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The influence of yaw rotation on spatial navigation during development

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ABSTRACT

Sensory cues enable navigation through space, as they inform us about movement properties, such as the amount of travelled distance and the heading direction. In this study, we focused on the ability to spatially update one's position when only proprioceptive and vestibular information is available. We aimed to investigate the effect of yaw rotation on path integration across development in the absence of visual feedback. To this end, we utilized the triangle completion task: participants were guided through two legs of a triangle and asked to close the shape by walking along its third imagined leg. To test the influence of yaw rotation across development, we tested children between 6 and 11 years old (y.o.) and adults on their perceptions of angles of different degrees. Our results demonstrated that the amount of turn while executing the angle influences performance at all ages, and in some aspects, also interacted with age. Indeed, whilst adults seemed to adjust their heading towards the end of their walked path, younger children took less advantage of this strategy. The amount of disorientation the path induced also affected participants' full maturational ability to spatially navigate with no visual feedback. Increasing induced disorientation required children to be older to reach adult-level performance. Overall, these results provide novel insights on the maturation of spatial navigation-related processes.

1. Introduction

When exploring an environment or moving along a predefined or novel route, we often rely on our ability to perceive our path's properties from the surroundings. If environmental features are absent or uninformative (e.g., in the absence of visual feedback), successful spatial navigation requires us to spatially update our location, mostly relying on vestibular and proprioceptive cues, which is known as inertial spatial navigation. This aspect of spatial navigation refers to path integration, based on an idiothetic reference used to code and monitor spatial navigation and generate a spatial representation of the travelled path. The triangle completion paradigm is one of the most commonly employed experimental tasks used to investigate path integration. In its classical version, the experimenter walks with the participant along two legs of a triangular path, and the participant is then asked to return to their starting position by walking along the triangle's third leg, without the experimenter's guidance. This methodology examines how well individuals can update their position in space by actively moving with or without visual feedback. Considerable research has implemented this task to disentangle perceptual properties of path integration (Loomis et al, 1993, 2001; Philbeck et al., 2001; Rieser and Rider, 1991; Smith et al., 2013). When visual feedback of environmental properties such as landmarks is absent, vestibular cues are fundamental to perform the triangle completion task. This aspect is confirmed by decayed performance in the case of clinical vestibular loss, mainly in older patients (Xie et al., 2017). In addition, galvanic vestibular stimulation can induce sensory perturbations that affect performance on the triangle completion task (Karn and Cinelli, 2019). Moreover, the presence of visual cues regarding self-motion, such as optic flow, which are non-informative about the environmental position to be reached, do not influence performance, suggesting a vestibular/proprioceptive dominance in spatial updates when moving (Kearns et al., 2002). In the context of sensory deprivation, visual experience appears to be significant: in the case of complete blindness, the onset of visual loss influences the ability to perform the task (Loomis et al, 1993, 2001). This result indicates that the amount of time experienced with vision, and likely the onset of blindness relative to development, affects the ontogenesis of spatial updating skills.

Developmental studies indicate that spatial navigation skills improve with age (for a review: Newcombe, 2019). The ability to orient oneself

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depends on development-related strategies that are acquired while growing up. Throughout development, children experience steady and rapid growth, both physically and cognitively. Such growth is especially accentuated during infancy, but slows down and reaches a plateau between adolescence and adulthood. In the context of spatial navigation, the ability to orient ourselves in the environment depends on the ability to process and represent contextual information. Specifically, this information includes geometric information, such as the shape of the navigated environment (e.g. left vs. right corner of a room), and non-geometric properties, such as the presence of landmarks. Such properties of spatial navigation have often been investigated with reorientation paradigms, where the participant, after exploring an environment to encode a target's location, is disoriented and asked to find the removed target's previous location. Contrary to adults, infants aged 18–24 months do not use non-geometric cues in reorientation tasks, but remain fixated on using geometric cues after being disoriented and asked to find previously observed target objects (Hermer and Spelke, 1994, 1996). Overall, young children aged 4–5 y.o. can encode non-geometric properties in their explored environment, but fail to use this information to reorient themselves (Hermer, 1997). After 6 y.o., children start using non-geometric properties to solve reorientation tasks; onset of this ability has been credited to language learning, specifically in the context of learning linguistic representations related to spatial navigation, such as using the words "left" and "right" (Hermer-Vazquez et al., 2001). Using non-geometric cues, such as landmarks, has received particular attention in the study of developmental changes related to spatial navigation. In the context of multisensory spatial navigation, initial studies on children demonstrated that visual information can interfere with spatial navigation skills in 2 year-olds (Rider and Rieser, 1988). In another study, 4 year-olds showed worse accuracy than adults in an inertial spatial navigation task where they were required to reach a previously seen target while blindfolded (Rieser and Rider, 1991). These findings indicate the significance of developmental changes in acquiring spatial navigation abilities, which are likely related to calibrating multiple sensory information cueing properties within one's environment while moving through space. In this context, studies show that children experience difficulties combining inertial spatial navigation cues (such as proprioceptive and vestibular) with the allocentric cues that visual landmarks provide. Such multisensory cue combination starts developing after 8–10 y.o. (Nardini et al., 2008), which is alike to observations regarding other perceptual dimensions such as size (Gori et al., 2008) and verticality (Cuturi and Gori, 2019). In such multisensory integration studies, children often show strong reliance on visual information. These results therefore support the multisensory recalibration theory (Gori et al, 2008, 2010) in which multisensory development is fostered by the most reliable sensory source (e.g. vision) that calibrates the processing of other sensory modalities (e.g. auditory, vestibular/proprioceptive). As a byproduct of this calibration process, 10–11 y.o. children can benefit from the combination of visual and inertial cues to spatial navigation, whereas adults do not (Petrini et al., 2016). Although controversial, this result might indicate the prominent role of visual information within the calibration processes taking place across development, causing children to combine visual and inertial cues. Meanwhile, adults rely solely on inertial cues, which have strengthened reliability due to their vision-driven calibration processes.

Overall, complex spatial navigation skills, such as moving towards a home location based on its relationship to the surroundings, are acquired at 6–7 y.o (Overman et al., 1996). and reach adult level at 11 y.o. (Hoesing et al., 2000). Interestingly, these age levels have been identified as age milestones in hippocampal growth (Uematsu et al., 2012; for a review, Wiener-Vacher et al., 2013). In the context of spatial navigation, considerable research on the role of hippocampus has focused on animal models and adapted similar methods with humans (Worsley et al., 2001). In Worsley and colleagues' pioneering study, epileptic patients who had unilateral resection of the temporal lobe were tested with a series of path integration tasks to unveil the hippocampus' role in human spatial navigation. Their results demonstrate that such patients show impairments in accomplishing a homing vector task (i.e. the triangle completion task), as well as more complex spatial navigation tasks. Given the outcome of this research, the authors suggest that patients with resected left temporal lobes might be able to calculate the correct direction, but will likely be unable to retain this information in memory.

