1	1	0	1	1
C160	M	4.83	Fail	0	0	1	1	0	1
C167 ^{sa1}	M	4.83	Fail	0	1	1	1	0	0
C187	F	5.00	Pass	1	1	1	1	1	1
C50 ^{sa2}	M	5.50	Pass	1	1	1	0	1	1
C53 ^{sa1}	F	5.50	Pass	0	1	1	1	1	1
C186	F	5.67	Fail	0	0	0	0	1	0
C27	M	5.83	Fail	1	1	0	0	1	0
C36 ^{sa1a2}	M	5.92	Pass	1	1	1	1	1	1
C34	F	6.67	Pass	1	1	1	1	1	1
C35	M	6.67	Fail	1	0	0	1	1	1
C48	F	6.67	Pass	0	1	1	0	1	1
C141	F	6.67	Pass	0	1	1	1	1	0
C42	M	6.92	Pass	0	1	1	1	1	1
C49	F	7.08	Fail	1	0	1	1	1	0
C143	F	7.08	Fail	0	0	0	1	0	0
C31	F	7.17	Pass	1	1	1	1	1	1
C25	M	7.25	Fail	0	0	0	1	0	1
C191	M	7.50	Pass	1	1	1	1	1	1
C26	F	7.92	Pass	0	1	1	1	1	1
C29	F	7.92	Pass	1	1	0	1	1	1
C52 ^{sa1}	M	8.08	Pass	1	1	1	1	1	1
C37	M	8.25	Pass	1	1	1	1	1	1
C138	F	8.42	Pass	1	1	1	1	1	1
C28	F	8.58	Pass	0	1	1	1	1	1
C30	F	8.92	Fail	1	0	1	1	1	1
C142	M	9.17	Pass	1	1	1	1	1	1
C43	M	9.67	Fail	0	0	1	1	1	1

Abbreviations: B-C: Bench to Chair. C-T: Chair to Table. T-S: Table to Shelf. S-T: Shelf to Table. T-C: Table to Chair. C-B: Chair to Bench. The * indicates the subjects who were considered to have failed one session of the homing task: s1, straight session 1; s2, straight session 2; a1, angled session 1; a2, angled session 2.

$r > -0.237$, $n = 28$, all $p > 0.225$).

3.4.3. Initial heading

In order to determine why some children were less accurate than adults at navigating to the target objects using novel paths, we first analyzed the initial heading of participants after they had walked one meter from the starting object (Supplementary Material 6). Adults' group average initial heading after one meter did not differ from the ideal heading except for the path from the table to the shelf. Children's group average initial heading after one meter did not differ from the ideal heading, or from the adults' initial heading for the paths that required a straight path, but it deviated from the ideal heading and from the adults' initial heading for the two paths requiring a 45° angle path. In addition, the angular deviation of the children's group was greater than the adults' for all of the paths except for the path from the table to the shelf. Children's unsigned angle of initial heading did not correlate with age for any of the paths (Bench to Chair: Pearson's $r = 0.047$, $p = 0.813$; Chair to Table: $r = -0.120$, $p = 0.543$; Table to Shelf: $r = 0.112$, $p = 0.569$; Shelf to Table: $r = -0.316$, $p = 0.101$; Table to Chair: $r = -0.309$, $p = 0.110$; Chair to Bench: $r = -0.251$, $p = 0.197$).

Children's less precise and overall less accurate initial headings, as compared to the adults' and to the ideal heading, are consistent with our findings from the homing task showing that children's integration of turns is overall less accurate and less precise than the adults'. However, the fact that the children's initial headings differed only for the two paths requiring a 45° turn may be better explained by the fact that whereas all adults had created a cognitive map of their environment during the learning phase, some children had not. Thus, as a group, the children's initial heading differed from the ideal initial heading, as well as from that of adults for the two paths that required a 45° turn.

3.4.4. Final heading

The average heading of the adults at the end of their path did not differ from the ideal heading for any of the trajectories (Supplementary Material 7). The average heading of the children at the end of their path only differed from the ideal heading for the first route (Bench to Chair), and from that of the adults for the first two routes (Bench to Chair and Chair to Table). In contrast, the angular deviation was greater for the children's group than for the adults for all of the paths except for the path from the table to the chair. The unsigned angle of children's final heading did not correlate with age, except for the path from the shelf to the table (Bench to Chair: $r = 0.094$, $p = 0.634$; Chair to Table: $r = -0.062$, $p = 0.753$; Table to Shelf: $r = -0.116$, $p = 0.558$; Shelf to Table: $r = -0.551$, $p = 0.002$; Table to Chair: $r = -0.235$, $p = 0.230$; Chair to Bench: $r = -0.245$, $p = 0.209$).

3.4.5. Headings correlations

There are two important differences between the children's initial and final headings to note. First, children's initial headings differed from the ideal headings for the two angled paths, between the chair and the table and between the table and the chair. However, at the end of their trajectory, children's headings no longer differed from the ideal heading. Nevertheless, children's initial heading and final heading correlated for all paths (Bench to Chair: $r = 0.781$, $p < 0.001$; Chair to Table: $r = 0.788$, $p < 0.001$, Table to Shelf: $r = 0.746$, $p < 0.001$; Shelf to Table: $r = 0.629$, $p < 0.001$; Table to Chair: $r = 0.709$, $p < 0.001$; Chair to Bench: $r = 0.823$, $p < 0.001$).

