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Report

# Development of Cue Integration in Human Navigation

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## Summary

**Mammalian navigation depends both on visual landmarks and on self-generated (e.g., vestibular and proprioceptive) cues that signal the organism's own movement [1–5]. When these conflict, landmarks can either reset estimates of self-motion or be integrated with them [6–9]. We asked how humans combine these information sources and whether children, who use both from a young age [10–12], combine them as adults do. Participants attempted to return an object to its original place in an arena when given either visual landmarks only, nonvisual self-motion information only, or both. Adults, but not 4- to 5-year-olds or 7- to 8-year-olds, reduced their response variance when both information sources were available. In an additional "conflict" condition that measured relative reliance on landmarks and self-motion, we predicted behavior under two models: integration (weighted averaging) of the cues and alternation between them. Adults' behavior was predicted by integration, in which the cues were weighted nearly optimally to reduce variance, whereas children's behavior was predicted by alternation. These results suggest that development of individual spatial-representational systems precedes development of the capacity to combine these within a common reference frame. Humans can integrate spatial cues nearly optimally to navigate, but this ability depends on an extended developmental process.**

## Results and Discussion

Adults and children aged 4–5 and 7–8 years took part in a homing task in a dark room with peripheral illuminated landmarks (Figure 1). Participants picked up a series of glowing objects and, after a delay in the center of the room, attempted to return the first object to its original location. Only the illuminated landmarks and objects (but no room features or boundaries) could be seen. For relocation of the object, participants could use two kinds of information: first, the visual cue to the object's initial position with respect to landmarks; and second, the self-motion cue to the direction and distance the participant had walked since picking up the object.

Relocation of the object depended only on nonvisual self-motion information when the landmarks were switched off and the room left in darkness (self-motion condition; "SM"). Relocation depended only on the landmarks when landmarks remained visible but participants were disoriented by turning (landmarks condition; "LM"), given that after disorientation the prior direction of self-motion is not known. Both information sources were available when participants remained oriented and landmarks remained visible (self-motion and landmarks condition; "SM+LM"). Conditions LM and SM+LM include the visual cue to self-motion provided by optic flow [13]; the task, therefore, distinguishes nonvisual self-motion information from all visual landmark information (including optic flow); however, optic flow was not useful for judging return angle (see Experimental Procedures).

On each trial, we recorded the distance (cm) between the participant's response and the correct location. Root mean-square errors (RMSEs) were calculated for each condition. As Figure 2A shows, in all three conditions participants' accuracy improved with age; repeated-measures ANOVA found main effects of group ($F [2] = 32.5$, $p < 0.001$) and condition ($F [2, 84] = 8.3$, $p < 0.001$). Age improvements in single-cue conditions SM and LM suggest the development of accuracy in the judging of distances and angles walked (SM) and of the object's place relative to landmarks (LM) [10, 11] (see Supplemental Data, available online, for individual age comparisons). A group × condition interaction ($F [4, 84] = 2.8$, $p < 0.05$) reflects a developmental change in profile across conditions. Whereas adults profited from the combined SM+LM condition relative to both single-cue conditions (paired $t [16] = 6.8$, $p < 0.001$ versus SM; paired $t [16] = 2.7$, $p < 0.02$ versus LM), children did not and were (nonsignificantly) less accurate with both cues available than with only LM available.

Why did having both information sources enable adults, but not children, to improve navigational accuracy? The error measure in Figure 2A includes "constant error," such as a tendency to overshoot or undershoot, and "variable error," which is the dispersion of responses. Variable error is of particular interest, given that human adults can reduce the variances of their sensory estimates by integrating multiple information sources [14–19]. Variance reduction by cue integration has previously been studied for perceptual tasks (e.g., judgments of height [17] or slant [19]), and a similar process has also recently been proposed for spatial behavior [20]. Here we provide a new test of this approach.

To measure variable error, we recorded standard deviations (SDs) of responses (i.e., the dispersion of each participant's responses about their own mean response location). Figure 2B plots mean SDs measured in SM, LM, and SM+LM conditions. Children did not significantly reduce SDs of their estimates relative to either single cue (see error bars, Figure 2B), whereas adults did ($t [16] = 5.2$, $p < 0.001$ compared with SM; $t [16] = 3.0$, $p < 0.01$ compared with LM). This suggests that adults' overall accuracy improvement (Figure 2A) is supported by an integration process that reduces response variance.