In the investigation of spatial navigation abilities, the triangle completion task represents a reliable method to investigate path integration strategies, as well as more general homing behaviors. Such behavioral abilities are important for understanding exploration strategies and abilities in child development. As Smith and colleagues state (Smith et al., 2013), such tasks provide the means to contemporarily investigate orientation and distance components of path integration. Since these two components cannot be separated in naturalistic settings, their combination improves the ecological aspects of laboratory testing. Following this observation, Smith and colleagues tested children on the triangle completion task, using turn angles of 90° to the right and left. The authors focused on the influence of path length on heading and distance errors while maintaining the turning angle at 90°. Their results showed developmental trends for both aspects of spatial navigation. However, the authors focused solely on the 90° turn angle, but in everyday life, we are faced with turn angles that can vary broadly.

Despite the importance of inertial spatial navigation, Smith and colleagues' contribution is the only report of developmental spatial navigation in the absence of external landmarks or cues, other than vestibular and proprioceptive. Investigating the isolated role and influence of such sensory cues is fundamental for a comprehensive understanding of spatial navigation across development, as these sensory modalities are more sensitive to the self-motion components of spatial navigation. Indeed, when turning, we experience self-rotation, which is the supplement of the inner angle between the two lines composing the path. For instance, an internal angle of 20° requires a rotation of 160° as the turn angle. This kind of rotation is defined as yaw rotation, which is a rotational movement about the vertical axis. When the latter coincides with gravity, yaw rotations can be expressed as clockwise or counterclockwise rotation of the erect body. When vision is not available, yaw rotation can induce disorientation, reducing the ability to spatially update one's location in relation to the surroundings and one's previous position. With the intent to test how yaw-based disorientation and development interact with the ability to spatially update one's position while moving, we used angles of increasing degree in a triangle completion task. Supported by previous findings showing the influence of turn angle (Loomis et al., 1993) and the strong role of vestibular information on path integration abilities, we hypothesized that the greater the yaw rotation experienced (thus the supplement of the interior angle), the greater the disorientation, resulting in greater spatial updating errors. In this context, the developmental properties of path integration would shed light on the maturation of vestibular-based path integration abilities. Regarding the role of development, given the above-mentioned work on the development of spatial updating skills, we hypothesize that younger children are less flexible in re-orienting themselves in a spatial updating task, and this aspect relates to the amount of yaw rotation experienced. Since we aimed to understand whether spatial updating progressively improves while moving, we tested the ability to point towards the home position, in terms of heading, at the beginning and end of the path to test for adjustment ability during spatial navigation. Our results indicated that the amount of yaw rotation differentially influenced performance across development, suggesting that path integration abilities emerge progressively throughout childhood.

2. Methods

2.1. Participants

Thirty-three children (6–11 y.o.) and 12 adults (22–37 y.o.) were recruited as participants. Subjects were divided into 4 subgroups depending on their ages. These are: 6–7 y.o. (n = 10; 5 females); 8–9 y.o. (n = 13; 7 females); 10–11 y.o. (n = 10; 7 females); >22 y.o. (n = 12; 6 females). All subjects were right-handed.

2.2. Set-up and stimuli

In the path integration task, participants were asked to return to the starting position by walking to complete the triangle with no vision. The first walked segment measured 200 cm, and the second walked segment measured 150 cm. We varied the interior angle between the first and second leg of the triangle as follows: +45°, +90°, +135°, −45°, −90° and −135°. The positive sign indicates a turn to the right, while the negative sign indicates a turn to the left. The supplement of the interior angle represents the amount of yaw motion while turning, which is the participant's actual turn angle. Therefore, the correspondence between the interior and turn angle is as followed: interior: ±45°, turn: ±135°; interior: ±90°, turn: ±90°; interior: ±135°, turn: ±45°. To maintain continuity with previous studies employing the triangle completion task, we will hereafter refer to the interior angles when indicating the angle magnitudes of ±45, ±90, and ±135. Each stimulus level was repeated four times, leading to 24 trials in total. The experiments were conducted in a silent room. The trajectories were recorded using the Kinect, which is a Microsoft motion-sensing input device, and the EyesWeb XMI platform: an open platform to support the design and development of real-time multimodal systems and interfaces (Volpe et al., 2016). We developed a portable body movement capture set-up. The Microsoft Kinect v2 depth sensor was connected to the computer running EyesWeb XMI through a router. This equipment was placed at one end of the experiment room to maximize the recording area. The experimenter used a smartphone-based remote controller to control the recording of the participants' path without interfering with their movement (see Fig. 1A). The remote control was implemented as an Android application on an Android Smartphone, which provided access to EyesWeb XMI's main functions (e.g. start or stop recordings) and allowed tuning of parameters such as participant ID and individual features (e.g. age). Microsoft's Kinect v2 interfaced with the main recording module in the EyesWeb XMI software for this purpose, providing access to the following data streams at 30 frames per second: a) Video (resolution of 1920 × 1080 pixels), b) Infrared (resolution of 512 × 424 pixels), c) Depth images (resolution of 512 × 424 pixels, e.g. see Fig. 1B), and d) Skeleton information (25 full body joints per tracked user, e.g. see Fig. 1C), with an available tracking volume (range of depth) between 0.5 and 4.5m.

2.3. Experimental procedure

On each trial, the experimenter guided the participant in walking along the triangle's two initial legs; on turns, the participants were told to turn while the experimenter gently pushed them in the turning direction with their hands on their shoulders. When the experimenter and participant reached the endpoint of the second triangle leg, the experimenter moved away from the participant and asked them to return to the start position without help from the experimenter. To make the task more enjoyable, children were told that they were walking through a wild forest, and they had to return to the start (indicated as "home") by using the shortest path and maintaining a constant velocity. Once away from the participant, the experimenter remotely started the motion recording of the participant's path. Between trials, the experimenter again walked the participant to the start while making random turns to avoid any performance feedback. Before starting the experiment,

