The development of path integration:

Combining estimations of distance and heading

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SHORT TITLE AND RUNNING HEAD: Development of path integration

ABSTRACT

Efficient daily navigation is underpinned by path integration, the mechanism by which we use self-movement information to update our position in space. This process is well-understood in adulthood, but there has been relatively little study of path integration in childhood, leading to an underrepresentation in accounts of navigational development. Previous research has shown that calculation of distance and heading both tend to be less accurate in children as they are in adults, although there have been no studies of the combined calculation of distance and heading that typifies naturalistic path integration. In the present study 5-year-olds and 7-year-olds took part in a triangle-completion task, where they were required to return to the startpoint of a multi-element path using only idiothetic information. Performance was compared to a sample of adult participants, who were found to be more accurate than children on measures of landing error, heading error, and distance error. 7-year-olds were significantly more accurate than 5-year-olds on measures of landing error and heading error, although the difference between groups was much smaller for distance error. All measures were reliably correlated with age, demonstrating a clear development of path integration abilities within the age range tested. Taken together, these data make a strong case for the inclusion of path integration within developmental models of spatial navigational processing.

Keywords: path integration; development; idiothetic

INTRODUCTION

Effective spatial navigation fundamentally depends on the ability to update our sense of position and heading as we move through an environment. This enables us to maintain a sense of where we are, where we are going, and where we have been, which is at the heart of daily wayfinding. According to Gallistel (1990), there are two distinct mechanisms that enable this spatial updating: a landmark-based system that uses the dynamic changes in visual surroundings to calculate movement and heading, and a path integration system that makes these calculations on the basis of idiothetic (self-movement) cues from vestibular and proprioceptive sources. In order to understand the functional basis of these processes it is important to address how they emerge in the developing brain (Plumert & Spencer, 2007). Accordingly, there have been a large number of studies that have explored the development of behaviours that support human navigational ability, largely focusing on the visually-guided components of navigation such as reorientation (e.g. Hermer & Spelke, 1994; Learmonth et al., 2001), landmark memory (e.g. Hund & Plumert, 2003; Presson, 1987), route learning (e.g. Allen & Kirasic, 1985; Cornell & Heth, 2000), large-scale search (e.g. Pellicano et al., 2011; Smith, Hood & Gilchrist, 2005) and map reading (e.g. Blades & Medlicott, 1992; Plester et al. 2002). In comparison, there have been relatively few studies of path integration in children. This has led to an underrepresentation of path integration in our accounts of navigational development, and an apparent absence from influential theoretical overviews (e.g. Gollege et al., 1985; Siegel & White, 1975).

Path integration involves the co-ordination of acceleration and velocity information with a representation of starting position, in order to update spatial location relative to that initial point (Loomis et al., 1999; Golledge et al., 1999). It is a core feature of navigational behaviour across human and non-human animal species, including insects (Wehner & Srinivasan, 1981), birds (Saint Paul, 1982) and mammals (Alyan & McNaughton, 1999). In order to study path integration in isolation (i.e. without additional guidance from visual or auditory input) scientists have adopted techniques whereby blindfolded participants are required to walk to a particular point in space. This could either involve navigating to a location that participants have previously seen before being blindfolded (Elliott, 1987; Philbeck et al., 1997), or returning to the starting position of a single-element (Mittelstaedt and Mittelstaedt, 2001) or multi-element (Loomis et al., 1993) path. Across such studies, participants are very systematic in the errors that they make, demonstrating the existence of clear non-random principles underlying performance. These errors have been very accurately predicted by computational models (Klatzky et al., 1990; Fujita et al., 2003), and appear to be related to the length of outbound paths traversed and the number of separate segments along them (also see: Wan, Wang & Crowell, 2013; Wiener & Mallot, 2006).

By calculating the Euclidian relationship between the endpoint of the response vector and the correct location (i.e. the start point) one gains a measure of two separate components of path integration: the individual’s estimation of the distance between the starting position and their endpoint, and the angular relationship between them. Although these components are inherently related to each other, it has been suggested that they are processed and represented by dissociable mechanisms (Berthoz et al., 1999). Neuropsychological evidence for this separation was presented in a study by Worsley and colleagues (2001): temporal lobe patients performed a triangle-completion task (see Loomis et al., 1993) where they were led along two legs of an imaginary triangle and then required to return to the start-point by completing the shape. There was no difference between left-hemisphere and right-hemisphere patients in terms of their distance error, although right-hemisphere patients were significantly more impaired in the angular (or, heading) component of their response vector. Complementary evidence for this separation in unimpaired adults comes from a study by Smith, Howard, Alcock, and Cater (2010), who studied two groups of trained athletes. Rugby players (trained at a large spatial scale) were significantly more accurate at estimating heading than martial artists (trained at a small spatial scale), whereas there was no difference between groups in their distance estimation. These data suggest that distance and heading are not only separately represented, but also separately amenable to modulation by experience (also see Bredin et al., 2005).