3.5. Cognitive mapping task: Results summary

Altogether, these findings indicate that 5–9-year-old children are capable of using path integration to build an allocentric spatial representation to take shortcuts, the hallmark of cognitive mapping abilities. Interestingly, children may have solved the 45° angle paths by starting to walk somewhat straight, and then by angling toward the target object at some point after one meter. By comparison, adults turned first, and then walked to the target object. Moreover, whereas children's final heading from the bench to the chair (the first novel path) differed from the ideal heading (indeed, this was the path on which the fewest children succeeded, and the distance from the participants' end location to the chair differed between adults and children who passed the cognitive mapping task), their initial heading did not differ from the ideal heading. This suggests that either (1) some children thought the chair was not positioned directly in front of the bench (they had the correct topological relation, but they miscalculated its precise angular relations with the bench) or (2) the children could not walk straight. The results from the homing task, and the fact that children's final heading for the reverse path from the chair to the bench did not differ from that of adults or the ideal trajectory, indicated that 5–9-year-old children are capable of walking sufficiently straight for seven meters in absence of visual information. It is thus most likely that some of the children's initial estimation of the location of the chair was somewhat distorted or imprecise, and may have to do with an inaccurate estimation or integration of the two 45° angles experienced during the learning phase between the bench and the shelf, and between the shelf and the chair.

4. Discussion

The aim of this study was to characterize the capacity of 5–9-year-old children to use path integration to build egocentric and allocentric spatial representations to navigate in their environment. We found that children from five years of age can use path integration in absence of visual information to (1) return to a home base and (2) build a cognitive map. Ninety percent of the children between 4.8 and 9.7 years of age could reliably return to the home area in the homing task, and sixty-four percent of the children were judged to have successfully built a cognitive map enabling them to take novel routes or shortcuts between different object locations. Importantly, age did not predict children's ability to construct a cognitive map, as the proportion of children younger than seven years of age who succeeded was the same as the proportion of children older than seven years of age. In fact, the youngest child in our study (4.8 years old) succeeded, whereas the oldest child (9.7 years old) did not.

4.1. Comparison with previous studies

Our results are consistent with previous reports that very young children can gain knowledge of the spatial relationships between objects, and that vision is not essential in the development of this knowledge (Landau et al., 1981, 1984). Using the same paradigm, Morrioniello et al. (1995) presented data showing that young children were less precise than older children at navigating to objects via novel routes without vision. However, they made no claim as to whether 5–9-year-old children could use path integration to build a cognitive map. Given the individual variation that Morrioniello et al. (1995) observed, they urged "caution in ascribing well developed Euclidean coding skills to very young children", as was proposed by Landau and colleagues. Our results complement these two series of studies, by affirming that 5–9-year-old children can use path integration to build a cognitive map in absence of visual information, yet demonstrating that their performance in both the homing and cognitive mapping tasks is less accurate and more variable than that of young adults. Our results suggest that the capacity to build a cognitive map without vision is developed and accessible to children by at least 5 years of age. Moreover, due to substantial individual variability, as was shown previously in allocentric spatial learning tasks performed in the presence of visual information (Ribordy Lambert et al., 2016), chronological age is not a reliable predictor of task performance for children in this age range.

With respect to the cognitive mapping abilities of children between 2.5 and 5 years of age, the study of Landau et al. (1984) included Kelli, a congenitally blind 2.6-year-old child, and five normally sighted but blindfolded children between 2.8 and 3.8 years of age. In contrast, Morrioniello et al. (1995) limited their study to children between 4.5 and 9 years of age because the 12 children who they tested between 3 and 4 years of age refused to keep the obscuring goggles on, and/or refused to perform the task and walk alone without vision. Similarly, three participants between 4 and 5 years of age that we attempted to test refused to wear the sleeping mask and/or walk alone without vision. Thus, although we could not confirm the findings of Landau and colleagues with normally sighted participants younger than 4.8 years of age, we have no reason to doubt them either. Indeed, it was previously shown by independent laboratories that from around two years of age children can build and use an allocentric representation of their environment to locate a hidden reward in presence of visual information (Newcombe et al., 1998; Ribordy et al., 2013; Ribordy Lambert et al., 2015), and that 3-year-old children benefit from external "room" landmarks to identify a toy's location in an array of cups (Nardini et al., 2006). Altogether, these findings indicate that children as young as 2.5 years of age are capable of building cognitive

maps of the spatial relationships between environmental objects. Importantly, although children's spatial representations of the environment, both in the absence and presence of visual information, are less precise than those of adults, our data reveal that adults' representations are also not perfectly accurate. Thus, although it is often argued that precise metric information, including angles and distances, must be accurately encoded in order to represent the Euclidean properties of space in cognitive maps (Gallistel, 1990; O'Keefe & Nadel, 1978; Warren, 2019), this does not appear to be the case, even in adults.

4.2. Path integration and a noisy cognitive mapping system

If a cognitive mapping system as proposed by O'Keefe and Nadel (1978) must necessarily encode precise metric information in order to build an exact Euclidean representation of space, then one must question the existence of cognitive maps in any organism, including adult humans. Nevertheless, behavioral and neurophysiological evidence suggest that both angular and distance information are represented in the brain, but that these representations are not exact replicates of the external world. In agreement with the concept of cognitive map as proposed by Tolman (1948), such representations encode the relationships between environmental objects and between the individual and other locations (Dabaghian, Brandt, & Frank, 2014; Poucet et al., 2015), and support flexible behavior (Behrens et al., 2018). Indeed, the representation of spatial information in the brain via individual head direction cells, place cells and grid cells is fundamentally noisy and thus imprecise in absolute terms (McNaughton et al., 1996; Taube, 2007). Yet, an animal's location can be decoded reliably from ensembles of place cells (Wilson & McNaughton, 1993) and grid cells (Fyhn, Molden, Witter, Moser, & Moser, 2004), and with increasing precision as the animal spends more time exploring the environment (Wilson & McNaughton, 1993). Accordingly, such spatial representations are sufficiently precise in order to enable successful navigation with or without visual information, as long as stable environmental visual, olfactory or somatosensory landmarks are occasionally available to update the representation of the animal's position (Etienne & Jeffery, 2004; McNaughton et al., 1996). In our study, both adults and children demonstrated the ability to take shortcuts to navigate between different objects, thus exhibiting their ability to use path integration to build a cognitive map of the relations between environmental objects in absence of visual information. However, all of our participants exhibited some degree of imprecision in their behavioral performance.