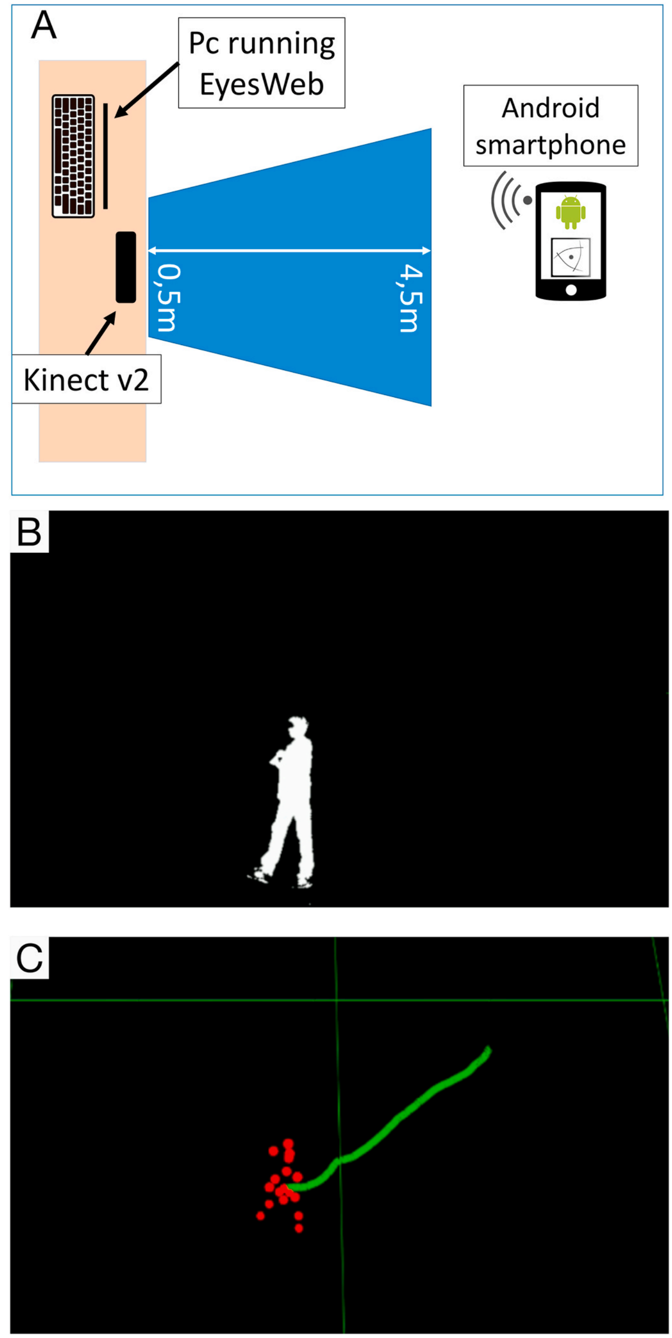

Fig. 1. Illustration of the EyesWeb recording set-up. (A) depicts a top-view representation of the experimental room and set-up. This was comprised of a Microsoft Kinect v2 depth sensor, a PC running the EyesWeb XMI software, a router connected to the PC (not represented), and an Android app implemented on an Android Smartphone for recording with a remote control (see Methods for details). The light blue area represents the approximate recording area covered by the Microsoft Kinect v2. In (B) and (C), an example trial is represented. (B) displays the participant's depth image at their instantaneous position while performing the trial. In (C), the red dots represent the tracked 25 full body joints, while the green line indicates the performed path. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

participants were informed that they had to complete the triangle by walking along the third leg; to make this point clear, the experimenter showed them the paths they would do with and without experimenter guidance on a paper printed triangle. Participants were blindfolded at the beginning of the experimenter using swimming goggles occluded with black tape, positioned over a blindfold that covered their eyes.

2.4. Data analysis

When analysing the data, we focused on four parameters: the *landing error*, the *path length error*, the *initial heading error,* and the *final heading error*. The *landing error* refers to the distance between the landing point and the home position. The *path length error* provides a measurement of the ability to compute the necessary amount of displacement to accomplish the task. The *heading error* is calculated over two phases of the performed path: the *initial* and *ending* heading. The *initial heading error* is calculated during the first portion of the walked path, which is the first 1/3 of the path from the end of the second triangle leg. This measure was taken to quantify the participants' ability to orient themselves towards the home position at the beginning of the walked path. The *ending heading* measures the last 1/3 of the walked path, referring to the participant's actual location and the home position. Similar to Smith and colleagues (Smith et al., 2013), we normalized the parameters depending on the angle magnitude. Since our paradigm leads to response paths that intrinsically change depending on the angle magnitude, we normalized the parameters to ensure the responses were comparable across angle magnitudes, while also removing potential artefacts, such as the possibility that a longer path would cause more errors (e.g. in the case of ±135°) compared to a shorter path (e.g. ±45°). In detail, the *path length error* was first calculated as the difference in cm between the total length of the path the participant walked and the correct path length for each angle. This difference is then processed as the percentage of the total length of the correct path for each angle. For instance, a path length after executing an angle of ±135° would by definition be longer than ±45°. A *path length error* value greater than 0 indicates that the participant walked a longer path than the correct one; if smaller than 0, the walked path was shorter than the correct one; while close to 0 indicates a path close to the correct path length. The *landing error* is presented both as non-normalized data, which is the distance in cm between the landing position and the target position (i.e. the home position), and as normalized data. As already observed in previous research (Loomis et al., 1993), the length of the required path to accomplish the task could influence overall performance. Therefore, by correcting the *landing error* for the path length for each angle, we aimed to evaluate participants' behavior by removing the path length's potentially spurious influence, which differs for each angle magnitude by definition. In detail, for longer paths with greater angles (e.g. ±135°), participants need to walk more compared to the other angle magnitudes (e.g. ±45°), and may consequently make greater errors simply due to the longer route. To correct this potential unbalance, we normalized the *landing error* by following a similar approach to Smith and colleagues (Smith et al., 2013). Thus, the normalized *landing error* is calculated as the percentage of the correct path length. A value close to 0 indicates that the participant landed close the home point, while a value greater than 0 indicates that the participant was farther away from the home landing point. For the *heading error*, we firstly calculated both *initial* and *ending heading errors* as the difference in degrees between the path the participant traced and the correct path for reaching the home position. Alike to the correction made for the *landing error,* we normalized the heading error depending on the amount of change in heading necessary to perform the task for each angle (see Fig. 2). In detail, we calculated the *heading error* as the error percentage relative to each required turn to accomplish the task, which was 160.89° for ±135°; 143.13° for ±90° and 131.53° for ±45°. If otherwise, that is by using the heading angle before normalization, we would include errors that might depend on the amount of yaw rotation needed to return to the home position; the normalization removes such influence, and thus provides a more appropriate measurement of the effect of angle magnitude on the performance.

2.5. Statistical analysis

For each parameter, we ran a 3-way mixed model ANOVA (ezANOVA package in R) for the three main factors that may influence performance. Considering the study's hypothesis and previous findings on development (see Introduction), we took age as a between factor, expressed as participants' age groups (i.e.: 6–7 y.o.; 8–9 y.o.; 10–11 y.o.; >22 y.o.). To test whether angle magnitude (i.e.: ±135°; ±90°; ±45°) and angle sign (either positive: towards the right, or negative: towards the left) influenced the ability to spatially update one's position while moving, we took these as within factors. *Post-hoc* analysis was conducted to test the significance level in subgroups defined by age or angle magnitude. We therefore used two-sample t-tests corrected for multiple comparisons (*Bonferroni* correction), with alpha set at 0.05. To examine whether participants' performance depended on age, and thus to test the presence of a developmental trend, we performed a correlation analysis between age and responses, wherein we treated age as a continuous variable, using decimal values.