Despite its functional primacy in human navigation, the development of path integration has been addressed in very few studies. Explorations of the mechanisms that support it have provided insight into, for example, the development of spatial orientation in infancy (e.g. Bremner, Hatton, Foster, & Mason, 2011; Acredolo & Evans, 1980) and this literature has been complemented by very useful reviews of the relationship between vision, locomotion, and spatial orientation in childhood, as provided by Campos et al. (2000) and Rieser & Pick (2007). More recently, a study by Nardini, Jones, Bedford, & Braddick (2008) has explored how information from path integration is combined with visual cues in order to support place memory. In their task, participants in a darkened arena were required to collect 3 objects sequentially and then return the first object to its original position. In some conditions participants could use both self-motion information and illuminated landmarks external to the arena to guide their response, whereas other conditions provided single cues (i.e. landmarks or path integration only). When both sources of information were available to participants, adults were able to combine them in order to reduce variance in their response. However, children aged 4-5 years and 7-8 years were unable to do this. Furthermore, in an additional condition where both cues were placed in conflict (i.e. the landmark positions were shifted before the response) children tended to alternate between one cue and the other, as opposed to a combination strategy adopted by adults.

The first study that focused specifically on the development of path integration itself was provided by Rider & Rieser (1988), who walked 2 year old and 4 year old children, in the dark, from one room into another room, via a short corridor. Children were then required to point to the location of their parents in the first room, and both age groups were able to accurately localise the room. However, in another condition when children walked with vision, the 2 year olds incorrectly pointed in the direction of the last segment of the journey. These data suggest that children can update orientation without vision as early as 2 years of age, although this may be subject to interference from competing inputs until later in development. Further insight was provided by Rieser & Rider (1991), who compared the performance of 4 year old children and adults in a paradigm that involved showing a location to participants, blindfolding them and leading them to a new point in the room, and then requiring them to point to the previously seen location. Both groups performed at a level of accuracy that was above chance, and neither group was affected by the inclusion of a

10 second interval between encoding and response. Furthermore, responses from both adults and children were systematically affected by the distance of the outbound path, and also the number of separate segments (i.e. translational sections without a turn) to the path. However, although the overall pattern of performance was comparable, children were significantly less accurate than adults in their estimations of orientation. It therefore seems that, although young children can efficiently and systematically utilise idiothetic information to update orientation, there is further development beyond the age of 4 years before their trajectory reaches an adult-like level. Rieser & Rider (1991) suggest that this may be due to developmental differences in sensory processes, or the calibration between them.

Studies such as those by Rider & Rieser (1988) and Rieser & Rider (1991) have addressed the orientation (or heading) component of path integration, but do not incorporate the distance estimation of the response. This latter component has received some attention; for example, a study by Giovannini et al. (2009) made a comparison of distance processing between typically developing children, adults, and children with autism spectrum disorders (ASD). In their first experiment, typically developing (TD) children of 7 years, 9 years, and adults, were blindfolded and led to a starting point. There were then shown a location between 3-6m ahead of them for 3s, the blindfold was replaced, and they were required to walk to that location. Proportional distance errors were close to zero for all of the age groups, and this contrasted with a perceptual distance matching task where accuracy increased with age. In their second experiment, Giovannini et al. (2009) compared a group of children with ASD, on the same task, to a matched group of TD children and an adult sample. There was no difference between any of the groups on the ‘blindwalking’ task, mirroring the findings of Experiment 1, although the ASD group were more accurate on the perceptual matching task. Interestingly, however, the overall pattern of findings for typical participants contrasts with data presented by Corlett, Patla & Williams (1985), who found that 9 year old children were significantly less accurate than adults on a similar task. They also reported that 9 year olds were more likely to be adversely affected by conditions were there was reduced time to visually encode the target location, and also by an increased retention delay before making their response.

It therefore seems that children as young as 4 years of age can accurately update orientation from idiothetic information (Rieser & Rider, 1991) and children of 7 years can accurately update distance (Giovannini et al., 2009). However, to date, it appears that there have been no published attempts to directly examine children's performance when both separate components of path integration are required in the same response, as required in accurate naturalistic behaviour. Studies of adult spatial updating behaviours have capitalised on the triangle-completion task in order to measure both factors working together, and we here report an experiment that, for the first time, uses this task in children. We also sought to examine if there was a developmental change in path integration abilities – this was motivated by a number of suggestions that children demonstrate particular advancement in their spatial abilities around the age of 6-7 years (Kovas, Kozma, Fehér & Benedek, 1999; Plumert & Spencer, 2007; Shemyakin, 1962). Since previous studies have found that the calculation of heading is more likely to dissociate between participant groups than distance (Smith et al., 2010), we predicted that heading estimations may improve faster between 5 years and 7 years than distance estimations. Both age groups were compared to adults –

although Giovannini et al. (2009) found no difference between adults and 7 year olds for distance estimation (c.f. Corlett et al., 1985), Rieser & Riser (1991) found that 4 year olds were less accurate than adults for orientation estimations.

METHOD

Participants

Thirty-eight children were recruited and tested at Summer Scientist Week, an annual public engagement of science event conducted at the University of Nottingham. The younger group consisted of 18 children aged between 5-6 years (M: 63.4 months; SD: 2.85), of whom 10 were female and 8 were male. The older group consisted of 20 children aged between 7-8 years (M: 91.1 months; SD: 4.28), of whom 10 were female and 10 were male. Forty students from the University of Nottingham formed the adult participant group, with an age range of 19-24 years (M: 20.6 years; SD 0.93) and equal numbers of males and females. Ethical approval was received from the School of Psychology ethics committee, and Criminal Records Bureau clearance was received for all experimenters working with the children.

Apparatus

Participants were examined in a large indoor room (6 x 6 m) with starting point and other vertices of the triangles marked in tape that could not be felt when walked over. Participants were fully blindfolded by use of an eye mask, with additional cotton wool pads placed between the eyes and the mask to ensure that the eyelids were closed. Participants also wore industrial ear defenders to remove extraneous ambient noise from the testing room (note that experimenter instructions could be clearly heard when enunciated).