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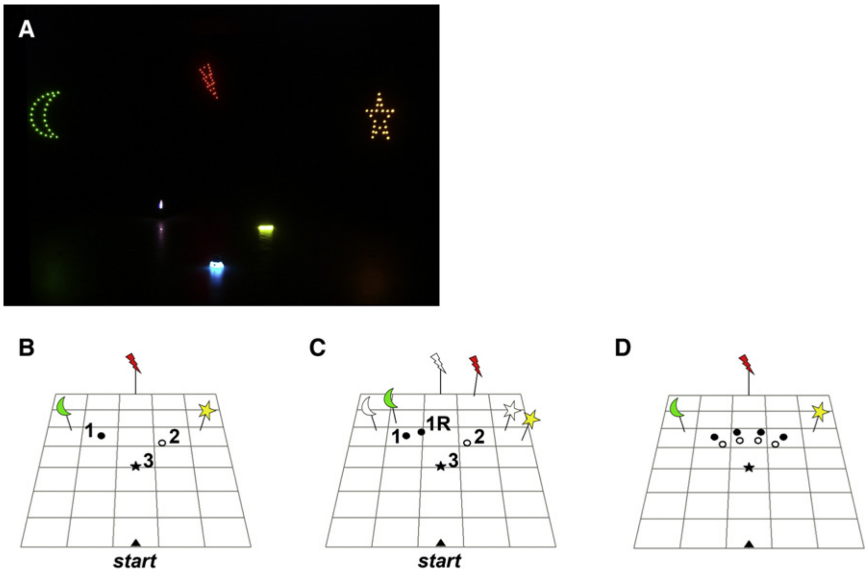


Figure 1. Layout and Procedure

(A and B) In a dark room with three illuminated landmarks ("moon," "lightning bolt," "star") and three illuminated objects (1–3) visible, participants viewed the layout from the "start" position, then collected the objects in sequence (1, 2, 3). They waited at object 3, facing away from the landmarks. Landmarks were turned off. Participants turned around and attempted to return object 1 to its original place, under one of the following conditions: landmarks left off, with only self-motion information available (condition SM); landmarks turned back on after the participant has been disoriented by turning, with only landmark information available (condition LM); or landmarks turned on and the participant not disoriented, with both kinds of information available (condition SM+LM).

(C) In an additional "conflict" condition, landmarks were covertly rotated around participants by 15°, after the participants had collected the objects but before they attempted to replace object 1. Self-motion still indicated the original location (1), whereas landmarks now indicated a location rotated by 15° (1R).

(D) The full set of locations for objects 1 (●) and 2 (○), which varied from trial to trial. Object 3′s location (*), from which participants attempted to return object 1, was constant. Grid squares represent 1 $m^2$.

Children's failure to reduce variance (Figure 2B) could be explained either by suboptimal integration or by failure to integrate the cues. To distinguish between these possibilities, we analyzed behavior in a "conflict" condition, which can reveal participants' relative reliance on the two cues. To model behavior, we approximated SM and LM estimates as normal distributions with random (Gaussian) noise [14–16, 20] (see Figure S1). We considered two models of cue combination: (1) integration of self-motion and landmark cues in a weighted average, and (2) no integration of the cues, but alternation between them—i.e., switching between the following of self-motion or of landmarks from trial to trial.

In the conflict condition (Figure 1C), landmarks were covertly rotated by 15° around the arena before participants made their response. Two response locations therefore indicate, respectively, exclusive use of self-motion and exclusive use of landmarks. The degree to which participants relied on each cue is given by the relative proximity of their mean search location to these locations (see also ref [21]). If distance to the self-motion-consistent location is $d_{SM}$ and distance to the landmark-consistent location is $d_{LM}$, relative proximity (i.e., 1/distance) to the landmark-defined location ($rprox_{LM}$) is:

$$rprox_{LM} = \frac{1/d_{LM}}{1/d_{SM} + 1/d_{LM}} = \frac{d_{SM}}{d_{SM} + d_{LM}} \quad (1)$$

We then tested how measured relative proximities and SDs fit the model predictions. In the integration model, self-motion and landmark estimates, with variances $\sigma^2_{SM}$ and $\sigma^2_{LM}$ (as measured in SM and LM conditions; i.e., squares of the SDs