3. Results

In Fig. 3, we present example trials that two different participants performed during the task. In the example of +45° angle magnitude, the participant did not show strong biases and managed to perform the task correctly, slightly undershooting the angle between the second and the third leg of the triangle (Fig. 3 - top panel). In the example of +135° angle magnitude, the participant tended to underestimate the angle between the first two legs of the triangle, thus overshooting the last turn angle, i.e., the one needed to complete the triangle (Fig. 3 - lower panel). The yaw rotation experienced while moving is the supplement of interior angle magnitude. In the last example, the individual participant

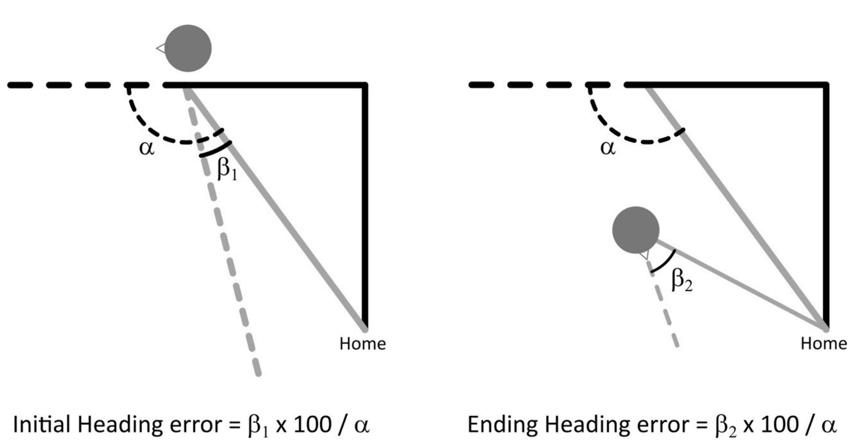

Fig. 2. Illustration of heading error calculation. A left angle of −90° is represented. The black lines indicate the path the participant walked under the experimenter's guidance. The grey line represents the ideal heading direction to reach the home position. The grey dotted lines represent the heading direction at the beginning of the response (left panel) and towards the end of the response (right panel). Formulas showing how the heading error was calculated are shown at the bottom of both panels.

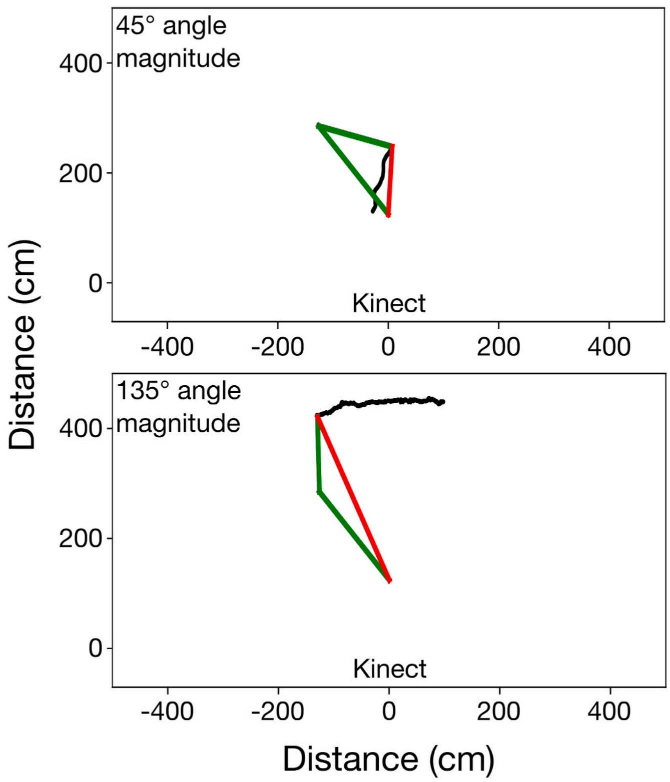

Fig. 3. Representation of individual participant's performance in the triangle completion task. The two panels represent performance for the right angles of +45° (top panel) and +135° (lower panel). Note that the participant's yaw rotation is the supplement of the angle magnitude. The green lines show the planned path along the first two legs of the triangle, the red line represents the correct path to close the triangle, and the black trace represents the participant's recorded motion path. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

overestimated the yaw motion experienced while going through the first two legs of the triangle and undershot the necessary yaw rotation to complete the triangle.

3.1. Path length error

When analysing the path length that participants travelled, we focused on the error relative to the correct path's total length, which is thus the *path length error*. In detail, we observed a significant effect given by angle magnitude ($F (2, 82) = 58.87$, $p < 0.0001$), demonstrating a trend due to age ($F (3, 41) = 2.86$, $p = 0.05$) but no significant interaction between the two factors ($F (6, 82) = 1.60$, $p = 0.15$). These results indicate that the ability to compute the length of the path to be executed does not depend on age, thus suggesting that children are able to disentangle such properties of path integration equally as well as adults. Exploratory analyses on the effect of age are reported in the Supplementary material. As confirmed by post-hoc analysis, participants performed longer paths as the angle magnitude decreases, regardless of their age (±90° vs. ±45°, $p < 0.0001$; ±135° vs. ±45°, $p < 0.0001$; ±90° vs. ±135°, $p = 0.03$; *Bonferroni* corrected see Fig. 4A). Since yaw rotation is the supplement of the angle magnitude, this result indicates that *path length error* increases with yaw motion experienced while executing the target angle magnitude. This result suggests that the greater amount of disorientation participants experienced while walking along the two legs of the triangle led to them completing a longer path to reach the home position. The analysis also revealed a significant effect of the sign of the angle ($F (1, 41) = 5.29$, $p = 0.02$), and a significant interaction between sign and angle magnitude ($F (2, 82) = 5.30$, $p < 0.01$), which might suggest asymmetries in path integration related to the movement's side. However, there was no overall significant difference between leftward vs. rightward angles ($p = 0.11$; see Fig. 4B), but there were significant differences when comparing +45° and −45° angles to the rest of the angle magnitudes, as represented in Fig. 4C (for detailed results see Table S2 in the Supplementary Materials). Moreover, we did not observe interaction between the sign and the age group ($F (3, 41) = 1.06$, $p = 0.37$), nor an interaction of the three factors ($F (6, 82) = 1.05$, $p = 0.39$). These results suggest that the ability to extract the total length of the path to be performed is generally not influenced by age or the side of the angle.

