



Early development of navigationally relevant location information in the retrosplenial complex

Yaelan Jung^a and Daniel D. Dilks^{a,1}

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Representing the locations of places so that we can use them as landmarks is critical to our ability to navigate through large-scale spaces—a process referred to as “map-based navigation.” While many neuroimaging studies in adults have revealed that this ability involves the retrosplenial complex (RSC)—a scene-selective region in the medial parietal cortex—nothing is known about how this cortical system develops. So, does it develop only late in childhood, as generally assumed from some behavioral studies? Or is it, perhaps counterintuitively, present in the first few years of life? To test this question, using functional magnetic resonance imaging (fMRI) multivoxel pattern analysis and a virtual town paradigm, we investigated the representation of location information in the RSC of 5-y-olds. We found that i) the RSC in 5-y-olds already represents the locations of particular buildings in the town (e.g., the ice cream store by the mountain versus by the lake), but not their category membership (e.g., ice cream store, regardless of location), and ii) this neural representation is correlated with their performance on a location task. Using multidimensional scaling, we also found that the neural representation of the buildings in RSC reflects the actual layout of the virtual town. Finally, the parahippocampal place area—a scene-selective region implicated in scene categorization, not map-based navigation—did not represent location information, but instead category information, the exact opposite of RSC. Taken together, these findings reveal the early development of navigationally relevant location information in RSC and thus the early origins of map-based navigation.

scene processing | navigation | fMRI | landmark | parahippocampal place area

Decades of neuroimaging research in adults have suggested that a scene-selective region—the retrosplenial complex (RSC)—is involved in “map-based navigation” (i.e., our ability to find our way from a specific place to some distant, out-of-sight place). Indeed, RSC has been shown to represent several kinds of information necessary for map-based navigation, including the locations of particular places so that we can use them as landmarks to orient ourselves while navigating large-scale environments (1–13). However, despite this now considerable understanding about the neural basis of map-based navigation in adulthood, a fundamental and yet unanswered question remains: How does map-based navigation (including RSC) develop? Does navigationally relevant information processing in RSC emerge much later in childhood, perhaps taking a decade or more of experience, as suggested by some behavioral studies (14–18)? Or is it detectable much earlier in childhood, emerging within the first few years of life even, challenging the pervasive view?

Here, we directly investigated this question using fMRI multivoxel pattern analysis (MVPA) and a virtual town paradigm in 5-y-old children ($N = 16$) and examined whether their RSC represents location information of landmarks, which is necessary for map-based navigation. Specifically, we scanned 5-y-old children after they learned about buildings in a virtual town called “Tiny Town.” The town consisted of a triangular layout with three distinct corners: a “Mountain corner,” a “Lake corner,” and a “Trees corner,” each containing two buildings, for a total of six buildings (Fig. 1*A*). Importantly, any two buildings located in the same corner were from *different* categories (i.e., ice cream store, playground, fire station), allowing the location information of the buildings to be dissociated from the general category membership of the buildings (Fig. 1*B*). In the scanner, children viewed static images of these buildings one at a time and made location judgments about them (e.g., whether the building was located in the Mountain corner? see *Methods* for details). Note that this paradigm is an adapted (child-friendly) version of the paradigm used in an adult fMRI MVPA study revealing that RSC represents location information, but not category information (10). Thus, while we are confident that this paradigm selectively

Significance

Using landmarks to navigate is a crucial human ability, yet its developmental origins remain unclear. Does it take over a decade to develop—as many assume—or might it come online much earlier, challenging this pervasive assumption? Here, using fMRI in young children, we show that by age five, children's retrosplenial complex—a brain region critical for large-scale navigation—already represents the locations of landmarks within a large-scale virtual environment. This finding suggests that while large-scale navigation abilities certainly continue to develop throughout childhood, the underlying neural system is established remarkably early.

Author affiliations: ^aDepartment of Psychology, Emory University, Atlanta, GA 30322

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¹To whom correspondence may be addressed. Email: dilks@emory.edu.

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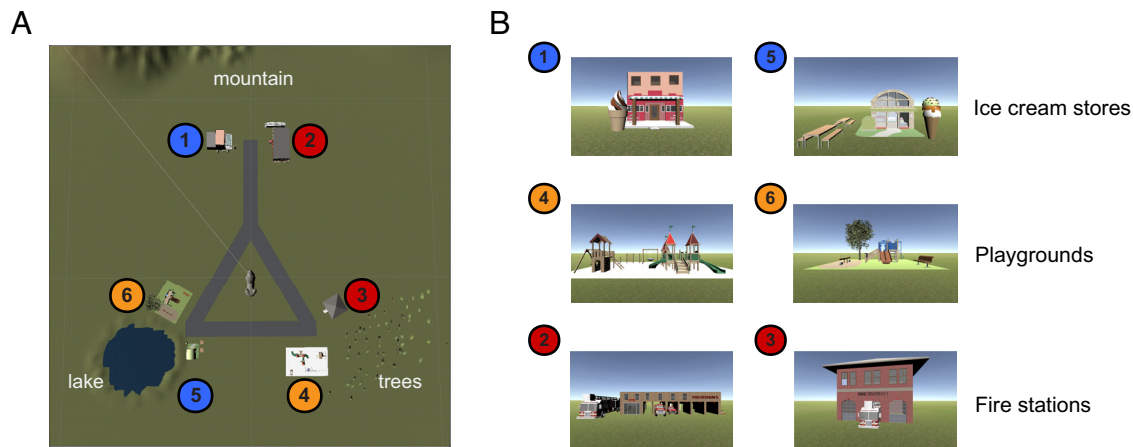