Our analyses of children's initial heading at one-meter in the homing task showed that they tended to under-rotate after being guided through the two-legged path (requiring an ideal left or right rotation of 135°), but they did not under-rotate following the straight path (requiring an ideal left or right rotation of 180°). Our results are consistent with those of Smith et al. (2013) who showed that 7–9-year-old blindfolded children under-rotated during a triangle completion task with a 90° guided turn, which also required an ideal 135° rotation before walking between 1.4 and 2.8 m to return home. Together, these results suggest that 5–9-year-old children are capable of producing turns of a specific desired angle, since they were capable of making a relatively precise 180° turn following the straight path journey in our experiment, but that their ability to integrate experienced rotations during the outward path is less precise than adults'. Indeed, previous authors have proposed that errors in path integration arise primarily from encoding errors of the experienced angles to be integrated (Fujita et al., 1993). However, across both the homing and the cognitive mapping tasks, even though children's initial heading was different from the ideal heading in four of ten paths (both angled paths in the homing task, and the two paths requiring a 45° turn in the cognitive mapping task), their final heading was only different from the ideal heading in one of these ten paths (the first path from the bench to the chair in the cognitive mapping task). Thus, children appeared to make less than ideal turns but continued to angle towards the goal while walking, whereas adults appear to have made more accurate turns first, and then walked straight to the goal. This difference in strategy between children and adults may be due to the fact that in our homing task participants repeated each of the four paths five times, and thus had the opportunity to correct their errors and compensate for their homing inaccuracies. Whereas adults had quite accurate initial and final headings and did not need to compensate, it is possible that some children recognized that they ended up to the left or the right of home (depending on the outward path) on the first trial or two, and then attempted to compensate while walking by veering more to the right or to the left, respectively.

In sum, when considering our data and the data from Smith et al. (2013), we believe that the most parsimonious explanation is that children are less precise than adults in integrating experienced rotations in the dark, leading them to systematically under-rotate when calculating the ideal return trajectory. Interestingly, however, Wiener, Berthoz, and Wolbers (2011) reported that when given specific instructions, adult individuals can either continuously update their position with respect to the start location (a.k.a. a continuous strategy) or remember the shape of the outbound path and calculate a homing vector based on this representation (a.k.a. a configural strategy). In their study, overall homing accuracy was better when subjects used the configural strategy, although experimental evidence indicated that these subjects also computed a homing vector continuously. Thus, an alternative explanation to our results may be that children relied more on a continuous computation to calculate their homing direction, whereas adults may have benefited from the added precision provided by a configural (cognitive) strategy in order to reconstruct the return path. Nevertheless, in our cognitive mapping task, there was a long temporal delay between when participants were guided to the first two objects and when they had to navigate the novel routes (usually more than 10 min for children), making the idea of a continuous computation strategy difficult to support theoretically.

If, however, children did systematically under-rotate when calculating a return trajectory, then this suggests that they overestimated the magnitude of the rotation experienced during the outward trajectory. This assumption is indeed consistent with the observed performance of some children in the cognitive mapping task. During the learning phase of this task, if these children similarly overestimated the experienced angles between the bench and the shelf (> 45°), and between the shelf and the chair (> 45°), their estimation of the position of the chair relative to the bench should place the chair to the right of the bench and not straight in front of it. Indeed, children's average final heading from the bench to the chair of 20.57° was outside of the 99% confidence interval (11.57°), and both their final heading and their angular deviation differed from that of adults. Moreover, 11 of the 12 children who

failed this route ended their path to the right of the chair, a distribution that is clearly not random. However, this was the only novel route for which children's final heading was outside the 99% confidence interval, suggesting that after they were guided to the chair from their end location they were able to quickly update their cognitive map, allowing them to more accurately navigate from the chair to the table (with 20/28 passing), and from the table to the shelf (with 22/28 passing), with final headings that were in the 99% confidence interval for both of these paths.

Altogether, the findings from the homing and cognitive mapping tasks suggest that from at least five years of age children are capable of turning sufficiently accurately and walking a straight line in order to perform low-resolution cognitive mapping without vision. Nonetheless, as compared to adults, 5–9-year-old children may integrate experienced angular rotations less well and be less precise in their path integration computations.

4.3. Why did some children fail to build a cognitive map?

Whereas the imprecise integration of angular displacements may have resulted in some children not passing by our subjective criteria, we can nonetheless identify a number of children who clearly had not built a cognitive map during the learning phase. These children can be seen going straight or in the opposite direction of the target in the chair to table and the table to chair paths. Our observations while these children were performing the task suggested that they were either inattentive, bored or dismissive of the experiment during the learning phase. However, a number of other children who succeeded in building a cognitive map in our study could also be described in this same manner.

