

Two cortical navigation systems and their differential development

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A couple of recent neuroimaging studies together led us to hypothesize—perhaps counterintuitively—that the occipital place area (OPA), which supports “visually-guided navigation” (ie making our way through the immediately visible environment, avoiding boundaries and obstacles), develops later than the retrosplenial complex (RSC), which supports “map-based navigation” (ie finding our way from a specific place to some distant, out-of-sight place). But is this true? We directly test this hypothesis using functional magnetic resonance imaging (fMRI) adaptation in 5- and 8-year-old children and ask when OPA and RSC represent left and right information—information that both regions represent in adulthood, albeit for different kinds of navigation. Our results revealed that in 5-year-olds, OPA does not represent left/right information and only does so in 8-year-olds. By contrast, RSC in 5-year-olds represents left/right information, like in 8-year-olds. These findings strongly support our hypothesis: the OPA, which is involved in visually-guided navigation, develops later than the RSC, which supports map-based navigation. This developmental timeline not only demonstrates that OPA and RSC develop at different rates but also strengthens the case that these regions serve distinct roles in adult human navigation—since a single system cannot follow two separate developmental trajectories.

Keywords: fmri adaptation; occipital place area; pediatric neuroimaging; retrosplenial complex; scene processing.

Introduction

Neuroimaging research in adult humans has suggested that navigation is not a monolithic system—perhaps not surprising given navigation is multifaceted—but rather composed of at least two distinct cortical systems, each supporting a distinct kind of navigation (Dilks et al. 2022). They are: (i) the occipital place area (OPA) that supports “visually-guided navigation” (ie our ability to move about the immediately visible environment, avoiding boundaries and obstacles) (Dilks et al. 2011; Kamps, Lall et al. 2016; Persichetti and Dilks 2016; Bonner and Epstein 2017; Dillon et al. 2018; Henriksson et al. 2019; Park and Park 2020; Suzuki et al. 2021; Kamps et al. 2024; Kang and Park 2024) and (ii) the retrosplenial complex (RSC, also known as the Medial Place Area, or MPA; Silson, Steel et al. 2016) that supports “map-based navigation” (ie our ability to find our way from a specific place to some distant, out-of-sight place) (Wolbers and Büchel 2005; Dilks et al. 2011; Auger et al. 2012; Vass and Epstein 2013; Marchette et al. 2014; Troiani et al. 2014; Auger et al. 2015; Marchette et al. 2015; Persichetti and Dilks 2016; Sulpizio et al. 2016; Persichetti and Dilks 2019; Steel et al. 2023). However, despite our growing understanding of the cortical systems underlying our ability to navigate in adulthood, how these systems develop remains relatively unknown. So, how then do these cortical systems develop? Are they both present in the first few years of life, or only develop after many years of experience? Or do they, instead, develop along different developmental timelines, with one present in the first few years of life, while the other develops much later?

Perhaps the couple of studies that have investigated the development of OPA and RSC separately can provide some clues. For

example, two studies (Kamps et al. 2020; Jung et al. 2024) found that first-person perspective motion information (ie mimicking the visual experience of actually navigating through a place) is represented in the OPA in 8-year-olds (like adults; Jones et al. 2023; Kamps, Lall et al. 2016; Yoon et al. 2025), but not at all in 5-year-olds. By contrast, one recent study (Jung and Dilks 2025) found that RSC in 5-year-olds represents landmark information (like adults; Maguire 2001; Auger et al. 2012; Vass and Epstein 2013; Auger et al. 2015; Persichetti and Dilks 2019). Critically, however, these prior studies did not test the development of information that both OPA and RSC share (in adulthood) and thus cannot directly test whether these regions develop differentially. Here we overcome this challenge by investigating the development of both regions simultaneously, in the same participants across two age groups, using information that both OPA and RSC represent in adulthood—namely, left and right information, which is critical for both visually-guided and map-based navigation, respectively (Dilks et al. 2011; Yoon et al. 2025). So, does OPA really develop later than RSC?