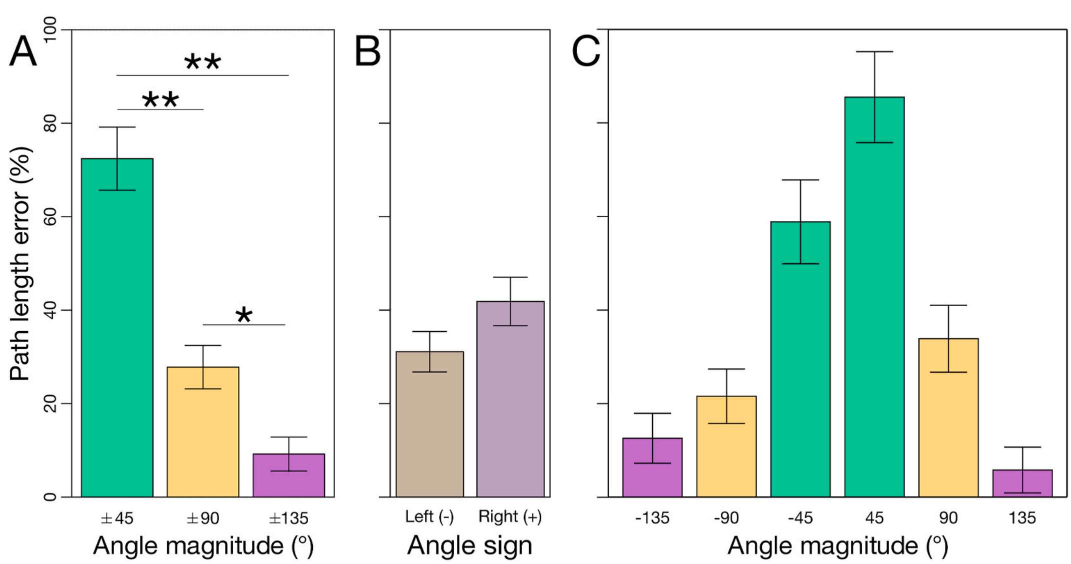

Fig. 4. Results for the *path length error* parameter. The *path length error* is calculated as the percentage of the required path length for each angle magnitude (see Methods). Positive values indicate a path length greater than required. The average path length across participants is reported. In (A), the bars represent the *path length error* for each interior angle, regardless of its sign. In (B), the bars represent the *path length error* for the right and left turns. In (C), the bars represent the *path length error* for each angle to the right (+) and to the left (−). Error bars represent standard error. One asterisk indicates $p < 0.05$, and two asterisks indicate $p < 0.01$. Significant comparisons for (C) are reported in.Table S2.

3.2. Landing error

Regarding the non-normalized *landing error*, which is the distance between the ending point of the trajectory and the home position, the 3-way mixed model ANOVA showed a significant effect of age ($F(3, 41) = 6.96$, $p < 0.001$) and angle magnitude ($F(2, 82) = 29.99$, $p < 0.0001$), but no significant interaction between the two factors ($F(6, 82) = 1.75$, $p = 0.12$). We observed no significant effect of the sign of the angle ($F(1, 41) = 0.38$, $p = 0.54$), nor an interaction between the sign and the age group ($F(3, 41) = 1.19$, $p = 0.32$), or between sign and angle magnitude ($F(2, 82) = 1.05$, $p = 0.35$). In addition, there was no interaction between the three factors ($F(6, 82) = 1.12$, $p = 0.36$). Children therefore behaved differently compared to adults. Additionally, we observed differences in the performance depending on the amount of yaw rotation experienced while encoding the first two legs of the triangle, regardless of the participant's age, which is the supplement of the angle magnitude. In detail, we observed that all participants made greater *landing errors* for the angle magnitude of ±135° compared to the angles of ±45° ($p < 0.0001$, *Bonferroni* corrected) and ±90° ($p < 0.001$, *Bonferroni* corrected). In other words, *landing errors* were greater with lesser yaw rotation (i.e. ±135°) compared to the angle magnitudes that induce greater yaw motion (i.e. angle magnitude = ±90° and ±45°). We observed no significant difference in performance for angles of ±90° vs. ±45° ($p = 0.25$, *Bonferroni* corrected). Given the effect of age on the performance, we performed post-hoc t-tests that revealed significant differences between age groups, with errors decreasing as age increases (6–7 vs. 10–11, $p < 0.01$; 6–7 vs. >22, $p < 0.0001$; 8–9 vs. >22, $p < 0.001$; 10–11 vs. >22, $p < 0.03$; *Bonferroni* corrected – see Fig. 5B). This pattern of results is confirmed by a significant negative correlation between *landing error* and age in decimal values ($R = -0.37$, $p < 0.0001$).

To account for the differences among angle magnitudes for the path to be performed and to specifically focus on the influence of yaw motion experienced while executing the first two legs of the triangle, we performed a similar analysis for the *landing error* normalized for each angle magnitude (see Data analysis for details). The 3-way mixed model, ANOVA, showed a significant effect of age ($F(3, 41) = 7.26$, $p < 0.001$), angle magnitude ($F(2, 82) = 57.06$, $p < 0.0001$), and a significant interaction between the two factors ($F(6, 82) = 3.46$, $p < 0.01$). We observed no significant effect of the angle's sign ($F(1, 41) = 0.91$, $p = 0.34$), nor an interaction between the sign and the age group ($F(3, 41) = 1.43$, $p = 0.24$). There was also no interaction between sign and angle magnitude ($F(2, 82) = 1.09$, $p = 0.34$), or between the three factors ($F(6, 82) = 1.64$, $p = 0.14$).

As shown in Fig. 6A, comparing the normalized *landing error* between angle magnitudes indicates that participants of all ages made greater errors for the angle magnitude of ±45° compared to the angles of ±90° ($p < 0.0001$, *Bonferroni* corrected) and ±135° ($p < 0.0001$, *Bonferroni* corrected), whereas there was no significant difference in performance for angles of ±90° vs. ±135° ($p = 1$, *Bonferroni* corrected). Since the sign of the angle had no effect, our correlation analysis focussed on the angle magnitude in relation to age. Firstly, we observed a developmental trend across all angles (see Fig. 6B), confirmed by *post-hoc* comparisons (6–7 vs. 10–11, $p < 0.001$; 6–7 vs. >22, $p < 0.0001$; 8–9 vs. >22, $p < 0.001$) and a significant negative correlation between age in decimal values and landing error ($R = -0.42$, $p < 0.0001$). These results indicate that the ability to land close to the home location changed with age, as performance improves as age increases and the participant reaches adulthood. Considering that we observed the same pattern of results with the non-normalized *landing errors,* this relationship appears to be quite robust and independent to the length of the path to reach the home position. In detail, young children (6–7 y.o.) demonstrated greater errors compared to older children and adults, who were more consistent in their errors across angles. By focusing on angle magnitudes, correlation analysis showed developmental trends for all angles. We observed significant negative correlations for the angle magnitudes of ±45° ($R = -0.47$, $p < 0.01$, *Bonferroni* corrected), ±90° ($R = -0.35$, $p < 0.01$, *Bonferroni* corrected), and ±135° ($R = -0.47$, $p < 0.0001$, *Bonferroni* corrected) (see Fig. 6C). *Post-hoc* comparisons (t-tests) revealed significant age differences when comparing performance for the angle of ±45°, indicating that adults and older children performed better than younger children (for detailed results, see Table S1 in the Supplementary Materials). This result can be observed in the developmental trends represented in Fig. 6C, as the landing error decreases with age. Moreover, the landing error is greater for the angle magnitude of ±45° compared to the other angles across all age groups.