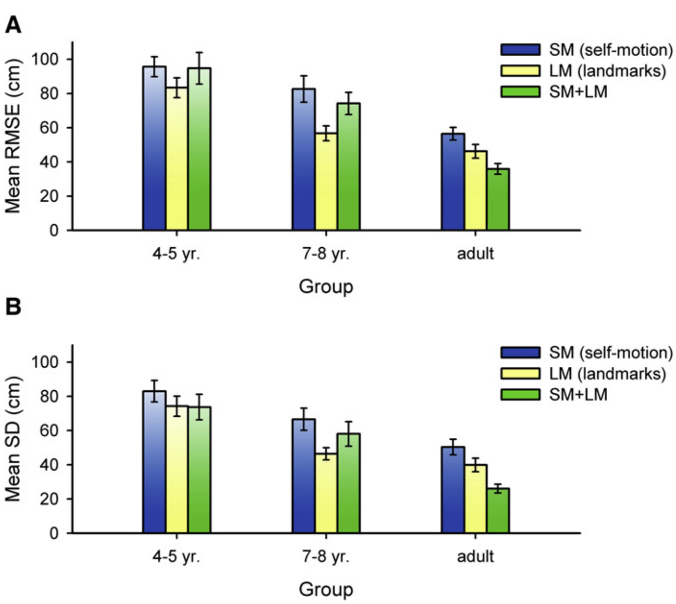


Figure 2. Results

(A) Mean root mean-square error (mean RMSE) by group, SE bars, for objects relocated under the self-motion condition (SM), the landmark condition (LM), or the combined condition (SM+LM).

(B) Mean standard deviation (SD) of participants' responses' distances from each participant's mean response location.

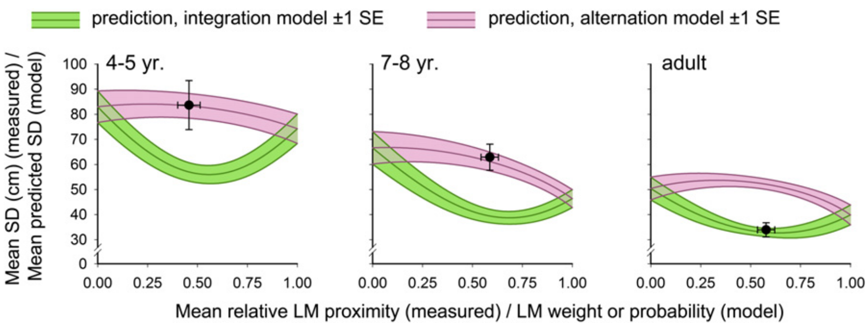


**Figure 3. Predictions and Behavior in the Conflict Condition**

The curves plot the means of functions predicting mean standard deviations (SDs) from different landmark weights (integration model) or landmark probabilities (alternation model), ±1 SE. The x axes correspond to progressively greater reliance on landmarks from left to right. The points plot measured mean SDs and mean relative proximities to the landmark-consistent locations (SE bars), interpreted as landmark weight (integration model) or landmark probability (alternation model).

plotted in Figure 2B), are integrated in a weighted average. The predicted variance for a condition in which SM and LM information is integrated, $\sigma^2_{SM+LM}$, is:

$$\sigma^2_{SM+LM} = w^2_{SM}\sigma^2_{SM} + w^2_{LM}\sigma^2_{LM} \quad (2)$$

in which $w_{SM}$ and $w_{LM}$ are the weights given to the two information sources and sum to unity ($w_{LM} = 1 - w_{SM}$). This model predicts a relationship between cue weighting and response variance (Figure 3). Variance can be reduced relative to the single cues, provided that appropriate weights are chosen [14–16]. In a weighted average of two distributions, the proximity of the combined mean to either underlying mean is a linear function of their weighting. Thus, if subjects combined cues in a weighted average, their relative proximity to the landmark location (Equation 1) would correspond to their weighting for the landmark cue (Equation 2). The data points (Figure 3) plot measured SDs and landmark proximities for the conflict condition. Interpreting relative proximity as weighting, we can thus determine whether the measured values differ from those predicted by the model.

The integration model predicts the same variance reduction irrespective of the distribution means. Thus, variance reduction is predicted even when the cues are in conflict. With too large a conflict, participants might not show integration behavior [20]; therefore, the conflict chosen for this study was relatively small (see Experimental Procedures).