Fig. 1. (A) A birds-eye view of the virtual town (note that participants never saw the town from this perspective nor were the corners denoted). The overlaid numbers in the circles correspond to the location of the buildings in the virtual town (clockwise, starting from the *Upper Left* corner), and (B) the colors of the circles correspond to the category of the building.

engages RSC, we are now asking whether (or not) RSC represents location information as early as 5 y of age.

If location information in RSC emerges early in childhood, within the first few years of life even, then the RSC in 5-y-olds must be able to discriminate between two places from the same category (e.g., ice cream store) based on their distinct locations (e.g., the ice cream store in the mountain corner versus the ice cream store in the lake corner). In other words, the RSC in 5-y-olds, like adults (10), will represent location information, but not category information. By contrast, we predict the exact opposite in the parahippocampal place area (PPA)—a scene-selective region shown to represent category information, but not location information, in adults (10)—in 5-y-olds, consistent with the recent hypothesis that PPA is also early developing (19).

Results

RSC in 5-Y-Olds Represents Location Information. To test whether the RSC in 5-y-olds represents location information, but not category information, we correlated the activity patterns in RSC (and PPA) to idealized matrices for both location and category (Fig. 2 *A* and *B*). Consistent with our prediction that the RSC in 5-y-olds represents location information, but not category information, we found that location coding was indeed significantly greater than category coding (Fig. 2*C*), $t(15) = 3.30$, $P = 0.005$, $d = 1.15$, mirroring the findings previously shown in adults (10). By contrast, we found the complete opposite pattern of response in PPA, with category coding significantly greater than location coding (Fig. 2*C*), $t(15) = 2.341$, $P = 0.033$, $d = 0.82$, again mirroring the finding previously shown in adults (10). Finally, testing this putative double dissociation between location and category coding in RSC and PPA in 5-y-olds, we conducted a 2 (Regions of Interest, ROI: RSC, PPA) $\times$ 2 (Information: Location, Category) repeated-measures ANOVA and found a significant interaction between ROI and Information, $F(1,15) = 16.33$, $P = 0.001$, $\eta_p^2 = 0.523$, with RSC representing location, not category, information and PPA representing category, not location, information, yet again mirroring the finding previously shown in adults (10). Additionally, we found that the location coding in RSC was significantly greater than zero, $t(15) = 2.151$, $P = 0.024$, $d = 0.54$, while the category coding was *not*, $t(15) = -2.447$, $P = 0.986$, $d = -0.61$. By contrast, PPA again showed the exact opposite, with the category coding in PPA significantly greater than zero, $t(15) = 1.948$, $P = 0.035$, $d = 0.49$, while the location coding was *not*, $t(15) = -1.306$, $P = 0.894$, $d = -0.33$. Taken together, these results strongly suggest that in

children as young as 5 y of age, RSC is already supporting some form of map-based navigation, while PPA is already supporting some form of scene categorization.