To directly compare when OPA and RSC develop, we used functional magnetic resonance imaging (fMRI) adaptation in children 5 and 8 years of age and examined when in development these regions represent left and right information in scenes (Dilks et al. 2011; Yoon et al. 2025). More specifically, borrowing from an adult fMRI study (Dilks et al. 2011), participants viewed images of scenes from three conditions: (i) completely different scene images (Different condition); (ii) a scene image followed by the mirror-reversed version of the same image; thus, manipulating left/right information (Mirror condition); or (iii) the same scene

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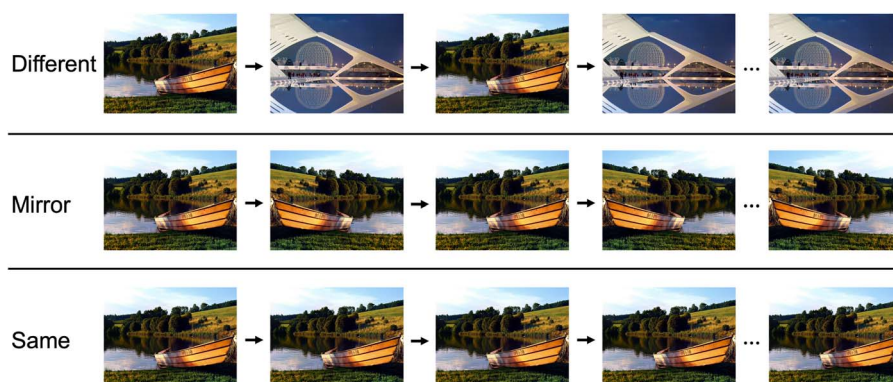


Fig. 1. Example stimuli images from the Different, Mirror, and Same condition blocks. Twelve images were displayed in each condition block and each condition block lasted 16 s. Each image was displayed for 800 ms and a 500 ms ISI was displayed after each image (not shown in the figure). In the Different condition, participants saw two completely different scene images repeated one after another. In the Mirror condition, participants saw a scene image and the mirror-reversal of that scene image repeated one after another. In the Same condition, participants saw the exact same scene image repeatedly. While the scene images are displayed in color here for clarity, the participants saw the images presented in greyscale.

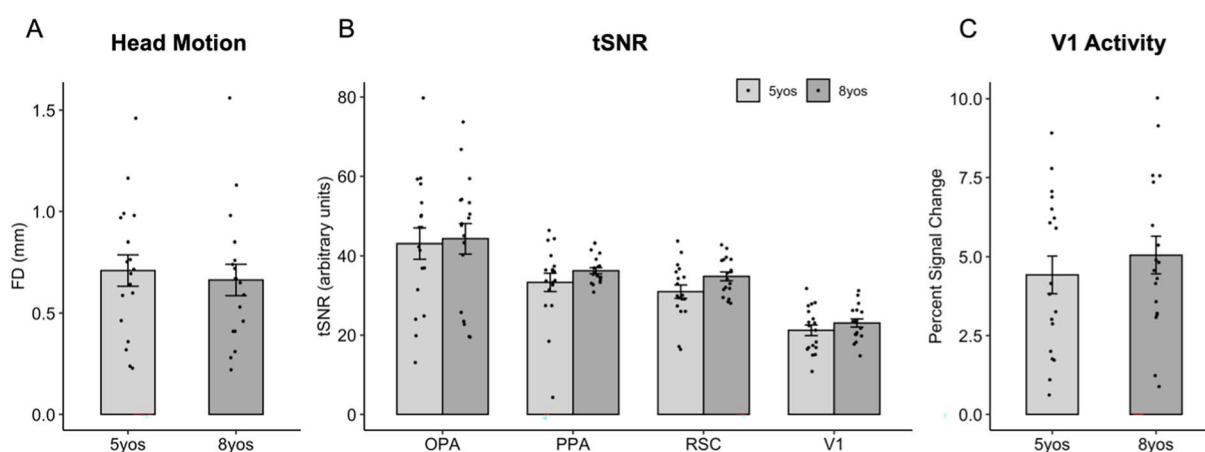


Fig. 2. No significant differences were found between the 5- and 8-year-olds for any of the following measures: a) head motion (average absolute frame-to-frame displacement for all useable runs); b) the tSNR in any ROI; or c) V1 activation (ie the average response in V1 across all conditions relative to fixation). Error bars depict the standard error of the mean and black dots represent individual subject data.

image (Same condition) (Fig. 1). If a region does not represent left-/right information, then mirror-reversed images of scenes will be treated as the same image, and the neural activity will show adaptation across mirror images of scenes. By contrast, if a region does represent left/right information, then mirror-reversed images of scenes will be treated as different images, and the neural activity will not show adaptation to mirror images. Consistent with our hypothesis that OPA develops later than RSC, we predict that in 5-year-olds, the OPA will not represent left/right information and only will do so by age 8. By contrast, we predict that the RSC in 5-year-olds will already represent left/right information, like in 8-year-olds. Importantly, data quality was matched between the two age groups (Fig. 2A–C), ensuring that data quality could not account for any observed developmental differences.