In the alternative model we considered, participants do not integrate the cues but alternate between them. The distribution of responses is therefore some mixture [22] of the SM and LM distributions. The predicted variance for a mixture of two distributions with variances of $\sigma^2_{SM}$ and $\sigma^2_{LM}$ and means of $\mu_{SM}$ and $\mu_{LM}$ is:

$$\sigma^2_{SM+LM} = p_{SM}\left(\mu^2_{SM} + \sigma^2_{SM}\right) + p_{LM}\left(\mu^2_{LM} + \sigma^2_{LM}\right) - \left(p_{SM}\mu_{SM} + p_{LM}\mu_{LM}\right)^2 \quad (3)$$

in which $p_{SM}$ and $p_{LM}$ are probabilities of following either cue and sum to unity. In the model, $\mu_{SM} = 0$ and $\mu_{LM} = 46$, because landmark rotation in the conflict condition shifts landmark-defined locations by 46 cm relative to self-motion-defined locations. The derivation of Equation 3 is explained in the Supplemental Data. The alternation model predicts a relationship between the probability of following either cue and the response variance (Figure 3). Variance cannot be reduced relative to the single cues, but it tends to increase slightly as both cues are used, owing to their separation. In a mixture of two distributions, the proximity of the mixture mean to either underlying mean is a linear function of their mixture probabilities. Thus, if subjects alternated between the cues, their relative proximity to the landmark location (Equation 1) would correspond to the probability with which they followed the landmark cue (Equation 3). Interpreting relative proximity as probability, we can thus determine whether the measured values differ from those predicted by the model.

As Figure 3 shows, children's behavior in the conflict condition was inconsistent with integration but consistent with alternation. By contrast, adults' behavior was consistent with integration but inconsistent with alternation. Mean relative proximity to the landmark-defined location (Figure 3, x axis) was 0.46 ± 0.06 at 4–5 years, 0.59 ± 0.04 at 7–8 years, and 0.58 ± 0.04 in adults. We compared measured and predicted SDs for these proximity values, i.e., the fit between data points and prediction curves along the y axis (Figure 3).

The mean SD of the 4- to 5-year-olds' searches, 83.7 ± 9.8 cm, was greater than the integration-model prediction of 57.0 ± 3.7 cm, $t(13) = 2.6$, $p < 0.03$, but did not differ from the alternation-model prediction of 83.3 ± 4.9 cm, $t(13) = 0.03$, $p = 0.97$. The mean SD for the 7- to 8-year-olds, 62.9 ± 5.2 cm, was likewise greater than the integration prediction of 39.4 ± 2.7 cm, $t(13) = 3.8$, $p < 0.01$ but did not differ from the alternation prediction of 61.2 ± 3.7 cm, $t(13) = 0.3$, $p = 0.80$. For adults, this pattern was reversed: their mean SD, 33.9 ± 2.8 cm, did not differ from the integration prediction of 32.9 ± 1.7 cm, $t(16) = 0.29$, $p = 0.78$, but was lower than the alternation prediction of 52.1 ± 2.1 cm, $t(16) = 4.8$, $p < 0.001$. Figure S1, plotting all searches, provides another way to visualize these patterns. Consistent with alternation, 7- to 8-year-olds' conflict-condition errors in the direction of landmark shift (x axis) appear possibly multimodal. For 4- to 5-year-olds, variances are large relative to the size of conflict, so there is less apparent change between SM+LM and conflict distributions.

Adults' mean SD is near the minimum of the integration curve in Figure 3, which suggests that their weighting of landmark and self-motion information was close to statistically optimal [14–16] for variance reduction. Variance reduction is greatest when cues are weighted according to their relative reliabilities (inverse variances; $1/\sigma^2_{SM}$ and $1/\sigma^2_{LM}$). Thus, the optimal weighting for landmarks, $w_{LM}$, would be:

$$w_{LM} = \frac{1/\sigma^2_{LM}}{1/\sigma^2_{SM} + 1/\sigma^2_{LM}} = \frac{\sigma^2_{SM}}{\sigma^2_{SM} + \sigma^2_{LM}} \quad (4)$$

The adult group's mean SM and LM variances (squares of values plotted in Figure 2B) predict an optimal landmark weight of 0.61 for the group as a whole. The measured mean weight, 0.58 ± 0.04, does not differ significantly from this value; $t(16) = 0.8$, $p = 0.41$. This implies that in the integration of spatial cues for navigation, adult humans take differences in their reliabilities into account, as they do in perceptual tasks [17–19].