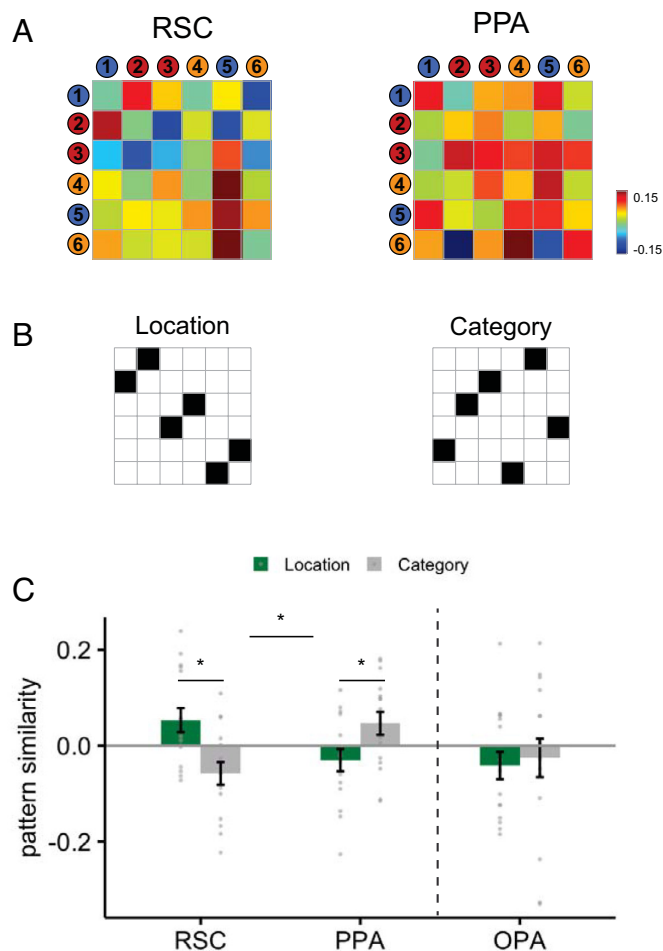


Fig. 2. (A) 6X6 representational similarity matrices, showing similarity between odd (column) and even (row) runs, for RSC (*Left*) and PPA (*Right*), averaged across participants. The colored circles refer to each building from the virtual town (Fig. 1), and the colors of the circles correspond to their category as in Fig. 1 (blue = ice cream store, red = fire station, orange = playground). (B) The idealized model matrices for each condition of interest (i.e., Location and Category). (C) The correlation coefficients between the representation similarity matrix and the model matrix averaged across participants (referred to here as Pattern Similarity). Error bars are ± 1 SEM. The asterisk indicates significant differences between conditions.

In addition to RSC and PPA, we also asked whether another scene-selective region—the occipital place area (OPA) (20)—contains either category or location information of buildings. We predicted that OPA would not represent either kind of information, since OPA is implicated in “visually guided navigation” (i.e., moving about the immediately visible environment, avoiding boundaries and obstacles), not map-based navigation or scene categorization as tested here, and moreover has been shown to represent neither category nor location information in adults (10). As predicted, we found that OPA does not contain information about the location or category of buildings. Specifically, there was no significant difference between location and category in OPA (Fig. 2C), $t(15) = 0.308$, $P = 0.763$, $d = 0.12$, and both location coding and category coding were *not* significantly greater than zero ($t(15) = -1.449$, $P = 0.916$, $d = -0.36$, for location coding; $t(15) = -0.626$, $P = 0.730$, $d = -0.15$, for category coding). Finally, to test for the complete functional dissociation among the three scene-selective regions, we conducted a 3 (ROI: RSC, PPA, OPA) $\times$ 2 (Information: Location, Category) repeated-measures ANOVA. We found a significant interaction between ROI and Information, $F(2,30) = 6.881$, $P = 0.003$, $\eta_p^2 = 0.314$, with RSC representing location information but not category information, PPA representing category but not location information, and OPA representing neither location nor category, again mirroring the previous adult finding (10).

Finally, another prominent brain region that may encode location information is the hippocampus. A mounting body of evidence suggests that the hippocampus plays a crucial role in map-based navigation (e.g., refs. 21–23), indicating that it may represent location information of buildings. Interestingly, some studies have also shown that the hippocampus is critical for visual categorization (24, 25), particularly in distinguishing places (26), suggesting that it may also encode category of buildings. Consistent with these predictions, we found that in 5-y-olds, the hippocampus represents both location information ($t(15) = 2.424$, $P = 0.014$; Fig. 3) and category information about buildings ($t(15) = 2.015$, $P = 0.029$; Fig. 3). This finding suggests that by age five, the hippocampus is already involved in map-based navigation—an idea previously supported only by behavioral evidence (27, 28).

But might it be the case that the representation of location information in RSC and the representation of category information in PPA are merely driven by similarities in the low-level visual features of the building images? To test this possibility, we used an idealized similarity matrix based on the pixel-level features of

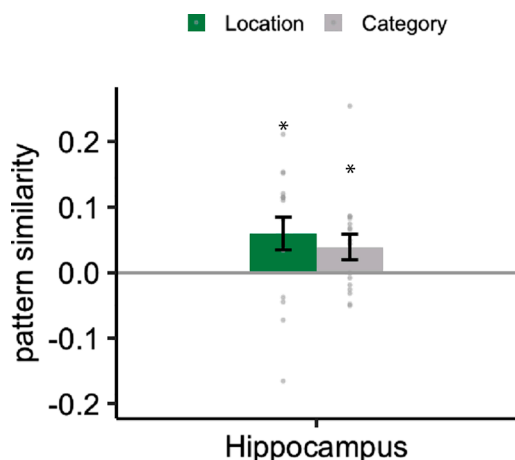


Fig. 3. The correlation coefficients between the representation similarity matrix from the hippocampus and the idealized model matrix (Location, Category from Fig. 1B) averaged across participants (referred to here as Pattern Similarity). Error bars are ± 1 SEM. The asterisk indicates significant differences from zero.