Materials and methods

Participants

Eighteen 5-year-olds (mean age: 5.66 years; range: 5.17–6.50 years; 8 female) and 18 8-year-olds (mean age: 8.58 years; range: 8.17–9.25 years; 10 female) were included in this study. However, 3 additional children (2 5-year-olds, 1 8-year-old) participated but were removed from analysis because they moved too much (2 participants) or were not paying attention to the stimuli

(1 participant). Participants were recruited from the Emory University Child Study Center. All parents or legal guardians gave informed consent, and verbal assent was additionally obtained for the 8-year-olds. All participants had normal or corrected-to-normal vision, and no history of neurological or psychiatric conditions. All procedures were approved by the Emory University Institutional Review Board (IRB Protocol #69592).

Design and stimuli

We used a region-of-interest (ROI) approach in which we used one set of runs to localize scene-selective ROIs (localizer runs) and a second set to investigate the responses of these same voxels (experimental runs). This ROI approach was facilitated by a group-constrained subject-specific (GSS) method, as detailed in the Data Analysis section.

For the localizer runs, a blocked design was used in which participants viewed videos from two different conditions (ie “scenes” and “objects”). The scene stimuli consisted of 32 3 s video clips from a first-person perspective walking through a scene (Kamps, Lall et al. 2016), and subtended approximately 12×9 degrees of visual angle. The object stimuli consisted of 32 3 s video clips of everyday objects moving (Pitcher et al. 2011), and also subtended approximately 12×9 degrees of visual angle. Each run was 180 s long and contained 3 blocks of each condition. The order

of conditions was pseudorandomized across participants. Each block contained 6 3 s videos with an interstimulus interval (ISI) of 500 ms. There were 4 12 s fixation blocks: one at the beginning, and then after every two stimuli blocks.

For the experimental runs, a blocked design was used in which participants viewed still images of scenes from three different conditions (ie “Different,” “Mirror,” and “Same”). The scene stimuli were identical to those used in a previous adult fMRI study investigating left/right representation across the scene-selective regions (Dilks et al. 2011). Specifically, the scene stimuli consisted of 32 images of outdoor scenes (64 total images including the mirror-reversals). The scene images were a mix of manmade and natural scenes (16 images each). All scene stimuli were non-chiral, such that making a mirror-image reversal of a stimulus image did not result in the exact same stimulus. When presented, each scene image subtended approximately 12×9 degrees of visual angle. Each run was 224 s long and contained 3 blocks of each condition. The order of condition blocks was pseudorandomized within each run and across participants. In the Different condition, participants saw a scene image and then a completely different scene image repeated one after another; in the Mirror condition, participants saw a scene image and then the mirror-reversal of the same scene image repeated one after another; in the Same condition, participants saw one repeated scene image (Fig. 1). Each scene image was displayed for 800 ms with an ISI (ie a gray screen) of 500 ms. There were 10 8 s fixation blocks: one at the beginning, and then after every stimulus block. Participants were not asked to do a formal task but were instructed to pay attention to the images. Importantly, results from adult fMRI studies with a task converge with other pediatric fMRI studies without a task (eg Kamps, Lall et al. 2016; Kamps et al. 2020; Jones et al. 2023; Jung et al. 2024; Kamps et al. 2024), so the results in the current study cannot be attributed to lack of task.

During each scanning session, we first took a high-resolution anatomical scan while the children watched a movie or show of their choice. Then, we collected fMRI data while participants viewed 2 localizer runs and 4 experimental runs.

fMRI scanning

All scanning was performed on a 3 T Siemens Trio scanner in the Facility for Education and Research in Neuroscience at Emory University. The functional images were collected using a 32-channel head matrix coil and a gradient-echo single-shot echoplanar imaging sequence (28 slices, TR = 2 s, TE = 30 ms, voxel size = $1.5 \times 1.5 \times 2.5$ mm, and a 0.5 interslice gap). For all scans, slices were acquired parallel to the anterior commissure and posterior commissure, covering all the occipital and temporal lobes, as well as the lower portion of the parietal lobe. Additionally, whole-brain, high-resolution anatomical images were acquired for each participant for registration and anatomical localization.