Design and Procedure

Participants were first led to the starting point, where the experimenter explained the task to them. They were then given two practice trials, one with full vision and one blindfolded, to ensure that they fully understood the requirements of the task. When they were ready to begin the experimental trials participants were blindfolded and the ear defenders were placed over their head. The experimenter reminded the participant that they were on the starting point and that they were going to be moved to another point in the room. With a hand on either shoulder, the experimenter then moved the participant forward either 1 or 2 metres, turned them 90^{o} either left or right, and then walked them a further 1 or 2 metres. Participants were then signalled (by a tap in the middle of the back) to find their way back to the starting point via the most direct route (i.e. the hypotenuse of the triangle) and to stop when they thought that they had arrived there. The experimenter followed the participant closely at all times to avoid any potential accidents, such as tripping and falling (note that this did not happen at all). Once the participant had stopped, the experimenter marked the location by placing a piece of numbered tape between the participant's feet.

Participants wore the blindfold and ear defenders for the duration of the experiment and no feedback on their performance was provided. Between trials participants were guided around the room in a figure of eight pattern to ensure that subsequent trials were not influenced by the perceived endpoint of the preceding trial. The participants were then placed on the same starting point at the beginning of each trial facing the correct direction to be moved forward for the first leg of their journey. All combinations of Leg 1 length (1 or 2 m), turn direction (left or right) and Leg 2 length

(1 or 2 m) were repeated twice, producing 16 separate trials that were conducted in a fully randomised order for each participant.

RESULTS

On each trial, performance can be expressed in terms of several different error measures as detailed below. On a trial where the participant landed at the exact location of the start of Leg 1, this would be perfect performance and would result in error magnitudes of zero on all error measures. We calculated two components of participants' performance: return trajectory errors and landing errors. Return trajectories were defined as the straight line between the end of Leg 2 and where the participant ended after making their response (see Figure 1). Each return trajectory yielded both a distance error and a heading error, defined as the difference between that participants' return trajectory and the correct return trajectory in terms of distance and heading. Errors were scaled by converting them into percentages of the correct return trajectory to normalise across triangles. Distance errors were expressed as a percentage of the magnitude of the correct return trajectory, and heading errors were expressed as a percentage of the correct return angle to be turned. Landing errors were then calculated by taking the distance between participants' finishing point and the correct finishing point (which is the same as the start point). As with the other errors, landing errors were scaled by expressing them as a percentage of the magnitude of the correct return trajectory. Error data for each of these dependent measures are contained in Table 1.

Return trajectory errors were analysed both in terms of unsigned error magnitudes, as a measure of accuracy, and also in terms of signed error magnitudes as a measure of bias. Positive signed distance errors are produced when participants take a route longer than the correct return trajectory (regardless of direction travelled). Negative signed distance errors are produced when participants take a route that is shorter than the correct return trajectory (regardless of direction travelled). Positive signed heading errors are produced when participants turn too far back towards Leg 1 (regardless of whether this turn is leftwards or rightwards towards Leg 1). Negative signed heading errors are produced when participants turn too little towards Leg 1.

----- Table 1 about here -----

----- Figure 1 about here -----

Landing errors

Children landed, on average, a distance of 64.083% (SD = 16.165) (of the correct return trajectory) away from the correct finishing point. The older children achieved a more accurate mean landing error of 58.258% (SD = 13.249), compared to the younger children's 70.556% (SD = 16.978). Adults landed closest to the correct endpoint (35.672%, SD = 13.132). There was a significant negative correlation between age and landing error for children ($r(36) = -0.464$, $p = 0.003$), indicating that children land closer to the correct landing position as they age, even within this restricted age range (see Figure 2). A significant regression slope fit ($r^2 = 0.215$, $F(36) = 9.899$, $p = 0.003$) indicates that children's landing errors improve 6.504 % per chronological year. This slope predicts that if they continue improving at the same rate, the older children's performance will reach adult levels in approximately 3.5 years (around 11 years of age). As a group, adults landed significantly closer to the correct finishing point than children ($t(76) = 8.539$, $p < 0.001$), and adults landed closer to the correct finishing point than the older children ($t(58) = 6.261$, $p < 0.001$).

In turn, older children produced significantly more accurate responses than younger children (t(36) = 2.502, p = 0.017).

Data were entered into a 3 (group: adults, 7 years, 5 years) x 3 (overall path length: 2m, 3m, 4m) x 2 (turn direction: left, right) mixed-design ANOVA. There was no effect of turn direction on landing error (F (1, 75) = 1.041, p = .311) although there was a main effect of overall path length (F (2, 150) = 36.042, p < .001), with greater error associated with shorter (2m: Mean = 65.343%, SEM = 2.570) rather than longer (3m: Mean = 51.100%, SEM = 1.806; 4m: Mean = 50.315%, SEM = 1.694) paths. There was a significant between-subjects effect of participant group (F (2, 75) = 46.229, p < .001), and Bonferroni post-hoc tests revealed that all groups performed significantly different from each other: adults were significantly more accurate than 7 year olds (p < .001), who were themselves significantly more accurate than 5 year olds (p = .010). There was no turn x group interaction (F (2, 75) = 1.094, p = .340), and no turn x length interaction (F < 1). There was, however, a significant length x group interaction (F (4, 150) = 8.826, p < .001), with children demonstrating greater improvements in accuracy with longer path lengths compared to adults. There was no three-way interaction between path length, turn direction, and group (F < 1).