We are thus left to conclude that all children from five years of age, or indeed even from 2.5 years of age if we consider other previous results (Landau et al., 1984; Newcombe et al., 1998; Ribordy et al., 2013; Ribordy Lambert et al., 2015), should be capable of building a cognitive map using path integration, but that some children simply fail to construct a cognitive map when the specific goals of the experiment have not been explicitly explained. Interestingly, in our experience using a number of tasks in which participants are given very few explicit verbal instructions concerning the aim of the experiment, we have found that about 15% of participants, be they children or adults, and with typical or atypical development, do not implicitly infer the aim of the experiment (Bostelmann et al., 2017, 2018; Ribordy et al., 2013). In the current study, we believe that all children between five and nine years of age would have exhibited the capacity to build a cognitive map had we explained that: "We are going to lead you on some paths between different pieces of furniture. At the end of the experiment, it will be your job to go to all of the different objects, so make sure that you think about and remember where all of the objects are."

However, implying that some children did not implicitly make cognitive maps because they were not paying attention implies that cognitive mapping is necessarily effortful or requires explicit attention (Newcombe, 2019). Instead, cognitive mapping has been assumed to be a continuous and automatic process (O'Keefe & Nadel, 1978; Tolman, 1948). Nevertheless, as we can all attest, from time to time we become lost in new or unfamiliar environments. Our capacity to build a cognitive map can be diminished when we are distracted or not paying attention when navigating, or when we are "blindly" following someone else who is doing the navigating. In our study, participants were never told that they should keep track of the locations of the objects in the room so that they could later navigate between them autonomously. Whereas all of our adult participants were able to construct a cognitive map (some or all of whom may have implicitly inferred the goal of the experiment), one third of the children did not. Interestingly, however, four of the eight children who failed the first 45° angle trajectory between the chair and the table were able to perform the second 45° angle trajectory and navigate appropriately from the table back to the chair, suggesting that once they understood the goal of the task they were able to quickly construct or improve an imprecise or incomplete cognitive map during the testing phase of the task. Indeed, if we use a more liberal criterion for determining whether children constructed a cognitive map, by considering only the trajectory from the table to the chair, we could conclude that 86% (24 of 28) of the 5–9-year-old children succeeded. In contrast to previous assertions that successful cognitive mapping is not exhibited by children until early adolescence (Newcombe, 2019), the current findings, as well as data from previous studies (Landau et al., 1981, 1984; Morrongiello et al., 1995), demonstrate that from at least 5 years of age children are capable of constructing and using a cognitive map, a representation of the relationships between objects' locations, in order to behave flexibly and navigate between these locations using novel routes (Behrens et al., 2018; Tolman, 1948). In contrast to the cognitive map concept proposed by O'Keefe and Nadel (1978), although the precision of these representations improves between childhood and adulthood, humans do not appear to encode the precise metric information necessary to build an exact Euclidean representation of space even in adulthood (Banta Lavenex, Colombo, Ribordy Lambert, & Lavenex, 2014). However, an exact Euclidean representation is likely not necessary since the perception of external landmarks from a distance can often be used to pinpoint the goal location and guide the final approach.

4.4. Path integration is less precise in children than in adults

Although a majority of 5–9-year-old children were able to build a cognitive map representing the spatial relationships between environmental objects, their variability in task performance was greater than that of adults. However, we did not find consistently reliable correlations between children's age and task performance in the homing or cognitive mapping tasks. This suggests that although the integration of directional and distance information may become more precise with age between childhood and adulthood, such integration remains highly variable both within and between individual children until at least nine years of age. Moreover, as previously described, path integration accrues error with every turn and every step. Obviously, children and adults had to integrate the same number of turns of the same magnitude. In contrast, due to their smaller size children had to take many more steps than adults in order to travel along the guided and non-guided paths. The fact that neither the task nor the environment was

scaled to the participants' size or step length may have contributed to the overall more variable performance of children as compared to adults. Note also that since children's size continues to evolve until young adulthood, the integration of sensory information derived from different sensory modalities must be constantly updated (Newcombe, 2019). This is another factor potentially contributing to the larger variability of behavioral performance observed in children, as compared to adults (Nardini et al., 2008; Ribordy et al., 2013; Ribordy Lambert et al., 2015, 2016). Interestingly, the calibration of path integration has been shown to change with experience (Jayakumar et al., 2019), and this plasticity may underlie developmental changes over the lifespan.

4.5. Distance estimation and cognitive maps

Whereas our experimental paradigm was very reliable for measuring the angular displacements (i.e., initial and final headings) of participants, it was less informative with respect to the linear displacements or distances traveled. First, in the homing task, participants repeated the same return path a total of 24 times, thus offering older children and adult participants the possibility of explicitly counting the number of steps required to return home, and adjusting this number based on trial and error (i.e., using a secondary cognitive strategy). Second, our experimental room was only 8 m × 8 m, thus limiting the maximal distance that participants could walk. Indeed, we found that children often had to be stopped before running into walls on their return paths, making the comparison of the distance traveled between adults and children invalid. However, it is impossible to know whether children were worse at estimating distance, or whether they had difficulties in understanding that they could consciously "estimate" distance and then explicitly use this knowledge to stop at a given point even though they had not reached a detectable goal location. Both explanations may have played a role in children's poor estimation of distance.