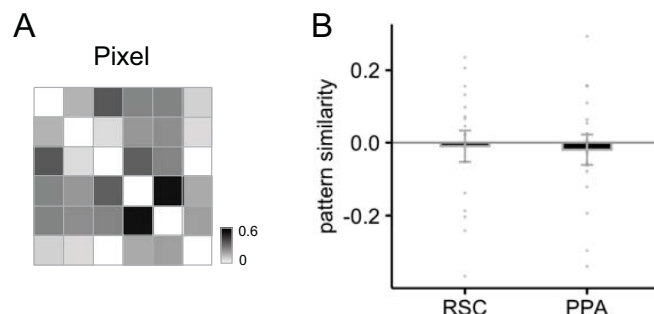


Fig. 4. (A) The idealized model matrix based on pixel-level similarity between the buildings. Note that the diagonal axis of the matrix, which indicates the identical buildings, was set to zero so that the model only reflects the similarity *between* the buildings. (B) The correlation coefficients between the representation similarity matrix and the pixel-level similarity matrix averaged across participants (referred to here as Pattern Similarity). Error bars are ± 1 SEM.

the building images (Fig. 4A) and then compared the pixel-based model to the activity patterns in RSC and PPA (Fig. 4B). We found that pixel-based coding was not significantly different between RSC and PPA, $t(15) = 0.219$, $P = 0.830$, $d = 0.06$. Furthermore, in both regions, pixel-based coding was *not* significantly greater from zero (RSC: $t(15) = 0.227$, $P = 0.824$, $d = 0.057$; PPA: $t(15) = -0.468$, $P = 0.646$, $d = -0.117$). Thus, these findings suggest that the observed location effect in RSC (and category effect in PPA) cannot be explained by low-level visual features alone.

Representation of Location Information in RSC Is Behaviorally Relevant. Next, we asked whether the representation of location information in the RSC of 5-y-olds is actually related to their performance on a location task. In other words, is the representation of location information in the RSC of 5-y-olds behaviorally relevant? The answer is yes. Indeed, there was a significant correlation between the location coding in RSC and the location task performance from the scanning session, $r(14) = 0.695$, $P = 0.003$, revealing that children who performed better showed stronger location coding in the RSC (Fig. 5A). Moreover, this correlation remained significant even when we controlled for participants' age, $r(14) = 0.737$, $P = 0.002$. Note that these correlations should still be interpreted with caution given our relatively small sample size. By contrast, this pattern was not found in PPA; there was no significant correlation between the location coding in PPA and the location task performance, $r(14) = 0.134$, $P = 0.621$ (Fig. 5B). Finally, we also confirmed that there was no significant correlation between the category coding in either RSC or PPA and the location task performance, $r(14) = -0.328$, $P = 0.214$; $r(14) = 0.07$, $P = 0.790$, respectively (Fig. 5C and D).

RSC in 5-Y-Olds Also Represents the Locations of Buildings Relative to Each Other. Thus far, we have shown that the RSC in 5-y-olds represents location information and that this neural representation is behaviorally relevant, suggesting the early development of map-based navigation. But does the coding of location information simply reflect an association between any particular building and its location (e.g., the ice cream store and the mountain go together), or does it actually reflect *map-like* information, including the locations of buildings relative to each other—as hypothesized here if map-based navigation is indeed early developing? To directly test this question, we assessed how the representation of the buildings in each ROI resembles the actual configuration of the buildings in the town. To do so, we used multidimensional scaling (MDS) to reconstruct how buildings were represented in each ROI. Specifically, we averaged correlation