----- Figure 2 about here -----

Heading errors

We first analysed unsigned performance values for heading error, and a similar pattern of performance can be seen as for landing errors. On average, adults showed the greatest accuracy with a mean of 12.762% (SD = 6.103) (of the magnitude of correct return trajectory heading turns) away from correct headings, whereas children produced errors that were 26.334% (SD = 10.076). Older children demonstrated a mean error of 23.427% (SD = 9.419), and the mean error of younger children was 29.565% (SD = 10.042).Within the child group, there was a negative relationship between age and heading error magnitudes (r(36) = -0.4013, p = 0.0125). A significant regression slope fit ($r^2 = 0.161$, F(36) = 6.908, p = 0.012) indicates that children were improving by 3.503 % per year. Adults produced significantly more accurate headings than children as a whole (t(76) = 7.236, p < 0.001) and more accurate headings than older children (t(58) = 5.293, p < 0.001). However, older children did not perform more accurately than younger children (t(36) = 1.943, p = 0.059) although this difference was approaching significance.

Data were entered into a 3 (group: adults, 7 years, 5 years) x 3 (overall path length: 2m, 3m, 4m) x 2 (turn direction: left, right) mixed-design ANOVA. There was a main effect of turn direction on heading error (F (2, 75) = 88.161, p < .001), with greater error for paths with left (Mean = 73.484%, SEM = 3.867) rather than right (Mean = 31.664%, SEM = 2.976) turns. There was also a main effect of overall path length (F (2, 150) = 6.657, p = .002), with error decreasing as paths became longer (2m: Mean = 58.100%, SEM = 3.721; 3m: Mean = 55.079%, SEM = 3.442; 4m: Mean = 44.543%, SEM = 3.219). There was also a significant effect of group (F (2, 75) = 40.172, p < .001): Bonferroni post-hoc tests revealed that all groups performed significantly different from each other: adults were significantly more accurate than 7 year olds (p < .001), who were themselves significantly more accurate than 5 year olds (p = .020). The factor of group interacted with turn direction (F (2, 75) = 4.322, p = .017), with adults demonstrating a smaller difference between paths with different turn directions than children. There was also an interaction between group and path length, (F (4, 150) = 3.043, p = .019): whereas adults demonstrated no effect of path length upon performance, children tended to become more accurate with longer paths. There was, however, no turn x length interaction (F (2, 150) = 1.976, p = .142), and no three-way interaction between path length, turn direction, and group (F < 1).

We next analysed signed heading error as a measure of bias, or the extent to which participants tend to turn too much or too little back towards Leg 1. Adults showed very slight negative bias, or the tendency not to turn enough back towards Leg 1 (M = -0.721%, SD = 8.450), although children displayed this tendency even more (M = -14.278%, SD = 10.195). Within the child group, older children had a lesser tendency to undershoot in their return headings (M = -13.212%, SD = 8.361) compared to younger children (M = -15.463%, SD = 12.053). The extent of undershoot was not significantly different from zero in adults (t(39) = -0.539, p = 0.592) but was significant in children (t(37) = -8.633, p < 0.001). There was no significant correlation in signed heading errors with age for children (r(36) = 0.203, p = 0.221). However, t-tests confirmed that children undershot on return headings more than adults (t(76) = 6.407, p < 0.001) and that even the older children did this to a greater extent than adults (t(58) = 5.416, p < 0.001). There was no significant difference between older and younger children on this measure (t(36) = 0.674, p = 0.504).

Signed data were entered into the same mixed-design ANOVA as the unsigned data. In this analysis there was no main effect of turn direction (F < 1) or path length (F < 1) on heading error. There was, however, a significant effect of group (F (2, 75) = 6.631, p = .002). Bonferroni post-hoc tests revealed no difference between 5 and 7 year olds, although adults were significantly more accurate than both child age groups (respectively: $p = .005$; $p = .041$). Group interacted with neither turn direction ($F < 1$) nor path length ($F < 1$), and there was no turn direction x path length interaction ($F < 1$). Finally, there was no three-way interaction between path length, turn direction, and group ($F < 1$).

Distance errors

As with landing errors and unsigned heading errors, there was a significant relationship between children's ages and their unsigned distance errors ($r(36) = -0.339$, $p = 0.036$). A significant regression slope fit ($r^2 = 0.115$, $F(36) = 4.701$, $p = 0.036$) indicates that children were benefitting from a 2.670 % decrease in distance errors per year. Note that the strength of this relationship is slighter smaller than the relationships between age and both heading error and landing error, although it still statistically reliable. Adults produced significantly smaller unsigned distance error magnitudes (M = 16.155%, SD = 5.761) than children (M = 30.115%, SD = 9.067), ($t(76) = 8.158$, $p < 0.001$). Adults were more accurate than older children, whose mean error was 27.5474% (SD = 10.010), and this difference was also significant, $t(58) = 5.601$, $p < 0.001$. However, older children were not significantly more accurate than younger children (M = 32.968%, SD = 7.11), although this difference approached significance ($t(36) = 1.904$, $p = 0.064$).