However, how important is distance estimation to the formation of cognitive maps? Whereas the critical role that precise angular estimation plays in cognitive map formation and navigation is obvious, the importance that distance estimation plays has long been disputed in the literature (Etienne & Jeffery, 2004; Etienne et al., 1996; M. L. Mittelstaedt & Mittelstaedt, 1980, 2001; O'Keefe & Nadel, 1978; Seguinot et al., 1993; Wehner & Wehner, 1986). Given that the distance travelled must be calculated via a combination of vestibular, proprioceptive and visual cues that integrate linear displacement, stride length and regularity, and visual flow (Campos, Butler, & Bulthoff, 2014; Souman, Freeman, Eikmeier, & Ernst, 2010), distance estimation must be highly sensitive to the age, size and health of the individual (Adamo, Briceno, Sindone, Alexander, & Moffat, 2012). Such integration must necessarily change across an individual's lifespan (Bullens et al., 2010), potentially making precise distance estimation difficult in long-lived and slowly-growing humans (Newcombe, 2019), even though the calibration of path integration changes with experience (Jayakumar et al., 2019). In contrast, a path integration system that has a relatively precise coding of angular displacement, combined with a gross and relative coding of linear displacement, may be accurate enough to support navigation over relatively short distances. Indeed, if one's angular estimation is correct, then navigating with a gross estimation of distance (a few meters away versus tens of meters away) will allow the individual to anticipate the location of the goal, and to recognize the goal or a familiar landmark that will help to localize the goal or the direction to the goal, when it is eventually approached (Etienne & Jeffery, 2004). In our cognitive mapping task, the target objects provided the necessary information to recalibrate the path integration system when building a cognitive map of the spatial relationships between these objects.

4.6. Early emergence of cognitive mapping abilities

In a recent review, Newcombe (2019) suggested that cognitive maps might not become widely evident in children until around 12 years of age. Evidence for such protracted development comes primarily from studies carried out in virtual environments (Broadbent et al., 2014; Buckley et al., 2015; Bullens et al., 2010), or from studies that dissociated different types of information in order to assess their role relative to, or in isolation from, other cues (e.g., Bullens et al., 2011; Nardini et al., 2008). However, as we and others have previously argued (Banta Lavenex et al., 2014; Cullen & Taube, 2017; Taube, Valerio, & Yoder, 2013), evidence from virtual reality paradigms, or from paradigms in which normally coherent cues are rendered incoherent, or from paradigms which require other higher order cognitive capacities (such as advanced linguistic, mental rotation, or theory of mind capacities) cannot be used to infer the absence of cognitive mapping capacities in the real world, in particular in developing individuals or in individuals with neurodevelopmental syndromes or acquired pathologies (i.e., the absence of evidence in an experimental setting cannot be considered as evidence of absence in the real world). Indeed, as described above, cognitive maps are constructed via the integration of coherent vestibular, proprioceptive, motor efference and visual information. In contrast, experiments carried out in virtual reality, for example, rely solely on visual information, and in fact oppose visual information with incoherent or absent vestibular and proprioceptive information (Adamo et al., 2012; Ravassard et al., 2013; Souman et al., 2010; Taube et al., 2013). This is especially problematic since experiments in rodents have shown that hippocampal place cell activity is abnormal without vestibular input (Ravassard et al., 2013; Stackman, Clark, & Taube, 2002), and since hippocampal place cells are at the core of cognitive maps (McNaughton et al., 2006; O'Keefe & Nadel, 1978). Similarly, although tasks that dissociate or render incoherent different cues may be informative about how the system performs under those specific conditions, they cannot inform about how the system works when all cues are present and coherent. Indeed, some experimental specificities may influence participants to use particular strategies, or to ignore other strategies, but this cannot be taken as evidence to conclude that the unused strategy is not available. In order to make such claims, paradigms that preclude the use of alternative strategies, yet afford participants the use of all normally coherent sensory information, and exclude the necessity of using other higher-order cognitive processes to understand or accomplish the task must be used (Nadel & Hardt, 2004). Our critique of these paradigms should not be taken to mean that we deny the interest and importance of using virtual reality and cue dissociation paradigms to study certain spatial processes. These paradigms can indeed be useful to tease

apart some basic cognitive processes and to understand how other implicit and explicit cognitive processes might interact with and impact these basic spatial processes. However, there is a serious logical confound in using the results from virtual reality experiments or cue dissociation tasks to infer that children or individuals with neurodevelopmental disorders or acquired pathologies are incapable of constructing allocentric spatial representations in the real world where the individuals have access to coherent information from all of the sensory modalities normally available to be integrated in a multimodal spatial representation.

4.7. Conclusion

The current findings, together with those of Landau et al. (1981, 1984) and Morrongiello et al. (1995), provide consistent evidence that by at least five years of age children can use path integration in absence of visual information to build a cognitive map representing the spatial relationships between environmental objects. Based on earlier findings in the presence of visual information (Newcombe et al., 1998; Ribordy et al., 2013; Ribordy Lambert et al., 2015, 2016), as well as Landau's initial reports, we may hypothesize that a cognitive mapping system integrating all types of sensory information may already be functional by two years of age. The present evidence also suggests that children's cognitive mapping capacities may improve with age, due to decreased intra-individual variability and increased encoding precision, but these improvements should be considered quantitative changes rather than qualitative changes.

Acknowledgments

This research was supported by the Swiss National Science Foundation: grant 100019_165481 to PBL and PL, and the Faculty of the Social and Political Sciences of the University of Lausanne. Neither the Swiss National Science Foundation nor the University of Lausanne had any involvement in the study design, nor in the collection, analysis or interpretation of the data, nor in the writing of this report or the decision to submit it for publication. The authors have no conflicts of interest to declare. The authors would like to thank all of the participants and their families for making this study possible.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cogpsych.2020.101307>.