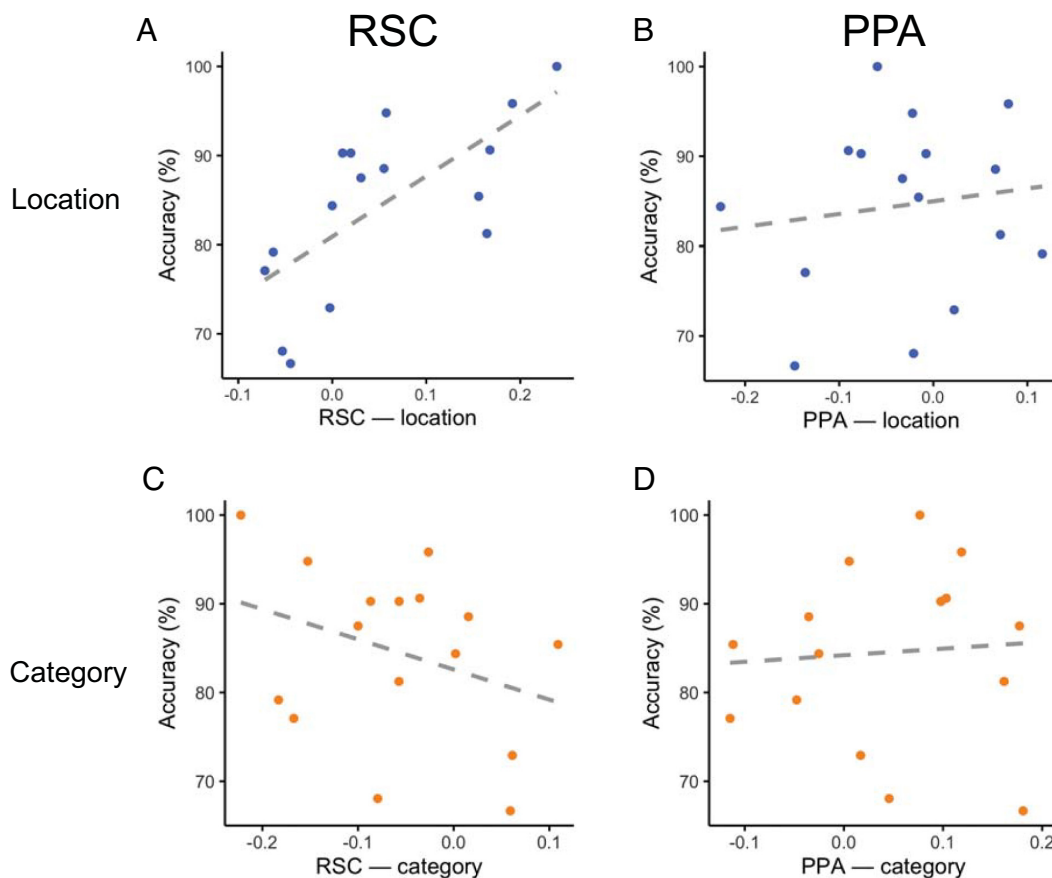


Fig. 5. The relationship between the location test performance (from the scanner) and the coding of location information in RSC (A) and PPA (B). There was a significant correlation between the location task performance and location coding in RSC. Note that there were no significant correlations between the task performance and category coding either in RSC (C) or in PPA (D).

matrices across participants for each ROI and applied MDS to produce a two-dimensional map showing how the buildings were represented relative to one another. (*Methods* for details). As a ground truth, we also created a correlation matrix based on the Euclidean distances between the buildings, which was then converted into a two-dimensional map using MDS to reflect the actual spatial layout. We used Procrustes analysis to quantify the distortion of each reconstructed map compared to the ground truth. We found that in RSC, the neural representation of buildings closely mirrored the actual map of the town, with buildings located in the same corner represented close to each other, $D = 0.415$, $P = 0.018$ (Fig. 6B). And, upon further inspection, interestingly, we found that this reconstructed map in RSC reflects children's behavior; the two buildings from Trees Corner, where children made more errors in the location task (Building #3 & #4 in Fig. 6A), were also the most distorted in their reconstructed positions within the neural "map" in RSC (Fig. 6B). By contrast, in PPA, the representation of the buildings did not reflect the actual layout of the town, $D = 0.543$, $P = 0.82$, but instead grouped the buildings by their category membership (Fig. 6C). Taken together, these results reveal that the RSC in 5-y-olds not only represents the locations of particular places but also how they are located relative to each other, while the PPA in 5-y-olds represents places by their category.

Discussion

In the current study, we investigated whether location information in RSC emerges early in childhood (by at least 5 y of age) using fMRI MVPA and a virtual town paradigm. We found that the

RSC in 5-y-olds, like adults, represents the locations of particular buildings in the town, and moreover, that this neural representation is correlated with the 5-y-olds' abilities to judge the locations of those same buildings. Using MDS, we also found that the

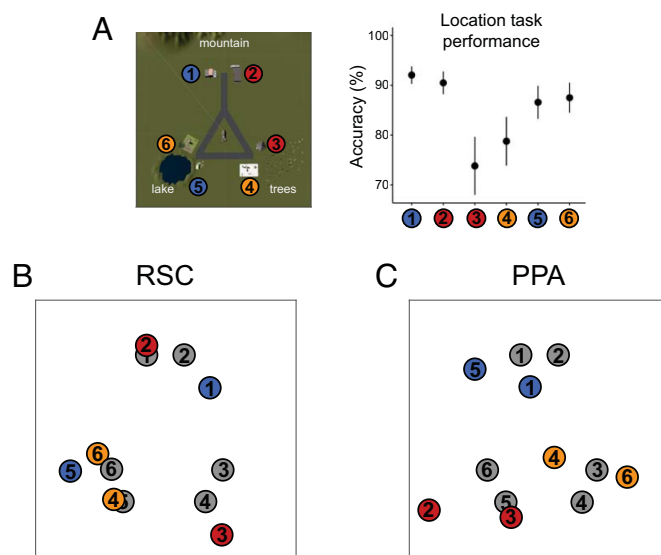


Fig. 6. (A) The actual layout of the buildings in the virtual town (Left) and the location task performance (from the scanning session) for each building (Right). (B and C) The results of the MDS analysis in RSC (B) and PPA (C). The gray circles are in the positions of the buildings in the virtual town, while the positions of the colored circles are the result of the MDS analysis. Note that color here indicates the category of the building (blue = ice cream store; red = fire station; orange = playground).

representation of the buildings in RSC reflects the actual map of the town. Finally, this representation of location information was specific to the RSC in 5-y-olds; the PPA in the same 5-y-olds, like adults, in fact represents category information, not location information, consistent with its hypothesized role in scene categorization (5) and hypothesized early development (19). Importantly, RSC in 5-y-olds, again like adults, did not represent category information. Taken together, these findings provide evidence of the early emergence of location information in RSC and hence the early emergence of map-based navigation.