Comparing the non-normalized to the normalized *landing error* demonstrates commonalities and differences. In the case of normalized data, the error is calculated by correcting the data by considering the total length of the correct path. By following this approach, we observed an interaction between age and angle magnitude, which is otherwise not present for the non-normalized *landing error.* Considering that the *path length error* is not influenced by age (see section 3.1), the interaction of age with angle magnitude on the non-normalized *landing error* might be masked by the absence of different path lengths across age groups. By correcting for the influence of differing path lengths for each angle magnitude, the analysis reveals interaction between the two factors. Interestingly, normalized *landing error* is greater when the experienced yaw motion during the first two legs of the triangle is also greater (i.e. for the angle magnitude of ±45°). When considering the non-normalized *landing error,* we observed the opposite tendency, with participants performing greater errors for angles with less yaw motion (e.g. ±135°), which might relate to the longer path. Indeed, in such conditions, the participant is farther away from the home position, which thus intrinsically increases the probability of greater *landing error.*

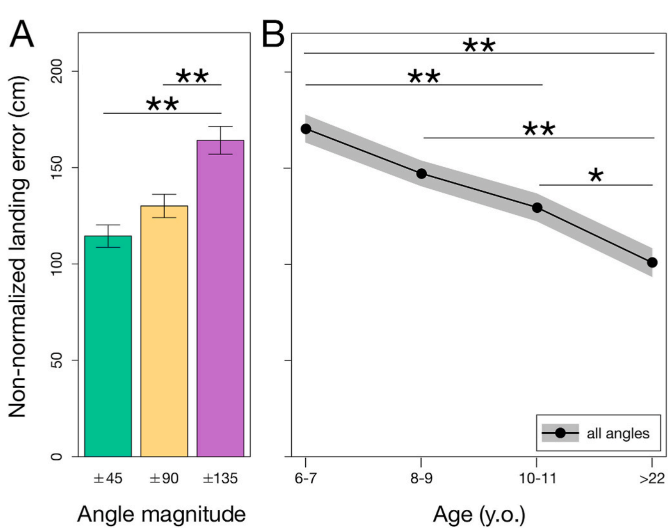

Fig. 5. Results for the non-normalized *landing error* parameter. The non-normalized *landing error* is calculated as the distance in cm between the reached position and the home position. The average *landing error* across participants is reported. In (A), the bars represent the *landing error* for each angle regardless of its sign; the error bars represent standard error. In (B) developmental trend, regardless of angle magnitude, is represented, with *landing error* as a function of age; shaded areas represent standard error. One asterisk indicates $p < 0.05$, while two asterisks indicate $p < 0.01$.

3.3. Heading error

When regarding participants' heading direction, we focused on two parameters: the *initial* and *ending heading error,* normalized for each angle magnitude (data before normalization are reported in the Supplementary material; for details on the normalization procedure, see Data analysis). Three participants had to be excluded from this analysis because of invalid readouts of their heading direction from the recorded traces. For the *initial heading*, the 3-way mixed ANOVA demonstrated a

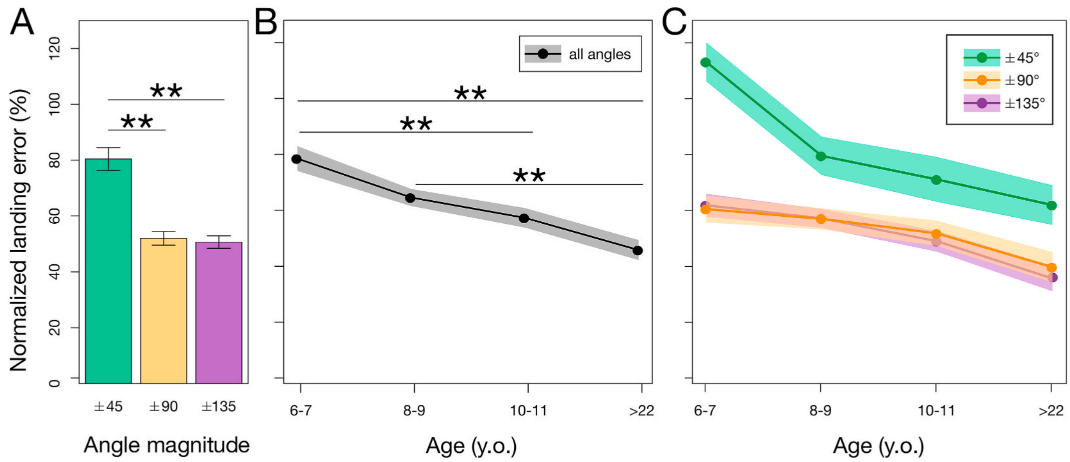

Fig. 6. Results for the normalized *landing error* parameter. The *landing error* is calculated as the percentage of the required path length for each angle (see Methods). The average *landing error* across participants is reported. In (A), the bars represent the *landing error* for each angle regardless of its sign, and error bars represent standard error. In (B) and (C), developmental trends are represented with the *landing error* in relation to age; shaded areas represent standard error. Two asterisks indicate $p < 0.01$. Significant comparisons for (C) are reported in Table S2 in the Supplementary Materials.

significant effect given by the angle magnitude ($F(2, 76) = 32.33$, $p < 0.0001$), but no significant effect of age ($F(3, 38) = 0.86$, $p = 0.46$, exploratory analyses on the effect of age are reported in the Supplementary material). A significant interaction was also not present between the two factors ($F(6, 76) = 1.90$, $p = 0.09$). We observed no significant effect of the sign of the angle ($F(1, 38) = 0.29$, $p = 0.59$), nor an interaction between the sign and the age group ($F(3, 38) = 0.47$, $p = 0.70$), or between sign and angle magnitude ($F(2, 76) = 2.09$, $p = 0.13$). Additionally, there was no interaction between the three factors ($F(6, 76) = 0.20$, $p = 0.97$). Post-hoc comparisons revealed *initial heading errors* to be significantly greater for the angle magnitude of ±45° compared to the angles of ±90° ($p < 0.0001$, *Bonferroni* corrected) and ±135° ($p < 0.0001$, *Bonferroni* corrected). There was no significant difference between the ±90° and ±135° angles ($p = 0.72$, *Bonferroni* corrected). These results indicate that when participants started the return, their orientation was not adequately aligned with the home location, and this error increased with decreasing angle magnitude and the increased yaw rotation experienced while walking along the first two legs of the triangle. Although we did not observe age-related differences in the overall *initial heading*, we found *initial heading errors* greater for ±45° than for ±90° and ±135° angle magnitudes. The absence of age's effect in the analysis of the *initial heading error* indicates that this pattern is maintained across age groups, thus suggesting a behavioral pattern uninfluenced by age but strongly related to angle magnitude. Such a result corroborates the abovementioned observation based on the analysis of *landing error* and *path length*, which show the overall influence the amount of yaw rotation experienced while walking along the first two legs of the triangle, which is the supplement of the angle magnitude, has on performance (see Data analysis for details).