Data analysis

Preprocessing was performed using AFNI (Cox 1996) (version 22.0.02). MRI data from the experimental runs were registered to a T1-weighted reference using `align_epi_anat.py` (AFNI) and corrected for head-motion using `3dvolreg` (AFNI). Before motion correction, volumes with large artifacts were corrected via interpolation between the nearest nonaffected volumes to reduce abrupt signal changes caused by head motion (`3dDespike`, AFNI). Spatial smoothing was applied with a Gaussian kernel with a 6 mm full width at half maximum (FWHM) (`3dmerge`, AFNI). High pass temporal filtering was performed using `3dTproject` (AFNI) to remove any frequencies above 0.2 Hz. Head-motion

parameters with respect to the BOLD reference were estimated before any spatial or temporal smoothing. Then, `3dDeconvolve` (AFNI) was used to model the data using a General Linear Model. Specifically, the onset and duration of each condition block (ie Different, Mirror, Same, Fixation) was convolved with a canonical hemodynamic response function. Six estimated motion parameters (three translations: x, y, z; and three rotations: roll, pitch, yaw) were also included in the model as nuisance regressors. Finally, any datapoints with motion displacement greater than 1.5 mm were censored from the regression. Together, this model yielded three beta values (each of the three experimental conditions relative to baseline fixation). Adaptation was thus measured in the following ways. The adaptation effect to scenes was calculated as the difference between the Different and Same conditions. Adaptation to mirror images of scenes (ie left/right sensitivity) was measured as the difference between the Mirror and Same conditions.

To ensure we only analyzed the highest quality data in our sample, we only analyzed runs where the average absolute frame-to-frame displacement was less than 1.5 mm (ie the approximate size of one voxel), and where activation could be detected in V1 ($Z > 2.3$, corrected cluster significance threshold of $P = 0.05$). As previously described, these criteria resulted in the exclusion of two participants for excessive motion across all runs, and one participant for no V1 activity across all runs. Additionally, we excluded three more participants who did not show the expected adaptation effect (ie a greater response to Different than Same condition) in all three of the scene-selective ROIs. (Note, however, the pattern of results remained the same when these children were included in the analysis.) As a result of these procedures, the final group of 18 5-year-olds and 18 8-year-olds were matched on head motion (average absolute frame displacement for all usable runs) ($t_{(34)} = 0.42$, $P = 0.67$, $d = 0.14$), temporal signal to noise ratio (tSNR) in all ROIs (all t 's < 1.91 , all P 's > 0.07 , all d 's < 0.41), and V1 activation (ie the average response in V1 across all conditions, $t_{(34)} = 0.70$, $P = 0.48$, $d = 0.23$) (Fig. 2A–C). The number of usable runs from each age group was also comparable ($t_{(34)} = 1.10$, $P = 0.28$, $d = 0.37$), resulting in an average of 3.3 usable runs per participant.

Given that hand-defining ROIs can be ambiguous, particularly at earlier stages of development, ROIs were facilitated by a GSS method that circumvents these challenges (Fedorenko et al. 2010; Julian et al. 2012). First, for each participant, we identified a search space for each ROI using previously published probabilistic atlases that predict the location in which each ROI is likely to fall given the typical distribution found in a large sample of adults. Search spaces for scene-selective regions (OPA, RSC, and the parahippocampal place area, or PPA—a third scene region hypothesized not to be involved in navigation) were derived from Julian et al. (2012), while search spaces for V1 were derived from Wang et al. (2015). Second, for each search space in each participant, voxels were ranked using the data from the localizer runs, based on parameter estimates for the contrasts of scenes > object videos (for the scene-selective regions), or all conditions > fixation (for V1). Based on these rankings, the top 10% of the voxels were then selected as the subject-specific ROI, as often done in pediatric fMRI studies (Kamps et al. 2020; Kamps et al. 2022; Schettini et al. 2023; Jung et al. 2024). Importantly, by selecting a small number of voxels that exhibited the strongest scene selectivity, we also reduced the possibility that OPA overlapped with nearby retinotopic visual areas (ie LO1, LO2, V3a, V3b, V7; see Silson, Groen et al. 2016). Indeed, upon visualization, we observed that OPA did not overlap with these retinotopic areas. Also, while we