Our finding that RSC in 5-y-olds represents location information, supporting the early development of map-based navigation, however, may seem at odds with the large body of behavioral literature, which has emphasized the protracted development in map-based navigation and related abilities (14, 16, 18, 29–33). For example, children's ability to encode and utilize landmarks improves with age between 6 to 10 y (16, 29, 30, 33) and is still not adultlike even at 10 y of age (18, 29, 31, 33). Relatedly, children's route learning and route integration skills also undergo substantial changes during childhood and mature around the age of 12 y (14, 18, 31). However, our findings do not actually contradict this literature as many of these studies have focused on when children's navigation abilities mature, not when they first emerge. Indeed, the findings from the current study are well aligned with some of the earlier behavioral work showing that young children have the foundational skills required for map-based navigation, even if these abilities are still developing (34, but also see ref. 35). For instance, with ample opportunities to explore the environment, children aged 5 to 7 y can encode fine-grained distance information between the buildings within a large-scale space (34), and children at age five can hold an allocentric spatial representation of objects within a large-scale space [e.g., recognizing the location of objects when their body position changed; (36)]. Our finding demonstrates that the neural system involved in such abilities in adulthood (8, 10, 37), RSC, emerges early in childhood and is involved with early navigation behaviors.

But how does the map-based navigation system (including RSC) change with development? Based on extensive behavioral research (e.g., refs. 14, 18, 31, 35, and 36), we propose that spatial representations may undergo two important developmental shifts: They become 1) broader in scale and 2) increasingly allocentric in nature. First, maturation of memory capacity and encoding efficiency in development (38, 39) is likely to allow children to represent larger and more complex environments. Indeed, in our own pilot work for this study, we observed that 5-y-old children had difficulty learning the locations of all eight buildings, whereas older children and adults did not, suggesting that the scope of children's cognitive maps expands with age. Second, survey-like, global knowledge of environments—such as the ability to take shortcuts or plan efficient routes (14, 18, 31, 36)—emerges later in childhood, around 10 y of age or older. Since these skills rely on allocentric representations, we predict that with age, spatial representations in the map-based navigation system may transition from predominantly egocentric to increasing allocentric coding.

Previous work in adults has demonstrated a strong relationship between neural representation in RSC and navigation behavior (3, 7, 40). For example, in good (proficient) navigators, the RSC exhibits a more robust representation of permanent (landmark-like) objects compared to less proficient navigators, suggesting that RSC plays a crucial role in map-based navigation (40). Additionally, good navigators show greater functional connectivity between the RSC and the hippocampus, indicating that connection between these brain regions may be critical for efficient map-based navigation behaviors (41). Our study builds on these findings by

demonstrating that, even in children, performance on a location memory task is closely linked to neural representation in RSC. Specifically, we show that children who perform better on the location task exhibit stronger neural representation of spatial location (Fig. 4A), and the reconstructed representations of buildings reflect their navigation behavior (Fig. 5A and B). These findings suggest that, like in adults, RSC plays a critical role in children's map-based navigation behaviors. This finding, however, still raises interesting questions about how the neural representation in RSC may become more refined over development, potentially paralleling the maturation of children's map-based navigation abilities—an exciting avenue for future research.

The double dissociation between RSC and PPA in 5-y-olds suggests that both RSC and PPA are dedicated to specific functions within the domain of scene processing by at least the age of 5, if not earlier. Although it has been shown that scene selectivity can be detected in young children (or infants) in RSC and PPA (42–45), it was not known whether the scene-selective regions in young children are dedicated to specific functions, as shown in adults (5). Our data fill this knowledge gap and show that these scene regions are indeed dedicated to specific (adult-like) functions at least by age five, with RSC involved in map-based navigation and PPA involved in scene categorization. Note, however, that it is still possible that RSC and PPA develop along different timelines, with scene categorization supported by PPA emerging before map-based navigation supported by RSC (for example, see ref. 19). Future research is required to determine the potential differential development then between RSC and PPA.

Unlike RSC and PPA, which exhibit their distinct adult-like function by 5 y of age, previous research has shown that the other scene-selective region, the OPA—a brain region dedicated to visually guided navigation—develops surprisingly late, with information necessary for visually guided navigation (i.e., first-person perspective motion and sensitivity to visual information about walking; (43, 44) only present around 8 y of age, but not 5 y of age (19). Thus, albeit seemingly counterintuitive, our finding suggests that the neural system involved in navigating large-scale environments (including RSC) may develop earlier than the neural system involved in navigating through a local environment (including OPA). These findings challenge a prevalent idea that moving around a local environment promotes, and is perhaps necessary (46), for spatial learning in large-scale spaces (47–49).