Data were entered into a 3 (group: adults, 7 years, 5 years) x 3 (overall path length: 2m, 3m, 4m) x 2 (turn direction: left, right) mixed-design ANOVA. There was no effect of turn direction on distance error ($F < 1$) although there was a main effect of overall path length ($F(2, 150) = 4.231$, $p = .016$): the greatest amount of error was associated with the 2m paths (Mean = 28.535%, SEM = 1.543), the least with 3m paths (Mean = 23.790%, SEM = .990), and an intermediate amount with 4m paths (Mean = 26.432%, SEM = 1.321). There was a significant effect of group ($F(2, 75) = 40.172$, $p < .001$). Bonferroni post-hoc tests revealed that all groups performed significantly different from each other: adults were significantly more accurate than 7 year olds ($p < .001$), who were themselves significantly more accurate than 5 year olds ($p = .035$). There was no turn x group interaction ($F(2, 75) = 1.395$, $p = .254$), no turn x length interaction ($F < 1$), and no length x group interaction ($F < 1$). There was, however, a significant three-way interaction between path length, turn direction, and group ($F(4, 150) = 5.636$, $p < .001$). For adults, there was no effect of either path length or turn direction, except for greater error on 2m paths with a left turn. For 7 year olds, paths with a right turn were performed more accurately as they became longer, whereas paths with a left turn showed the inverse relationship. For 5 year olds, there was no apparent difference between turn directions, and more accurate performance in 3m paths, compared to 2m and 4m trials.

Analysis of signed distance error illustrated that, just as all groups tended to undershoot in terms of return headings, they also tended to undershoot in terms of return trajectory distances. Signed distance errors reveal the tendency for return trajectories to be biased towards smaller distances than the correct return trajectory for adults (M = -1.330%, SD = 11.685), for children (M = -9.963%, SD = 18.433), for younger children (M = -8.020%, SD = 18.943) and for older children (M = -11.711%, SD = 18.271). There was, however, no significant improvement in this measure for children as they age ($r(36) = -0.016$, $p = 0.923$). As with the other performance measures, adults performed more accurately than children overall ($t(76) = 2.4833$, p =

0.0152), and significantly more accurately than the older children ($t(58) = 2.672$, $p = 0.009$). Interestingly, this was the only measure on which the mean error magnitude was larger for older children than for younger children, though this difference was not significant ($t(36) = 0.611$, $p = 0.545$). The extent of undershoot was not significantly different from zero in adults ($t(39) = -0.720$, $p = 0.475$) but was significant in children ($t(37) = -3.331$, $p = 0.002$).

Signed data were entered into the same mixed-design ANOVA as the unsigned data. Here, there was no effect of turn direction on landing error ($F < 1$) although there was a main effect of overall path length ($F (2, 150) = 36.042$, $p < .001$), with a small amount of overshooting associated with short path lengths (2m: Mean = 6.257%, SEM = 2.837) and increasing amounts of undershooting with longer path lengths (3m: Mean = -8.306%, SEM = 1.855; 4m: Mean = -18.310%, SEM = 2.057). The between-subjects comparison between groups approached significance ($F (2, 75) = 2.934$, $p = .059$), although Bonferroni post-hoc tests revealed no significant difference between groups. There was no turn x group interaction ($F < 1$), and no turn x length interaction ($F < 1$). There was, however, a significant length x group interaction ($F (4, 150) = 9.277$, $p < .001$): whilst all participants overshot with shorter paths and undershot with longer paths, children demonstrated more pronounced errors in either direction than adults. Finally, there was no three-way interaction between path length, turn direction, and group ($F (4, 150) = 1.817$, $p = .128$).

DISCUSSION

Adults and children participated in a triangle-completion task that required calculation of both heading and distance in the reproduction of the response vector. On all measures of performance, adults produced more accurate responses than children: errors in their landing position were smaller, and their estimations of both distance and heading of the return trajectory were more accurate. Some of these data contrast with the findings of Giovannini et al. (2009), who found no difference between children and adults on a distance estimation task. However, they are in line with other demonstrations that adults produce more accurate estimations of orientation (Rieser & Rider, 1991) and distance (Corlett et al., 1985) than children. What makes the present paradigm different to those previous studies is that the response required participants to make estimations of both distance and heading, rather than heading (i.e. pointing towards a hidden location) or distance (i.e. walking to a previously-viewed location) alone. This may therefore explain the differences between our data and those of Giovannini et al. (2009) – it could be that integrating estimations is harder for children, and so distance estimations, which may sometimes be comparable to those of adults when calculated alone, are adversely affected by the concurrent estimations of heading.

Previous research by Nardini et al. (2008) supports the notion that adults may be more adept at combining spatial cues: their findings demonstrated that the ability to effectively integrate multi-modal cues develops over time in humans, and children of at least 8 years of age and below are unable to perform at a similar level to adults. It could be argued that responses in the present study required a combination of information within modality (i.e. distance and heading calculations from self-motion), and it may therefore be the case that children also have similar difficulties integrating intra-modal cues as much as they do multi-modal ones. In contrast, since idiothetic cues usually include information from vestibular sources (providing signals indicating balance and movement) and proprioceptive sources (providing signals indicating spatial position) (see Mittelstaedt and Mittelstaedt, 1980; 1982), it seems equally tenable to argue that the integration of these cues is itself multi-modal process. Indeed, the signals result from different biological systems, and are manifest in different electrophysiological forms, which thus requires some form of multisensory integration to produce a coherent motion-based account of translation through space. As such, the theoretical account of integration provided by Nardini et al. (2008) may be just as applicable to the present data, with adults combining these multi-modal sources of information more effectively than children. However, this analogy might not be entirely appropriate when it comes to the distinction between representations of distance and heading (and the necessity for them to be combined in the triangle-completion task). Although vestibular and proprioceptive mechanisms are differentially suitable for calculating each of these representations, calculation of distance and heading will naturally make use of both sources of information throughout the outbound path (e.g. heading towards the origin will be updated by increased distance of leg 2). Thus, the final homing response in a triangle-completion task is not necessarily informed by a weighted combination of the two sensory cues in quite the same way as search for an object location that is informed by visual and idiothetic cues. It does, though, remain possible that there is a developmental trajectory for the combination of vestibular and proprioceptive information during active translation, which presents an interesting possibility for future enquiry.