Figure 3 illustrates the behavior predicted if the whole group adopted the same integration weight or mixture probability. In fact, even greater variance reduction is possible in the integration model if each participant sets his or her own optimal weight (Equation 4). The mean optimal SD predicted in this way for the adult group is 27.0 ± 1.5 cm. Adults did not achieve this reduction in the conflict condition, $t(16) = 2.2$, $p < 0.05$, but they did so in the consistent SM+LM condition with mean SD 26.1 ± 2.6 cm (Figure 2B); $t(16) = 0.4$, $p = 0.69$. Adults' greater conflict-condition SD suggests that the conflict disrupted integration to a small degree, and it is consistent with a minority of participants' detection of the conflict (see Experimental Procedures).

A probabilistic analysis of behavior requires that a number of assumptions are met [14–16]: normal distributions, uncorrelated noise, and an account of all significant noise sources. Errors were well approximated by normal distributions (see Figure S1). Given that the object could be localized relative to landmarks before being picked up but relative to self-motion after being picked up, noise in these information sources should not be correlated (although memory or attention noise in the subsequent delay period could potentially be correlated). The contributions of motor noise and decision noise to our data are unknown, but purely motor errors (in pointing to a marked location; [23]) are around 1.5 cm in 5- to 6-year-olds, whereas we recorded mean RMSEs of around 90 cm in 4- to 5-year-olds and of 70 cm in 7- to 8-year-olds. It is therefore likely that the great majority of the error we measured was in the spatial-localization processes under study, although modeling of all potential noise sources is an important aim for future studies.

In summary, we found that in short-range navigation, human adults, but not 4- to 5-year-olds or 7- to 8-year-olds, reduced localization errors by combining nonvisual self-motion information and visual landmark information (Figure 2A). A major factor in this was a reduction in response variance (Figure 2B). We modeled two ways of combining self-motion and landmark cues: integrating them in a weighted average, which would reduce variance, and alternating between them, which would not. Adults' behavior was consistent with integration, whereas 4- to 5-year-olds' and 7- to 8-year-olds' behavior was consistent with alternation (Figure 3). Adults' chosen weights and attained variances were close to optimal in terms of variance reduction (Figure 3), which implies that adults weight spatial cues according to their reliabilities. Children's failure to reduce variance did not indicate integration with suboptimal weights but, rather, a failure to integrate the cues at all. This suggests that development of individual spatial representational systems precedes development of the capacity to combine these within a common reference frame.

These results raise an important question for navigation: can mammals' preferred use of landmarks [6–9] be explained solely by the fact that they usually enable more accurate localization than does self-motion, or is there some additional landmark bias? This can be tested with "noisy" landmarks. Probabilistic analyses of cue combination can also provide insight into many other processes in spatial cognition [20], such as effects of biases or "priors" in spatial coding [24].

Another important question is: What enables mature sensory integration to develop? For multisensory integration, it is necessary to know which cues go together and to be able to translate between different frames of reference. Successful cross-modal perception in the first year of life [25] suggests that these basic conditions are met early. However, our results, and those showing that 8-year-olds do not integrate visual and haptic cues to shape [ref. 26, in this issue], indicate that the combining of sensory information to reduce variance develops much later. Current models propose that neural coding and integration of sensory probabilities could be relatively simply achieved [27, 28]; these models could now be extended to make predictions about development. Spatial-cue integration might depend both on low-level processes (e.g., accurate neural coding of sensory reliabilities) and on major anatomical changes, such as the development of pathways to supramodal areas that can combine multiple sources of spatial information (though see ref [29]). One way to distinguish between these possibilities will be to compare the developmental time courses of within-modality and between-modality integration. Studies of this kind can provide new insight into how mature cue integration is achieved.

## Experimental Procedures

### Participants

Participants were 17 adults (mean age = 24.9, SD = 3.5 years; 7 male), 14 7- to 8-year-olds (mean age = 7.9, SD = 0.5 years; 7 male), and 14 4- to 5-year-olds (mean age = 5.0, SD = 0.2 years; 6 male). Two additional subjects (one adult, one 7-year-old) who did not follow the procedure were excluded. The study conformed with ethical approval from the Oxford Applied and Qualitative Research Ethics Committee, and participants or their parents gave informed consent.