Taken together, the current study demonstrates that by at least 5 y of age, RSC represents location information within a large-scale virtual town. This finding suggests that despite the protracted development of map-based navigational skills (14, 16, 18, 29, 31, 50), the neural system supporting navigation in large-scale spaces develops remarkably early in childhood.

Methods

Participants. Twenty-one children (mean age of 68.9 mo; 63 to 78 mo, nine females; see *SI Appendix, Fig. S1* for the distribution of age in our sample and the effect of age in our findings) participated in this study. One child (70 mo old, female) did not complete the fMRI session due to fear of the scanner. Two children (ages of 69 mo old and 70 mo old, one male and one female, respectively) failed to learn about the locations in the town and were not included in the fMRI session. Of the 18 children who participated in the fMRI session, two children (ages of 65 mo old and 71 mo old, both male) were excluded due to excessive motion. Thus, a total of 16 child participants were included in the data analysis. All participants were recruited through the Emory Child Study Center from metro Atlanta area. Consent was given for all children by their parent or guardian. All participants had normal or corrected to normal vision, and no history of neurological or psychiatric conditions. All procedures of the experiment

were approved by the Emory University Institutional Review Board (IRB reference number: 69592).

Design and Procedure. The experiment consisted of two sessions: a behavioral session, where children learned about the buildings and their locations in a virtual town (Tiny town), and an fMRI session, where children were scanned while performing a location task about the buildings from the virtual town.

We used the Unity software (Unity Technologies) and OpenMaze (51) to create a virtual town with a triangular layout comprising three corners—Mountain corner, Lake corner, and Tree corner. Each corner had two buildings, and the buildings in each corner did not share category membership. The six buildings in the town belonged to one of three categories (two buildings per category): fire station, playground, and ice cream shop (Fig. 1B). This virtual town paradigm is an adapted, child-friendly version of the paradigm used in ref. 10, where they examined location and category coding in RSC and PPA in adults. Using the exact Persichetti & Dilks paradigm in child pilot testing, we found that 5-y-olds, unlike adults, could not reliably learn the locations of the *eight* buildings (the town was a square with two building in each corner). Therefore, we needed to modify the virtual town to have a triangular layout with six buildings (two in each corner). Due to this change though, we then could not investigate how the RSC in 5-y-olds represents facing direction information (another kind of information necessary for map-based navigation and tested in ref. 10, as location information and facing direction information were now confounded in our adapted paradigm. Specifically, buildings that shared the same location (e.g., the ice cream shop and the fire station at Mountain Corner) also shared the same facing direction (e.g., facing north within the town). Nevertheless, we obviously were able to investigate location information, information still necessary for map-based navigation.

The behavioral session had three phases: introduction, learning, and testing. During the introduction phase, the experimenter showed the child participant the lion statue at the center of the town, followed by the mountain, lake, and tree corners, in that exact order. The child also learned how to “navigate” in the virtual town using four keys (forward, backward, left, right). During the learning phase, participants perform the learning task in three blocks. They were asked to navigate to a specific building (e.g., go to the ice cream store in the mountain corner) from a distant, starting point. In the first block, the starting point of the trial was always in front of the lion statue. In the next two blocks, participants started from random spots in the town and had to find their way to the target building.

After the learning phase, two tests were conducted to ensure that participants knew the particular buildings from the virtual town and their locations. First, participants performed the “identity” test, where they were presented with either a building from the town or a novel building from the same category (e.g., a different fire station). The experimenter verbally asked, “Did you see this building in the town?”, and the child responded “yes” or “no.” Participants also performed a “location” test, where they were shown a front view of a building (Fig. 1B) along with a probe of one of the three corners (e.g., Mountain corner). The experimenter verbally asked, “Was this building in the Mountain corner?”, and the child responded Yes or No. For both tests, each trial ended when the child responded, and they were encouraged to make a guess when they were unsure about the answer. The order of the location and the identity tests were counterbalanced across the participants. On average, participants successfully learned both the locations and identities of the buildings in the virtual town, achieving 91.2% accuracy on the location task and 99.2% on the identity task. Participants with an accuracy of 75% or less on the location test or the identity test were not invited to the fMRI session; two children were excluded due to low performance on the location test (*Participants*).

During the fMRI session, participants completed the experimental runs and the localizer runs. In the Experimental runs, we used an event-related design, where each trial featured an image of a building. Participants completed 2 to 4 runs (average: 3.63, SD = 0.95), each consisting of 24 experimental trials. In the experimental trials, a building image was presented for 2 s, followed by a location probe (e.g., mountain) for an additional 3.75 s, with a 0.25-s intertrial interval. While the location probe was displayed, participants indicated whether the building was in the given location via button press (yes or no). Notably, this location task during the fMRI session was similar to the prescan location task (see above), but there were two key differences. First, participants responded via button press rather than verbally. Second, they were given a limited time (5.75 s from the onset of the image) to provide their response. During this fMRI location

task, participants showed an average accuracy of 84.54% (SD = 9.73). This task performance was then used to investigate whether neural representations in children’s RSC were behaviorally relevant (Figs. 5 and 6A).