Another prediction was that there would be a developmental difference between younger and older children. This was based upon various accounts of change in spatial abilities around the age of 7 years (see Plumert & Spencer, 2007). Analysis of landing error did indeed reveal a group difference between 5 year old and 7 year olds, with the latter performing more accurately. There was also a significant linear relationship between age and landing accuracy, with children improving around 6.5% per year, on course to attain adult levels of accuracy around 11 years of age. Analysis of absolute heading and distance errors also uncovered a similar relationship, with group differences between younger and older children, and a significant linear relationship between age and performance. However, the relationship was somewhat different for signed errors, which provide a measure of bias in the response. Both older and younger children demonstrated a tendency to undershoot, in terms of both heading (i.e. not turning sufficiently toward the startpoint) and distance (i.e. not walking far enough). There was, though, no group difference between older and younger children on these measures, and no linear relationship with age. Previous adult data (e.g. Klatzky et al., 1990; Loomis et al., 1993) have shown that smaller distances (i.e. leg lengths of around 2m) tend to engender overshooting, whereas longer distances (i.e. leg lengths of around 6m) produce undershooting. Thus, there is the possibility that this relationship scales to the relative size of the individual. It has also been suggested that the differences between adults and children are due to greater experience calibrating spatial updating from idiothetic information that is associated with adulthood (Rieser & Rider, 1991).

An additional component to our developmental predictions was that estimations of heading would be more likely to undergo a developmental change than distance estimations. This was a result of previous studies, including work from our own laboratory, which have drawn a distinction between the two forms of information (see Berthoz et al., 1999). In particular, heading information appears to be more susceptible to damage (Worsley et al., 2002) and more amenable to improvement through training (Smith et al., 2010). We therefore reasoned that the developmental course of heading calculation may differ from that of distance. However, we did not find strong evidence for dissociation between these two components of the path integration response: both estimations improved with age, with heading gaining around 3.5% accuracy per year, and distance gaining around 2.7%. Children's accuracy was more susceptible to changes in path length and turn direction than that of adults, and this variability was particularly apparent for estimations of heading, compared to distance. This difference might support argument for a functional separation, although it might also reflect inherent differences in the calculation of these separate components on the basis of their underlying substrates. As mentioned above, what may change over time is our ability to integrate them in order to reduce the variability of the response. This is an interesting issue for future research – the present paradigm was not designed to place the cues in competition with each other, and so it is not possible to ascertain whether children were relying on one form of information over the other.

Taken together, the present data show that the accuracy of full path integration (i.e. combining heading and distance) improves with age. Furthermore, there is evidence for improvement across a relatively short period of time (i.e. between 5 and 7 years of age). It is therefore clear that theories of navigational development need to include path integration as a component. Existing accounts (such as those of: Gollege et al., 1985; Siegel & White, 1975) primarily focus of the use of landmarks and the formation of cognitive maps, with no place for idiothetic representations of movement in space. This is despite other accounts of the fundamental role of proprioception in cognitive mapping (Gallistel, 1990), along with clear empirical demonstrations that self-motion cues scaffold landmark learning (Müller and Wehner, 2010) and route learning (Ruddle and Lessels, 2006). One reason why path integration has not previously been incorporated into theories of navigational development may be that it had mostly been explored and characterised in closed biological systems, such as continuous online vector summation in the desert ant (Wehner & Srinivasan, 1981). However, recent accounts of path integration in humans have characterised the process not as a continuous low-level calculation, but more of a configural response that is more likely to require cognitive processing. For example, the Error Encoding Model (EEM) proffered by Fujita et al. (2003) states that the individual stores individual legs and turns in working memory as they traverse the route. It is only when they are required to return to the startpoint that this information is configured into a map-like survey representation, allowing individuals to then calculate the distance and heading of the return vector.

The difference between continuous and configural strategies in path integration has recently been explored by Wiener, Berthoz and Wolbers (2011), who required participants to adopt either one strategy or the other during a triangle-completion task. They found that participants were more accurate when adopting a configural strategy (i.e. remembering the shape of the path) but that they were quicker to respond when adopting a continuous strategy (i.e. continuously updating the position of the startpoint as they moved). These data show that humans are able to employ two different strategies to spatially update through self-movement. Combined with the EEM account put forward by Fujita et al. (2003), it therefore seems likely that there is a cognitive component to human path integration that can and should be accounted for in theories of navigational development. Just as children's ability to encode landmarks and the metric relations between them improves with age (Gollege et al., 1985; Siegel & White, 1975), it appears that their ability to use self-movement cues to update their position within that space also improves. It is likely that these abilities will directly affect each other (Müller and Wehner, 2010) and we must therefore seek to characterise them both. Furthermore, just as we might wish to assess how changes in other cognitive functions, such as visuospatial working memory, attentional capacity, and processing speed (see Pickering, 2001), might affect memory for routes and landmarks, we should also address how they impact upon the efficiency of path integration.