### Apparatus

The 540 × 720 cm space (Figure 1) was enclosed by floor-to-ceiling blackout curtains. LED arrays measuring 30 cm x 15 cm formed a "moon," a "lightning bolt," and a "star." Relative to the central location from which subjects attempted to return the first object, the moon and star were 45° to the left or right, at a distance of 258 cm, at a height of 50 cm; the lightning bolt was straight ahead at a distance of 400 cm, at a height of 150 cm. Each landmark had a duplicate, rotated by 15° about the central location (Figure 1C); on conflict trials, landmarks were "rotated" by switching between these. Of 45 subjects, 19 experienced clockwise rotation. A speaker above the central location played white noise to mask external sound. The glowing toys (Figure 1B) were a "rocket", some "fuel," and an "alien." Relative to the central location, the rocket was 33° or 11° to the left or right at a distance of 175 cm, the fuel was 33° or 11° to the left or right at a distance of 131 cm; and the alien was always in the central location (Figure 1D). Participants, who wore sunglasses, could see only the illuminated landmarks and objects but not the floor, ceiling, or curtain walls of the space.

### Design and Procedure

On each trial, participants were led inside the enclosure to a position 300 cm behind the central homing place (Figure 1B, "start"). Participants were told to pick up the rocket (object 1), remembering where it was; then pick up the fuel (object 2) and put it in the rocket, then pick up the alien (object 3) and put it in the rocket. Participants faced back toward the start position, and landmarks were switched off. On SM, SM+LM, and conflict trials, the experimenter stood in front of the participant and counted down from 10, then the participant attempted to replace the rocket. On disoriented (LM) trials, the participant was seated in a rotating chair and turned rapidly during the countdown. To encourage reorientation, once landmarks were turned back on participants were slowly rotated in the chair to face the landmarks and prompted to use these to relocate the rocket.

Following one practice trial each of SM+LM, SM, and LM conditions, subjects completed four blocks of four trials, each including one trial of every type (SM, LM, SM+LM, conflict) in random order. Each of the four possible rocket places was used once in each condition. The position of the second object ("fuel") was chosen randomly from the two positions (11°, 33°) in the half of the room opposite to the rocket. Thus, from the point of view of one standing at the central position facing straight ahead (Figure 1D), when the rocket was in one of the left ● positions the fuel was in one of the right ○ positions, and vice versa.

To calibrate speed of turning for the disorientation procedure, in the LM practice trial, participants were asked to point to the "moon" before landmarks were reilluminated. Those able to localize it were turned more rapidly and asked to point again, which was repeated until they showed pointing error consistent with disorientation. For the conflict condition, the degree of rotation (15°) was chosen, after piloting, to be unnoticeable. After the study, all participants were asked whether they noticed anything unusual about the landmarks. Only four (three adults, one 7-year-old) noticed that they moved. Therefore, on the whole the conflict was subtle enough to be undetected. Because landmarks were behind participants before they turned around to respond (Figure 1A), optic flow was not useful for calibration of the correct turn angle, although optic flow could be used to calibrate return distance.

### Analysis

Before calculation of each participant's RMSE for a condition (Figure 2A), individual trial data were filtered to remove errors that were extreme outliers in the distribution of all errors recorded for that age and condition. "Extreme outliers" were defined as errors greater than the third quartile plus three times the interquartile range [30]; in a normal distribution, fewer than 0.0002% of values would meet this criterion. Eighteen trials (2.5%; three of adults, nine of 7- to 8-year-olds, and six of 4- to 5-yearolds) were excluded as extreme outliers. We interpret these values as signifying lapses of concentration, or, in the LM condition, failures to use the landmarks to reestablish orientation.

To analyze response variance (Figure 2B), each participant's four responses in a condition were first standardised to account for the fact that they were aiming for four different locations in the room (Figure 1D, "●" locations) at which the following of landmarks (in the conflict condition) would predict different angles of shift relative to the room. Response coordinates were transposed and rotated so that they could be considered as responses around a single point, at which the direction of the correct return path to the target is "north" and the axis of landmark rotation is orthogonal. For conflict trials, x coordinates of search were inverted for anticlockwise-rotation participants, so that the direction of landmark rotation was always "east." A participant's standard deviation for a condition was then calculated on the basis of the participant's searches' distances from his or her mean search location for that condition. Extreme outliers were removed as in the analysis of RMSE, based on distance from the grand mean response location for each age and condition. Twenty-seven trials (3.7%) were excluded (nine of adults, thirteen of 7- to 8-year olds, and five of 4- to 5-year-olds).

### Supplemental Data

Supplemental experimental procedures and one figure are available with this article online at http://www.current-biology.com/cgi/content/full/18/9/689/DC1/.

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