did not enforce spatial continuity when selecting these voxels, most of these voxels formed a contiguous cluster when visualized. Third, responses to each condition (minus fixation) in each ROI and participant were measured using the remaining, independent experimental runs (see above for more information about how the experimental runs were modeled). Percent signal change was calculated as the average response to each condition relative to baseline fixation (averaged over blocks). For each ROI, GSS analysis was conducted separately in each hemisphere. None of the ROIs had a significant hemisphere $\times$ condition interaction, and thus the responses from the ROIs in each hemisphere were subsequently averaged together.

Results

As predicted, we found that, in 5-year-olds, the OPA does not represent left/right information, but rather only does so by age 8. In 8-year-olds, a 3-level (Different, Mirror, Same) repeated-measures ANOVA revealed a significant effect of condition ($F_{(2,34)} = 18.28$, $P < 0.001$, $\eta_p^2 = 0.52$), with a significantly greater response to both the Different and Mirror conditions compared to the Same condition (main effect contrasts, both P 's < 0.001), and no significant difference between the Different and Mirror conditions (main effect contrast, $P = 1$) (Fig. 3). These results demonstrate the expected fMRI adaptation effect (ie Different $>$ Same) in OPA in 8-year-olds, but no adaptation across mirror images of scenes (ie Mirror $>$ Same), revealing that OPA in 8-year-olds represents mirror images of scenes as two different images. By contrast, in 5-year-olds, a 3-level (Different, Mirror, Same) repeated-measures ANOVA also revealed a significant effect of condition ($F_{(2,34)} = 12.93$, $P < 0.001$, $\eta_p^2 = 0.43$), but with a significantly greater response to the Different condition compared to both the Mirror and Same conditions (main effect contrasts, both P 's < 0.002), and no significant difference between the Mirror and Same conditions (main effect contrast, $P = 0.39$) (Fig. 3). These results demonstrate the expected fMRI adaptation effect in OPA in 5-year-olds, as well as adaptation across mirror images of scenes, revealing that OPA in 5-year-olds represents mirror-reversed images of scenes similar to the exact same scene image. Furthermore, 17 out of 18 (and conservatively, 15 out of 18) 5-year-olds showed this effect (Fig. 4). Critically, directly comparing OPA in 5- and 8-year-olds then, a 2 (Age: 5-year-olds, 8-year-olds) $\times$ 3 (Condition: Different, Mirror, Same) mixed-model ANOVA revealed a significant age by condition interaction ($F_{(2,68)} = 5.65$, $P < 0.005$, $\eta_p^2 = 0.14$), with a significant difference in left/right sensitivity across age (interaction contrast, Mirror condition minus Same condition, $P < 0.05$), but not a significant difference in adaptation to scenes (interaction contrast, Different condition minus Same condition, $P = 0.21$). Taken together then, OPA represents left/right information late in development—by 8 years of age, and not at all at 5 years of age.

As predicted, we also found the RSC already represents left/right information in 5-year-olds, like in 8-year-olds. In 8-year-olds, a 3-level (Different, Mirror, Same) repeated-measures ANOVA revealed a significant effect of condition ($F_{(2,34)} = 22.55$, $P < 0.001$, $\eta_p^2 = 0.57$), with a significantly greater response to both the Different and Mirror conditions compared to the Same condition (main effect contrasts, both P 's < 0.001), as well as the Different condition compared to the Mirror condition (main effect contrast, $P < 0.01$) (Fig. 3). These results demonstrate the expected fMRI adaptation effect in RSC in 8-year-olds, but no adaptation across mirror images of scenes, revealing that RSC in 8-year-olds represents mirror images of scenes as two different images. Similarly, in