It is important to note the constraints of the present design within discussion of these issues: Compared to previous studies of path integration, we employed a relatively limited range of path components. For example, Loomis and colleagues (1993), manipulated leg lengths between 2m – 6m and turns between 60^o – 120^o. In contrast, we used a smaller range and size of leg lengths (i.e. 1m – 2m), and all turns were of 90^o. These constraints may therefore carry implications for the behaviours we observed. One possibility is that participants could have recognised the regularity in the angle of turn, which may be especially likely as cardinal directions can often be treated as qualitative (rather than quantitative) data (see Frank, 1991).Equally, although there were effects of path length and turn direction on performance, participants could have been sensitive to the fact that there was little variability overall. As such, it is possible that participants were more likely to use some form of configural strategy (Fujita et al., 1993; Wiener et al., 2011) than they would if we had manipulated a greater range of leg lengths and turns. It would therefore be of great interest to more systematically manipulate these properties in future in order to assess whether children adopt different strategies according to the nature of the route, or if they are more likely to rely on one form. The ability to switch between strategies may itself be something that possesses an interesting developmental profile (c.f. Nardini et al., 2008).

With this in mind, it is clear that further research is necessary to more closely assess the strategies that children may be using to make their response, and how they relate to other aspects of both navigational behaviour and more general cognitive abilities. Wiener et al. (2011) state that head orientation is reliably associated with the use of a continuous path integration strategy, so it would be useful to measure this in children as an assay of the cognitive foundations of their response. Equally, it may also be useful to employ other techniques to more closely model their behaviour, such as manipulating additional properties of the outbound path (e.g. the number of route segments). The ability to construct a configural survey representation of a route experienced only through self-movement may be an ability that is unique to humans (Wiener et al., 2011). As such, we need to devote more attention to understanding its developmental origins and fully characterising how it interacts with other navigational systems – if we are to develop a comprehensive account of a fundamental human behaviour then we must be sure to incorporate perception, cognition, and action into our thinking.

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LEGENDS

TABLE 1. Mean (and SD) percentage error data for each triangle type.

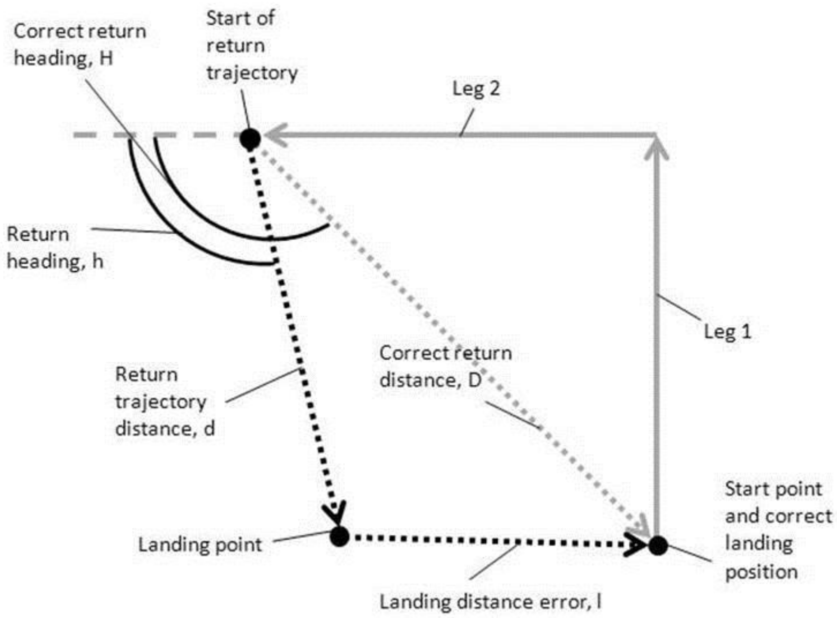
FIGURE 1. Schematic diagram of return trajectory taken on a trial with equal leg lengths and a leftward turn. In this trial, the participant undershoots in terms of heading by failing to turn back far enough towards Leg 1. This will produce a negative signed heading error. The participant also undershoots in terms of trajectory distance, producing a negative signed distance error. The return trajectory taken here results in a substantial landing error of approximately 60% which is indicative of the magnitude of older children's landing error magnitudes. Heading errors are calculated by taking the difference between the return heading taken and the correct return heading, and scaling this as a percentage of the magnitude of the correct return heading. The equivalent calculation is done for distance errors using the correct return distance. Landing error is also scaled as a percentage of the magnitude of the correct return distance.

FIGURE 2. Children's mean landing errors scaled as a percentage of the distance of the correct return distance. The mean value for adults is shown together with 1 standard error above and below the mean.