References

- Acredolo, L. P. (1978). Development of spatial orientation in infancy. *Developmental Psychology, 14*(3), 224.
- Acredolo, L. P., Adams, A., & Goodwyn, S. W. (1984). The role of self-produced movement and visual tracking in infant spatial orientation. *Journal of Experimental Child Psychology, 38*(2), 312–327.
- Acredolo, L. P., & Evans, D. (1980). Developmental changes in the effects of landmarks on infant spatial behavior. *Developmental Psychology, 16*(4), 312.
- Adamo, D. E., Briceno, E. M., Sindone, J. A., Alexander, N. B., & Moffat, S. D. (2012). Age differences in virtual environment and real world path integration. *Frontiers in Aging Neuroscience, 4*, 26.
- Allen, G. L. (2004). *Human spatial memory: Remembering where*. Psychology Press.
- Alyan, S., & McNaughton, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience, 113*(1), 19–31.
- Banta Lavenex, P., Colombo, F., Ribordy Lambert, F., & Lavenex, P. (2014). The human hippocampus beyond the cognitive map: evidence from a densely amnesic patient. *Frontiers in Human Neuroscience, 8*.
- Behrens, T. E. J., Muller, T. H., Whittington, J. C. R., Mark, S., Baram, A. B., Stachenfeld, K. L., et al. (2018). What is a cognitive map? Organizing knowledge for flexible behavior. *Neuron, 100*(2), 490–509.
- Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology, 199*(1), 219–224.
- Bostelmann, M., Costanzo, F., Martorana, L., Menghini, D., Vicari, S., Lavenex, P. B., & Lavenex, P. (2018). Low-resolution place and response learning capacities in Down syndrome. *Frontiers in Psychology, 9*, 2049.
- Bostelmann, M., Fragniere, E., Costanzo, F., Di Vara, S., Menghini, D., Vicari, S., ... Lavenex, P. B. (2017). Dissociation of spatial memory systems in Williams syndrome. *Hippocampus, 27*(11), 1192–1203.
- Bremner, J. G. (1978). Egocentric versus allocentric spatial coding in nine-month-old infants: Factors influencing the choice of code. *Developmental Psychology, 14*(4), 346.
- Bremner, J. G., Knowles, L., & Andreassen, G. (1994). Processes underlying young children's spatial orientation during movement. *Journal of Experimental Child Psychology, 57*(3), 355–376.
- Broadbent, H. J., Farran, E. K., & Tolmie, A. (2014). Egocentric and allocentric navigation strategies in Williams syndrome and typical development. *Developmental Science, 17*(6), 920–934.
- Buckley, M. G., Haselgrove, M., & Smith, A. D. (2015). The developmental trajectory of intramaze and extramaze landmark biases in spatial navigation: An unexpected journey. *Developmental Psychology, 51*(6), 771–791.
- Bullens, J., Klugkist, I., & Postma, A. (2011). The role of local and distal landmarks in the development of object location memory. *Developmental Psychology, 47*(6), 1515–1524.
- Bullens, J., Nardini, M., Doeller, C. F., Braddick, O., Postma, A., & Burgess, N. (2010). The role of landmarks and boundaries in the development of spatial memory. *Developmental Science, 13*(1), 170–180.
- Bushnell, E. W., McKenzie, B. E., Lawrence, D. A., & Connell, S. (1995). The spatial coding strategies of one-year-old infants in a locomotor search task. *Child Development, 66*(4), 937–958.
- Campos, J. L., Butler, J. S., & Bulthoff, H. H. (2014). Contributions of visual and proprioceptive information to travelled distance estimation during changing sensory congruencies. *Experimental Brain Research, 232*(10), 3277–3289.
- Corlett, J. T., Patla, A. E., & Williams, J. G. (1985). Locomotion estimation of distance after visual scanning by children and adults. *Perception, 14*, 257–263.
- Cornell, E. H., & Heth, C. D. (1979). Response versus place learning by human infants. *Journal of Experimental Psychology: Human Learning and Memory, 5*(2), 188–196.
- Cullen, K. E., & Taube, J. S. (2017). Our sense of direction: Progress, controversies and challenges. *Nature Neuroscience, 20*(11), 1465–1473.
- Dabaghian, Y., Brandt, V., & Frank, L. M. (2014). Reconciling the hippocampal map as a topological template. *Elife, 3*.
- Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*, 180–192.
- Etienne, A. S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J., & Séguinot, V. (1998). Navigation through vector addition. *Nature, 396*(6707),