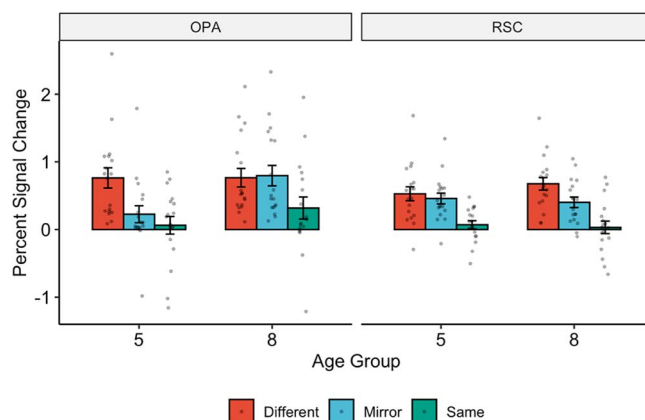


Fig. 3. OPA and RSC responses to the Different, Mirror, and Same conditions relative to fixation by age. In OPA, 5- and 8-year-olds respond differently to these conditions; despite successful adaptation in both groups (Different $>$ Same), only 8-year-olds are sensitive to left/right information (Mirror $>$ Same), and not 5-year-olds (Mirror $\approx$ Same). By contrast, in RSC, 5- and 8-year-olds respond similarly to these conditions; both age groups show successful adaptation (Different $>$ Same), as well as sensitivity to left/right information (Mirror $>$ Same). These response patterns, when compared across age and ROI, reveal that OPA and RSC develop differentially, insofar as RSC represents left/right information earlier in development (ie by 5 years of age) but OPA represents this information much later (ie by 8 years of age). Error bars depict the standard error of the mean and black dots represent individual subject data.

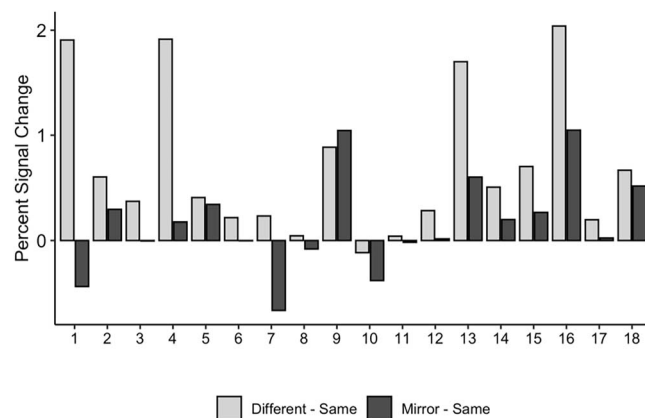


Fig. 4. The average response of OPA for the different minus same conditions (labeled “Different-Same”) and mirror minus same conditions (labeled “Mirror-Same”) for individual 5-year-old participants.

5-year-olds, a 3-level (Different, Mirror, Same) repeated-measures ANOVA revealed a significant effect of condition ($F_{(2,34)} = 20.54$, $P < 0.001$, $\eta_p^2 = 0.55$), with a significantly greater response to both the Different condition and Mirror conditions compared to the Same condition (main effect contrasts, both P 's < 0.001), and no significant difference between the Different condition compared to the Mirror condition (main effect contrast, $P = 0.39$) (Fig. 3). These results demonstrate the expected fMRI adaptation effect in RSC in 5-year-olds, but no adaptation across mirror images of scenes, revealing that RSC in 5-year-olds also represents mirror images of scenes as two different images. Critically, directly comparing RSC in 5- and 8-year-olds then, a 2 (Age: 5-year-olds, 8-year-olds) $\times$ 3 (Condition: Different, Mirror, Same) mixed-model ANOVA did not reveal a significant age by condition interaction ($F_{(2,68)} = 1.68$, $P = 0.20$, $\eta_p^2 = 0.05$), revealing that RSC represents

left/right information early in development—by at least 5 years of age.

Although these findings suggest that left/right information is represented by 8 years of age in OPA, and by 5 years of age in RSC, does this information really develop earlier in RSC than OPA? To answer this question, we directly compared responses in OPA and RSC across our participants. A 2 (Age: 5-year-olds, 8-year-olds) $\times$ 3 (Condition: Different, Mirror, Same) $\times$ 2 (ROI: OPA, RSC) mixed-model ANOVA revealed a significant Age $\times$ ROI $\times$ Condition interaction ($F_{(2,68)} = 9.75$, $P < 0.002$, $\eta_p^2 = 0.22$), with significant difference not only in left/right sensitivity between the 5- and 8-year-olds OPA (interaction contrast, Mirror minus Same condition, $P < 0.05$) but, critically, also between the 5-year-olds OPA and RSC (interaction contrast, Mirror minus Same condition, $P < 0.01$). There was no significant difference in adaptation to scenes across age and ROI (Different minus Same condition, all P 's > 0.11). Additionally, to ensure these results were not driven by potential outliers, specifically in 5-year-olds OPA's response to the Mirror condition, we removed two participants whose average response to the Mirror condition was greater or less than two standard deviations from the group mean. However, the removal of either outlier, or both, still yielded a significant Age $\times$ ROI $\times$ Condition interaction (all P 's < 0.002), with the same significant interaction contrasts found in the full sample analysis. These results reveal that OPA represents left/right information later in development than RSC and support our hypothesis OPA and RSC develop along different timelines, with OPA indeed developing later than RSC.