To disclose whether the ability to spatially update one's location while walking changes while performing the path, we also analyzed the error in the heading direction when approaching the destination. We therefore measured the *ending heading error* in the last 1/3 of the walked path. For the *ending heading error*, we observed a significant effect given by the angle magnitude ($F(2, 76) = 36.33$, $p < 0.0001$), which is thus coherent with the initial heading result where we observed improved performance with increasing angle magnitude. However, we observed no significant effect of the sign of the angle ($F(1, 38) = 1.24$, $p = 0.27$), nor an interaction between the sign and the age group ($F(3, 38) = 1.04$, $p = 0.38$), or between sign and angle magnitude ($F(2, 76) = 0.64$, $p = 0.52$). There was also no interaction between the three factors ($F(6, 76) = 1.82$, $p = 0.10$). In contrast to the *initial heading error*, we observed a significant effect of age ($F(3, 38) = 5.18$, $p < 0.01$), but no significant interaction between the two factors ($F(6, 76) = 0.51$, $p = 0.79$, exploratory analyses on the interaction between age and angle magnitude are reported in the Supplementary material.). *Ending heading error* decreased as the angle increases (i.e. as experienced yaw rotation decreases), with the lowest errors made for the ±135° angle (±90° vs. ±45°, $p < 0.0001$; ±135° vs. ±45°, $p < 0.0001$; ±90° vs. ±135°, $p = 0.0270$; *Bonferroni* corrected) as shown in Fig. 7B. In Fig. 7C, the effect of age is represented, demonstrating that adults performed significantly better compared to the other age groups, as confirmed by the post-hoc comparisons (>22 y.o. vs. 6–7 y.o., $p < 0.01$; >22 y.o. vs. 8–9 y.o., $p < 0.001$; >22 y.o. vs. 10–11 y.o., $p = 0.0239$; 8–9 y.o. vs. 6–7 y.o., $p = 1$; 10–11 y.o. vs. 6–7 y.o., $p = 1$; 10–11 y.o. vs. 8–9 y.o., $p = 1$ - *Bonferroni* corrected). The observation that the *ending heading error* was lower for adults compared to children of all ages suggests a developmental trend. Correlation analysis supports this developmental trend by demonstrating a significant negative correlation between *ending heading error* and age, thus indicating that performance improves with age ($R = -0.28$, $p < 0.001$). Although adults show similar disorientation behavior as children when pointing towards the home destination at the beginning of the walked path, they were able to adjust their path while walking. Adults therefore finished with less *heading* and *landing errors* when approaching the destination. The developing ability to spatially navigate and update one's location while moving might underlie this pattern of results. Alternatively, it can be argued that performance at the end of the path reflects greater veering behavior in children compared to adults. Although such interpretation cannot be excluded, most of the research on veering behavior has focused on path lengths that substantially exceed the lengths executed in the present study (e.g.: Boyadjian et al., 1999). Nevertheless, literature lacks studies on veering behavior in children, and our results thus posit an interesting indicator on the possibility that children might show veering behavior for shorter walked distances compared to adults.

4. Discussion

To investigate developmental changes in the ability to spatially update one's location while moving, we adopted the well-known triangle completion task. We asked participants to complete the shape by walking along the third leg of a triangular path based on vestibular and proprioceptive information. We then measured how angles of different magnitude and side influenced spatial updating. Participants needed to base their response solely on the spatial information arising from the experienced movement of walking along the first two legs of the

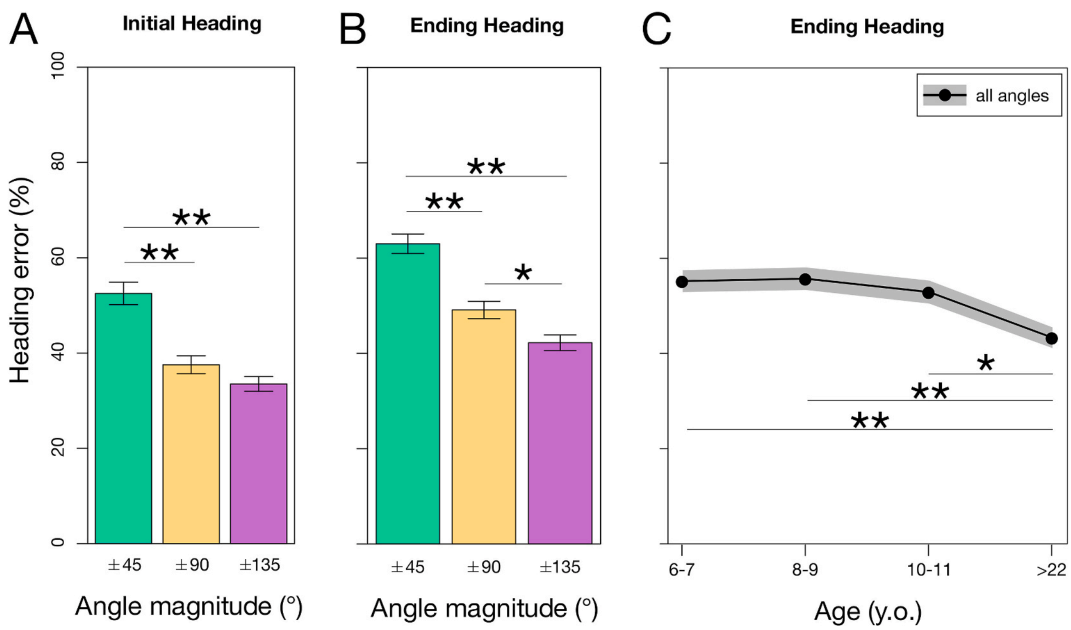

Fig. 7. Results for the *heading error* parameters. The *heading error* is calculated as the percentage error of the turn required to complete the triangle (see Methods and Fig. 2). The average *heading error* across participants is reported. In (A) and (B), the bars represent the *heading error* at the beginning of the path (A) and towards the end of the path (B) for each interior angle, regardless of its sign; the error bars represent standard error. In (C), developmental trends are represented with *ending heading error* in relation to age; the shaded areas represent standard error. One asterisk indicates $p < 0.05$, while two asterisks indicate $p < 0.01$.

triangle. Therefore, to accomplish the task, the participant's path to reach the home position is based on a complex representation of the spatial relationship between the passively reached position and the home position. Such a representation is built while the experimenter guides them through spatial updating abilities. The youngest group of participants (6–7 y.o.) demonstrated worse performance than older peers, especially when angle magnitude was small (i.e., ±45°) but the amount of yaw motion was greater, which is the supplement of the interior angle between the two first legs of the triangle. The ability to land close to the home location changed with age, and the adult group demonstrated better performance. At the same time, performance differed depending on the angle magnitude, as smaller angle magnitude (i.e., ±45°) resulted in worse performance compared to the other angles for all ages. This result was the same when considering the length of the travelled path, as well as the heading error. Interestingly, we observed age-related differences in heading error when considering the final portion of the path, thus indicating that older participants were better at adjusting their path to find the home position.