- 161–164.
- Etienne, A. S., Maurer, R., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology*, 199(1), 201–209.
- Foster, T. C., Castro, C. A., & McNaughton, B. L. (1989). Spatial selectivity of rat hippocampal neurons: Dependence on preparedness for movement. *Science*, 244(4912), 1580–1582.
- Fujita, N., Klatzky, R. L., Loomis, J. M., & Golledge, R. G. (1993). The encoding-error model of pathway completion without vision. *Geographical Analysis*, 25(4), 295–314.
- Fyhn, M., Molden, S., Witter, M. P., Moser, E. I., & Moser, M. B. (2004). Spatial representation in the entorhinal cortex. *Science*, 305(5688), 1258–1264.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Giovannini, L., Jacomuzzi, A. C., Bruno, N., Semenza, C., & Surian, L. (2009). Distance perception in autism and typical development. *Perception*, 38(3), 429–441.
- Giudice, N. A. (2018). Navigating without vision: Principles of blind spatial cognition. In D. R. Montello (Ed.), *Handbook of behavioral and cognitive geography* (pp. 260–288). Northampton, MA, USA: Edward Elgar Publishing.
- Golledge, R. G., Klatzky, R. L., & Loomis, J. M. (1996). Cognitive mapping and wayfinding by adults without vision. In J. Portugali (Ed.), *The construction of cognitive maps* (pp. 215–246). Kluwer Academic Press.
- Jabès, A., Banta Lavenex, P., Amaral, D. G., & Lavenex, P. (2011). Postnatal development of the hippocampal formation: A stereological study in macaque monkeys. *Journal of Comparative Neurology*, 519(6), 1051–1070.
- Jayakumar, R. P., Madhav, M. S., Savelli, F., Blair, H. T., Cowan, N. J., & Knierim, J. J. (2019). Recalibration of path integration in hippocampal place cells. *Nature*, 566(7745), 533–537.
- Keating, M. B., McKenzie, B. E., & Day, R. H. (1986). Spatial localization in infancy: Position constancy in a square and circular room with and without a landmark. *Child Development*, 57(1), 115–124.
- Klatzky, R. L., Loomis, J. M., Golledge, R. G., Cicinelli, J. G., Doherty, S., & Pellegrino, J. W. (1990). Acquisition of route and survey knowledge in the absence of vision. *Journal of Motor Behavior*, 22(1), 19–43.
- Landau, B., Gleitman, H., & Spelke, E. (1981). Spatial knowledge and geometric representation in a child blind from birth. *Science*, 213(4513), 1275–1278.
- Landau, B., & Spelke, E. (1988). Geometric complexity and object search in infancy. *Developmental Psychology*, 24(4), 512.
- Landau, B., Spelke, E., & Gleitman, H. (1984). Spatial knowledge in a young blind child. *Cognition*, 16(3), 225–260.
- Langston, R. F., Ainge, J. A., Couey, J. J., Canto, C. B., Bjerknes, T. L., Witter, M. P., ... Moser, M. B. (2010). Development of the spatial representation system in the rat. *Science*, 328(5985), 1576–1580.
- Lavenex, P., & Banta Lavenex, P. (2006). Spatial relational memory in 9-month-old macaque monkeys. *Learning and Memory*, 13(1), 84–96.
- Lavenex, P., & Banta Lavenex, P. (2013). Building hippocampal circuits to learn and remember: Insights into the development of human memory. *Behavioural Brain Research*, 254, 8–21.
- Lavenex, P., Banta Lavenex, P., & Amaral, D. G. (2004). Nonphosphorylated high-molecular-weight neurofilament expression suggests early maturation of the monkey subiculum. *Hippocampus*, 14(7), 797–801.
- Lavenex, P., Banta Lavenex, P., & Amaral, D. G. (2007). Postnatal development of the primate hippocampal formation. *Developmental Neuroscience*, 29(1–2), 179–192.
- Lavenex, P., Sugden, S. G., Davis, R. R., Gregg, J. P., & Banta Lavenex, P. (2011). Developmental regulation of gene expression and astrocytic processes may explain selective hippocampal vulnerability. *Hippocampus*, 21(2), 142–149.
- Lew, A. R., Bremner, J. G., & Lefkovich, L. P. (2000). The development of relational landmark use in six- to twelve-month-old infants in a spatial orientation task. *Child Development*, 71(5), 1179–1190.
- Loomis, J. M., Klatzky, R. L., & Golledge, R. G. (2001). Navigating without vision: Basic and applied research. *Optometry and Vision Science*, 78(5), 282–289.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, 122(1), 73–91.
- McKenzie, B. E., Day, R. H., & Ihlsen, E. (1984). Localization of events in space - Young infants are not always egocentric. *British Journal of Developmental Psychology*, 2(Mar), 1–9.
- McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M. W., Knierim, J. J., ... Weaver, K. L. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology*, 199(Pt 1), 173–185.
- McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M. B. (2006). Path integration and the neural basis of the 'cognitive map'. *Nature Reviews Neuroscience*, 7(8), 663–678.
- Mittelstaedt, H. (1999). The role of the otoliths in perception of the vertical and in path integration. *Annals of the New York Academy of Sciences*, 871, 334–344.
- Mittelstaedt, M. L., & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, 67(11), 566–567.
- Mittelstaedt, M. L., & Mittelstaedt, H. (2001). Idiopathic navigation in humans: Estimation of path length. *Experimental Brain Research*, 139(3), 318–332.
- Morrongiello, B. A., Timney, B., Humphrey, G. K., Anderson, S., & Skory, C. (1995). Spatial knowledge in blind and sighted children. *Journal of Experimental Child Psychology*, 59(2), 211–233.
- Muller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences USA*, 85(14), 5287–5290.
- Nadel, L., & Hardt, O. (2004). The spatial brain. *Neuropsychology*, 18(3), 473–476.
- Nardini, M., Burgess, N., Breckenridge, K., & Atkinson, J. (2006). Differential developmental trajectories for egocentric, environmental and intrinsic frames of reference in spatial memory. *Cognition*, 101(1), 153–172.
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, 18(9), 689–693.
- Nardini, M., Thomas, R. L., Knowland, V. C. P., Braddick, O. J., & Atkinson, J. (2009). A viewpoint-independent process for spatial reorientation. *Cognition*, 112(2), 241–248.
- Negen, J., Heywood-Everett, E., Roome, H. E., & Nardini, M. (2018). Development of allocentric spatial recall from new viewpoints in virtual reality. *Developmental Science*, 21(1).
- Newcombe, N. S. (2019). Navigation and the developing brain. *Journal of Experimental Biology*, 222, jeb186460.
- Newcombe, N. S., & Huttenlocher, J. (2000). *Making space. The development of spatial representation and reasoning*. Cambridge, MA: MIT Press.
- Newcombe, N. S., Huttenlocher, J., Drumme, A. B., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development*, 13(2), 185–200.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.
- Passini, R., & Proulx, G. (1988). Wayfinding without vision - an experiment with congenitally totally blind people. *Environment and Behavior*, 20(2), 227–252.
- Poucet, B., Chailion, F., Truchet, B., Save, E., Sargolini, F., & Hok, V. (2015). Is there a pilot in the brain? Contribution of the self-positioning system to spatial navigation. *Frontiers in Behavioral Neuroscience*, 9.
- Ravassard, P., Kees, A., Willers, B., Ho, D., Aharoni, D., Cushman, J., ... Mehta, M. R. (2013). Multisensory control of hippocampal spatiotemporal selectivity. *Science*, 340(6138), 1342–1346.
- Ribordy, F., Jabès, A., Banta Lavenex, P., & Lavenex, P. (2013). Development of allocentric spatial memory abilities in children from 18 months to 5 years of age. *Cognitive Psychology*, 66(1), 1–29.
- Ribordy Lambert, F., Lavenex, P., & Banta Lavenex, P. (2015). Improvement of allocentric spatial memory resolution in children from 2 to 4 years of age. *International Journal of Behavioral Development*, 39(4), 318–331.
- Ribordy Lambert, F., Lavenex, P., & Banta Lavenex, P. (2016). The “when” and the “where” of single-trial allocentric spatial memory performance in young children: Insights into the development of episodic memory. *Developmental Psychobiology*, 59(2), 185–196.
- Rider, E., & Rieser, J. (1988). Pointing at objects in other rooms: Young children's sensitivity to perspective after walking with and without vision. *Child Development*, 59(2), 480–494. <https://doi.org/10.2307/1130326>.
- Rieser, J., & Heiman, M. (1982). Spatial self-reference systems and shortest-route behavior in toddlers. *Child Development*, 53(2), 524–533. <https://doi.org/10.2307/>