But could this late development of left/right information in OPA simply reflect a lack of *scene selectivity* (ie responding significantly more to images of scenes than objects) in OPA at age 5? This possibility is unlikely, given that prior work has revealed that OPA is scene selective by age 5 (Kamps et al. 2020; Kamps et al. 2022; Jung et al. 2024). However, to directly test whether OPA is scene selective in the 5-year-old participants in the current study, we used the GSS method (see Methods) to compare responses in OPA to scenes and objects from the localizer runs, using half the runs to localize and the other half to test. Indeed, in 5-year-olds, the OPA responded significantly more to scenes than to objects ($t_{(12)} = 3.19$, $P < 0.01$, $d = 0.92$), as well as in 8-year-olds ($t_{(14)} = 6.17$, $P < 0.001$, $d = 1.65$). For completeness, we also investigated the scene selectivity of RSC. Not surprisingly, RSC in 5-year-olds also demonstrated scene selectivity ($t_{(12)} = 8.46$, $P < 0.001$, $d = 2.44$), as well as in 8-year-olds ($t_{(14)} = 9.09$, $P < 0.001$, $d = 2.43$). Thus, the late development of left/right information in OPA is not due to a lack of scene selectivity.

Similarly, could the observed responses in either OPA or RSC in 5- and 8-year-olds simply reflect information inherited from low-level vision? Unlike both scene-selective regions, early visual cortex (V1; see Methods) did not even show the adaptation effect (ie no significant difference between Different and Same in either age group; both P 's > 0.21), suggesting the responses in OPA and RSC are not reflecting information simply inherited from V1 and are instead specific to OPA and RSC. Note that we did not expect V1 to show the adaptation effect because we did not ask participants to fixate, similar to a recent adult fMRI study (Yoon et al. 2025).

Finally, we also investigated how the PPA represents left/right information in 5- and 8-year-olds—a scene-selective region that does not represent left/right information in adults and thus is not involved in any kind of navigation (Dilks et al. 2011; Yoon et al. 2025). As expected, a 2 (Age: 5-year-olds, 8-year-olds)

$\times$ 3 (Condition: Different, Mirror, Same) repeated-measures ANOVA did not reveal a significant Age $\times$ Condition interaction ($F_{(2,68)} = 0.01$, $P = 0.99$, $\eta_p^2 = 0.0004$), but did reveal a main effect of Condition ($F_{(2,68)} = 23.16$, $P < 0.001$, $\eta_p^2 = 0.41$). Specifically, in both 5- and 8-year-olds, PPA responded significantly more to the Different compared to either the Mirror or Same conditions (main effect contrasts, all P 's < 0.001), with no significant difference between the Mirror and Same conditions (main effect contrasts, both P 's > 0.17). Taken together, these results suggest that, like in adults, the PPA in 5- and 8-year-old children does not represent left/right information in scenes. Moreover, this result is not due to lack of scene selectivity in either the 5- or 8-year-olds (5: $t_{(12)} = 7.47$, $P < 0.001$, $d = 2.16$; 8: $t_{(14)} = 10.10$, $P < 0.001$, $d = 2.69$).

Discussion

The current study directly compared the development of visually-guided navigation (including OPA) and map-based navigation (including RSC), specifically asking whether left/right information—one kind of information necessary for both visually-guided navigation and map-based navigation—develops later in OPA than in RSC. Consistent with our hypothesis, we found that OPA develops later (by age 8), while RSC develops earlier (at least by age 5), insofar as RSC represents left/right information in scenes earlier in development than OPA. Furthermore, neither PPA in 5- nor 8-year-olds—like adults—represents left/right information, which is consistent with the hypothesis that PPA is not involved in navigation (Dilks et al. 2022). Importantly, the different pattern of responses in the scene-selective regions across development is not due to differences in head motion, data quality, attention, or scene selectivity.