TABLE 1

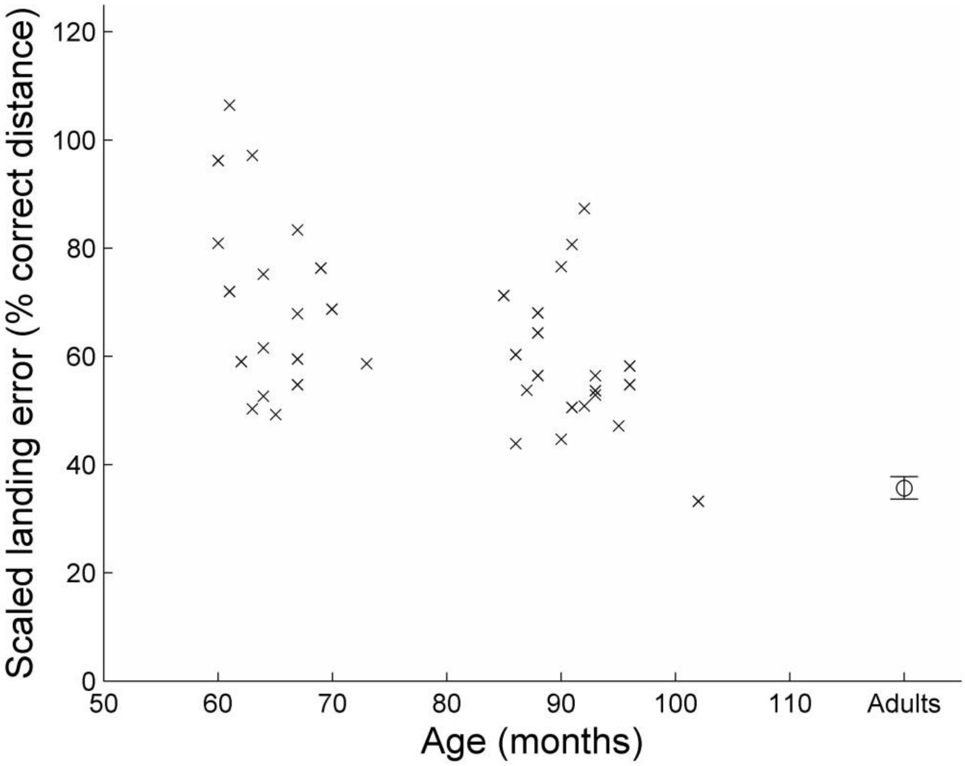
	Triangle	Leg 1	1m	1m	2m	2m	1m	1m	2m	2m
		Leg 2	1m	2m	1m	2m	1m	2m	1m	2m
		Turn	left	left	left	left	right	right	right	right
Adults	Landing	Mean	42.16	39.01	37.28	35.93	34.46	31.01	34.20	31.32
		SD	21.95	20.91	19.29	19.48	18.15	20.22	16.90	17.64
	Distance (signed)	Mean	3.83	-0.07	-1.52	-5.82	4.46	0.36	-5.38	-6.51
		SD	22.07	18.84	14.70	15.92	17.03	16.80	16.20	13.45
	Distance (unsigned)	Mean	21.72	17.08	13.69	14.91	16.10	14.57	15.78	15.39
		SD	14.05	11.24	9.21	10.24	11.89	9.47	7.75	6.97
	Heading (signed)	Mean	-7.79	-17.71	3.21	-1.85	-5.24	-25.46	5.67	-10.23
		SD	51.72	80.92	32.81	47.67	26.87	54.85	14.07	43.03
	Heading (unsigned)	Mean	43.81	70.88	29.15	40.20	15.95	30.29	14.00	19.73
		SD	32.49	48.86	18.62	29.14	22.65	53.41	9.53	41.07
7 years	Landing	Mean	70.10	57.91	61.98	52.98	63.65	54.59	49.24	52.98
		SD	30.37	20.54	24.53	19.07	23.97	22.85	16.04	17.07
	Distance (signed)	Mean	3.92	-8.88	-9.52	-24.71	-3.03	-14.75	-15.03	-19.64
		SD	27.68	29.39	27.54	22.03	35.53	22.42	22.59	22.59
	Distance (unsigned)	Mean	24.03	27.90	26.14	30.57	35.69	27.96	23.82	25.10
		SD	16.28	16.35	16.07	14.96	19.13	16.28	15.72	16.30
	Heading (signed)	Mean	-48.81	-11.62	-24.92	-14.77	-24.88	-38.07	-17.51	-19.66
		SD	75.37	126.64	46.28	70.22	25.88	54.28	28.02	25.13
	Heading (unsigned)	Mean	85.04	115.81	57.52	61.95	27.52	40.71	25.28	24.04
		SD	52.43	62.88	43.83	43.91	26.77	53.31	22.93	22.25
5 years	Landing	Mean	90.80	55.41	60.29	64.28	90.89	63.34	65.68	64.39
		SD	32.91	19.30	30.61	16.59	52.37	27.34	30.04	23.60
	Distance (signed)	Mean	8.97	-15.34	-13.03	-24.60	19.41	-1.90	-17.08	-28.58
		SD	42.18	14.59	25.94	27.88	35.10	32.56	25.84	32.12
	Distance (unsigned)	Mean	38.61	26.04	27.27	33.22	35.07	32.85	32.04	39.40
		SD	22.84	9.78	12.68	17.55	23.12	16.11	13.16	17.16
	Heading (signed)	Mean	-28.14	-27.88	-26.70	-16.78	-50.29	-59.88	-19.56	-30.44
		SD	111.30	116.01	41.94	88.23	58.37	67.50	32.86	38.57
	Heading (unsigned)	Mean	120.35	124.04	51.92	83.34	55.93	65.02	34.05	37.99
		SD	84.56	82.75	34.75	41.29	54.04	64.50	26.28	37.15

FIGURE 1



Heading error = (h – H)*100 / H
Distance error = (d – D)*100 / D
Landing error = (l – D)*100 / D

FIGURE 2


Scaled landing error (% correct distance)
0
20
40
60
80
100
120
50
60
70
80
90
100
110
Adults
Age (months)