1128995.

- Rieser, J., & Rider, E. (1991). Young children's spatial orientation with respect to multiple targets when walking without vision. *Developmental Psychology*, 27(1), 97–107. <https://doi.org/10.1037/0012-1649.27.1.97>.
- Ruddle, R. A., & Lessels, S. (2006). For efficient navigational search, humans require full physical movement, but not a rich visual scene. *Psychological Science*, 17(6), 460–465.
- Savelli, F., & Knierim, J. J. (2019). Origin and role of path integration in the cognitive representations of the hippocampus: Computational insights into open questions. *Journal of Experimental Biology*, 222(Pt Suppl 1).
- Seguinot, V., Cattet, J., & Benhamou, S. (1998). Path integration in dogs. *Animal Behaviour*, 55(4), 787–797.
- Seguinot, V., Maurer, R., & Etienne, A. S. (1993). Dead reckoning in a small mammal: The evaluation of distance. *Journal of Comparative Physiology A*, 173(1), 103–113.
- Smith, A. D., McKeith, L., & Howard, C. J. (2013). The development of path integration: Combining estimations of distance and heading. *Experimental Brain Research*, 231(4), 445–455.
- Souman, J. L., Freeman, T. C. A., Eikmeier, V., & Ernst, M. O. (2010). Humans do not have direct access to retinal flow during walking. *Journal of Vision*, 10(11).
- Spiers, H. J., & Barry, C. (2015). Neural systems supporting navigation. *Current Opinion in Behavioral Sciences*, 1, 47–55.
- Stackman, R. W., Clark, A. S., & Taube, J. S. (2002). Hippocampal spatial representations require vestibular input. *Hippocampus*, 12(3), 291–303.
- Taube, J. S. (2007). The head direction signal: Origins and sensory-motor integration. *Annual Review of Neuroscience*, 30, 181–207.
- Taube, J. S., Valerio, S., & Yoder, R. M. (2013). Is navigation in virtual reality with fMRI really navigation? *Journal of Cognitive Neuroscience*, 25(7), 1008–1019.
- Tcheang, L., Bulthoff, H. H., & Burgess, N. (2011). Visual influence on path integration in darkness indicates a multimodal representation of large-scale space. *Proceedings of the National Academy of Sciences USA*, 108(3), 1152–1157.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55, 189–208.
- Wang, C., Chen, X., & Knierim, J. J. (2019). Egocentric and allocentric representations of space in the rodent brain. *Current Opinion in Neurobiology*, 60, 12–20.
- Warren, W. H. (2019). Non-Euclidean navigation. *Journal of Experimental Biology*, 222(Pt Suppl 1).
- Wehner, R., & Wehner, S. (1986). Path integration in desert ants - Approaching a long-standing puzzle in insect navigation. *Monitore Zoologico Italiano-Italian Journal of Zoology*, 20(3), 309–331.
- Wiener, J. M., Berthoz, A., & Wolbers, T. (2011). Dissociable cognitive mechanisms underlying human path integration. *Experimental Brain Research*, 208(1), 61–71.
- Wills, T. J., Cacucci, F., Burgess, N., & O'Keefe, J. (2010). Development of the hippocampal cognitive map in preweanling rats. *Science*, 328(5985), 1573–1576.
- Wilson, M. A., & McNaughton, B. L. (1993). Dynamics of the hippocampal ensemble code for space. *Science*, 261(5124), 1055–1058.
- Zar, J. H. (1999). *Biostatistical analysis* (4th ed.). Upper Saddle River, New Jersey: Prentice Hall.