Our finding of differential development of the cortical regions each supporting map-based navigation and visually-guided navigation dovetails with behavioral findings suggesting these systems develop along different timelines. For instance, a large body of behavioral literature reveals that children's map-based navigation abilities, particularly their use of landmarks and allocentric cues, are at least present by age 5, if not earlier (Acredolo 1977; Landau 1984; Huttenlocher et al. 1994; Newcombe et al. 1998; Newcombe and Huttenlocher 2000; Lee et al. 2006; Balcomb et al. 2011; Ribordy et al. 2013; Ribordy et al. 2013; Negen et al. 2018; Newcombe 2019; Fernandez-Baizan et al. 2021; Van Hoogmoed et al. 2022). By contrast, several other behavioral studies find that children's visually-guided navigation abilities develop by around age 8 (Julian et al. 2019; Kamps et al. 2023). Additionally, obstacle avoidance and efficient path-taking (two key features of visually-guided navigation) are also slow to develop, again not reaching adult-like levels of performance until around 8 (Pryde et al. 1997; Berard and Vallis 2006; Michel et al. 2010; Choi et al. 2016).

However, pure observation tells us that children move around their environment well before they are 8 years of age. So, how can we reconcile this “early” walking (or even crawling) with the hypothesis that OPA develops late? One possibility is that early visually-guided navigation abilities also rely on OPA and that, despite development extending well into childhood (as found here), the foundations of this system are nevertheless intact early, and sufficient to support these early navigational behaviors. Thus, although left/right (and first-person perspective motion, as previously described; Kamps et al. 2020; Jung et al. 2024) information is represented late in OPA, it is possible that other types of navigationally relevant information, such as egocentric

distance (Persichetti and Dilks 2016), is still represented earlier. A second possibility, given that OPA does not represent at least two kinds of navigationally relevant information at all at age 5 (left/right and first-person perspective motion; Kamps et al. 2020; Jung et al. 2024) is that OPA develops abruptly around age 8 and another system entirely supports early visually-guided navigation behavior. Intriguingly, our finding that RSC represents left/right information earlier than OPA, raises the possibility that RSC may be supporting visually-guided navigation behavior before OPA develops. Future work is needed to directly test whether OPA develops discontinuously, as well as what neural system may support visually-guided navigation in children younger than 8.

Finally, the finding that OPA and RSC develop along different developmental trajectories supports the hypothesis that OPA and RSC support distinct functions within the broader domain of adult human navigation. While previous fMRI evidence in adults had suggested that OPA and RSC support independent navigation systems, the converging data presented here—that is, the finding that OPA and RSC develop along different timelines—provides stronger evidence for the two-navigation-systems hypothesis, since one system cannot develop along two different timelines. Note, however, that the present study did not explicitly test (eg using an explicit task) the development of visually-guided and map-based navigation (as supported by the OPA and RSC, respectively), but instead relied on the development of left/right information as a proxy for the development of functions, like many adult fMRI studies that use information processing as a proxy for function (eg Wolbers and Büchel 2005; Iaria et al. 2007; Auger et al. 2012; Vass and Epstein 2013; Marchette et al. 2014; Auger et al. 2015; Marchette et al. 2015; Kamps, Lall et al. 2016; Kamps, Julian et al. 2016; Persichetti and Dilks 2016; Bonner and Epstein 2017; Dillon et al. 2018; Henriksson et al. 2019; Persichetti and Dilks 2019; Pitcher et al. 2019; Park and Park 2020; Suzuki et al. 2021; Jones et al. 2023; Steel et al. 2023; Kamps et al. 2024; Kang and Park 2024). Thus, future research should address the two-navigation-systems hypothesis more directly by investigating the development of visually-guided navigation, as supported by OPA, and map-based navigation, as supported by RSC, using an explicit task.

In conclusion, here we found that left/right information in scenes is represented late—by 8 years of age—in OPA, but represented much earlier—by at least 5 years of age—in RSC. These findings suggest that, perhaps surprisingly, OPA (supporting visually-guided navigation) develops later than RSC (supporting map-based navigation).

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Author contributions

Rebecca J. Rennert (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing) and Daniel D. Dilks (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing—review & editing).

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