Our study shows that path integration depends on the amount of yaw motion required by the tested angle, and this property of spatial updating changes across development. For *landing error*, *path length error,* and *heading errors*, we observed greater errors for the ±45° angle. While performing the ±45° angle, participants were guided through a yaw rotation of 135° to their straight ahead. Such yaw rotation is greater compared to the other tested angles, like 90° for the ±90° angle and 45° for the ±135° angle. Contrary to roll rotation, yaw rotation impacts the ability to spatially localize and memorize items (Klier et al., 2006). Indeed, our results indicate that the amount of yaw rotation influences spatial updating while walking. Isolating vestibular-based yaw rotation in tasks analogous to route and inferential spatial navigation has shown that the ability to spatially update one's location decreases in precision and accuracy in the latter case (Seemungal et al., 2007). These results consequently highlight the strong connection between vestibular processing of yaw rotation and spatial navigation. Considering the strong role of vestibular information in path integration (Péruch et al., 1999), and specifically in the triangle completion task (Glasauer et al., 2002; Xie et al., 2017), we observed that a greater yaw rotation results in a stronger disorientation. This relationship is demonstrated by greater errors made in relation to the length of the travelled path, the *landing error,* and both *initial* and *ending heading errors*. This result can be ascribed to the effect of spatial updating processes, whose perturbation increases with the amount of experienced yaw rotation. In detail, experiencing larger yaw rotations while performing the angles affected the participant's ability to spatially update their location with respect to the home position while walking along the triangle's first two legs. Such disorientation might have resulted in a worse performance throughout the task. Specifically, participants' ability to maintain a reference to the home position seemed to worsen while walking. Overall, our results suggest an influence of age and development on spatial navigation abilities, specifically the ability to spatially update one's position in the environment, based on inferential cues from encoding proprioceptive and vestibular information. Since adults performed better than children, the results strongly indicate that using such information improves with age. This improvement may depend on an improved ability to encode spatial information due to multisensory recalibration. Research has indeed shown that congenital blind individuals perform worse in vestibular inferential task compared to sighted individuals (Seemungal et al., 2007). As observed for the use of landmarks in spatial navigation tasks (Nardini et al., 2008), visual experience might also influence an individual's ability to spatially navigate when visual cues are absent, as Petrini and colleagues suggest (Petrini et al., 2014). Consequently, adults demonstrate improved spatial navigation abilities, while younger children are still developing their multisensory recalibration process.

The ability to spatially update after turning depends on the participants' age. When considering the ability to return to the home position, with focus on the *landing error*, young children (6–7 y.o.) showed worse spatial updating skills compared to older children and adults, who were more consistent in their ability to complete the triangle across angles. This pattern of results corroborates previous findings on spatial updating with angles of ±90° (Smith et al., 2013). However, when considering the interaction between age and angle magnitude, we observed that adults performed better than all children for the ±45° angle, whereas for angles of ±90° and ±135° magnitudes, we observed significant differences only between adults and 6–7 y.o. children. This aspect might be related to the above-mentioned observation on the greater amount of yaw rotation required while completing a ±45° angle. The developmental trend observed in the *landing error,* as well as in the *initial* end *ending heading error,* suggests that adults better integrate vestibular and proprioceptive orientation cues regarding yaw rotation. These findings add fundamental insights on how the ability to spatially navigate develops across age. The complexity of the movement, in terms of turn angle of different degrees, is indeed a non-negligible aspect to delineate a full picture of path integration development. Age milestones in spatial navigation have been identified at 6–7 and 11 y.o. which coincide with milestones in hippocampal growth (Uematsu et al., 2012; for a review, Wiener-Vacher et al., 2013). Considering the close relationship between vestibular processing and hippocampal functioning, as demonstrated by hippocampal atrophies for vestibular dysfunction (Brandt et al., 2005; Hüfner et al., 2007), suggests a strong interconnection between developing navigation skills and vestibular processing (Wiener-Vacher et al., 2013). At the same time, hippocampal ablated patients show impairments in performing path integration tasks, thus supporting the significant impact of hippocampal activation in spatial updating (Worsley et al., 2001). The linear relationship observed between vestibular-induced disorientation and performance in the triangle completion task supports this hypothesis. Additionally, the decreasing impact of the amount of yaw rotation with age suggests the presence of developmental trends in between the milestones abovementioned, thus suggesting a progressive development of path integration skills.

In this presented study, we maintained the same length for the first two guided path segments for all angles. This choice led to a longer path for the third triangle segment with an increasing angle. When considering the ability to reproduce the correct walked path length, we did not observe an influence of age, as results were mostly influenced by angle magnitude. Specifically, all participants tended to overshoot the walked path for 45° angles, both to the right and left, compared to the greater angles, where they seemed to accurately compute the correct path length. Although we focused on the influence of angles on the ability to spatially update across development, overall path length can also influence spatial updating across development (Smith et al., 2013). Future studies would be needed to investigate how child development influences the interaction of these two spatial navigation properties. In this context, Smith and colleagues (Smith et al., 2013) argued that limited variation of path properties (e.g. only path length), might lead to the participant taking advantage of a configurational strategy to solve the task, forming a cognitive map-like representation of the path to be performed (Fujita et al., 1993; Wiener et al., 2011). Such a strategy contrasts to the continuous strategy for which low-level path information, such as distance and turns, is stored in the working memory and used to perform path integration (Fujita et al., 1993). Although we varied an aspect of spatial navigation that is likely to increase participants' disorientation in this study, as previously discussed, it cannot be excluded that repeating the same angle magnitudes led to a preferred configurational over continuous strategy. Adding another variable would likely reduce a potential learning process, leading to such a preferential strategy. To overcome this issue, manipulating path properties, such as overall path length and angle magnitude, could be combined with specific testing of navigational strategies to unveil whether these can influence the developmental trend observed in this and previous studies.

To summarize, in the research presented here, we provided novel insights on how spatial representation changes while moving through space, demonstrating that greater amounts of yaw rotation induce stronger disorientation, and the ability to spatially update body position in the environment changes across development. The maturational steps to achieve successful spatial navigation seem to be related to the specific feature of path integration. On the one hand, the ability to quantify the amount of path to be walked might already be acquired at the first steps of development. This aspect indeed represents one of the essential aspects in the complex scenario of abilities needed to spatially navigate and spatially update one's location while moving. On the other hand, more elaborated properties of spatial navigation, such as the ability to adjust the walking path and likely the consequent ability to land close to the home location, seem to occur later in development. Although some of these properties appear to be acquired after the age of 10–11 y.o., developmental trends suggest that this process may gradually improve throughout development, until the full maturational level is reached in adulthood.

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Credit author statement

Luigi F. Cuturi: Conceptualization, Methodology, Formal analysis, Data curation, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Paolo Alborno**: Software, Methodology, Data curation, Investigation, Visualization. **Giulia Cappagli**: Conceptualization, Methodology, Writing – review & editing; **Erica Volta**: Conceptualization, Writing – review & editing, Visualization; **Gualtiero Volpe**: Conceptualization, Methodology, Writing – review & editing, Supervision. **Monica Gori**: Conceptualization, Methodology, Writing – review & editing, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2021.107774.

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