In addition to the experimental trials, each run included 6 fixation trials, in which a gray fixation point was displayed for 6 s at the center of the screen. Each run began and ended with a fixation trial, with each run lasting 180 s.

The localizer runs, used to identify scene-selective regions in each participant, employed a blocked design in which participants viewed videos of objects and scenes (52). Each participant completed two runs of the localizer scan, with each run lasting 180 s and consisting of three blocks per stimulus category (scenes and objects). Each block contained six 3-s-long videos from the same category with a 500 ms interstimulus interval, for a total of 21 s per block. The order of the blocks was counterbalanced across runs, and four 12-s fixation blocks were included: one at the beginning, two interleaved between blocks, and one at the end of each run (see *SI Appendix, Fig. S2* for more information).

fMRI Scanning. All scanning was performed on a 3T Siemens Prisma 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 for the localizer scans (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), and for the resting state scan (60 slices, TR = 2 s, TE = 30 ms, voxel size = $2 \times 2 \times 2$ mm). For all scans, slices were oriented approximately to the anterior commissure and the posterior commissure (AC–PC). Additionally, whole-brain, high-resolution anatomical images were acquired for each participant for registration and anatomical localization.

fMRI Data Analysis. Preprocessing was performed using AFNI (Analysis of Functional Neuroimages) (53) (version 20.3.02). MRI data from the experiment runs were registered to a T1w reference using `align_epi_anat.py` (AFNI) and corrected for head-motion using `3dvolreg` (AFNI). Before motion correction, volumes with movement >2 mm were corrected via interpolation between the nearest nonaffected volumes to reduce abrupt signal changes caused by head motion (`3dDespike`, AFNI). Spatial smoothing was applied to the data from the Localizer runs with a Gaussian kernel with 6 mm full width at half maximum using `3dmerge` in AFNI, and no spatial smoothing was applied to the data from the Experimental runs. Temporal smoothing was performed to remove frequencies above 0.2 Hz. Head-motion parameters with respect to the BOLD reference were estimated before any spatial or temporal smoothing.

To ensure the data quality, we excluded runs where the average absolute frame-to-frame displacement (FD) exceeded 1.5 mm (the approximate size of one voxel), and where activation could not be detected in V1 ($Z < 2.3$). Participants with fewer than two runs meeting these criteria were excluded, as at least two runs are required to independently localize and then test responses in each ROI (see below for details). As previously reported, this resulted in the exclusion of two children (ages 65 mo and 71 mo, both male). The final sample of 5-y-olds had an average framewise displacement (FD) of 0.72 mm (SD = 0.21; *SI Appendix, Fig. S3A*), which is comparable to that reported in previous studies with a similar age range (43, 44). Importantly, the amount of head motion was *not* significantly correlated with task performance or RSC location decoding (*SI Appendix, Fig. S3*).

After preprocessing, both the localizer and the experimental data were processed using a general linear model (GLM; `3dDeconvolve` in AFNI). The GLM for the localizer runs included the regressors for the two video conditions (scenes and objects), and the GLM for the experimental runs included the regressors for each of the six buildings and another for the fixation trials. Both of the GLMs also included six nuisance regressors of motion artifacts, and frames in which head motion exceeded 1.5 mm were censored (including those that had been despiked).

We defined the ROIs, except the hippocampus, using the Group-Constrained Subject-Specific method, which was conducted with the following steps: First, for each participant, we identified a search space for each ROI, across both hemispheres, using probabilistic atlases that predict the typical location of each scene-selective region in a large adult sample. Second, for each search space, voxels were ranked using data from the localizer runs based on parameter estimates for the scenes > objects contrast. The top 100 voxels were selected as the subject-specific ROI and used to analyze the data from the experimental runs. For the hippocampus, we used FreeSurfer segmentation (54).

Next, to test whether an ROI contained information about the location or category of the buildings, we calculated the correlation between activity patterns associated with each of the six buildings. To do this, we first split the experimental runs into even and odd runs and normalized the data by subtracting the grand mean of all runs in each voxel within each ROI for each half of the dataset. We then assessed the similarity of activity patterns for the six buildings by computing Pearson correlations between all possible building pairs across the two data splits (odd and even runs). This resulted in a 6×6 correlation matrix for each participant (see Fig. 2A for the average correlation matrix in RSC and PPA across participants).

To test for coding of location and category information, we created idealized matrices for both location and category (Fig. 2B) and compared them to the neural correlation matrices using Pearson correlation. These correlation coefficients were computed for each participant and each ROI, then transformed into Fisher Z-scores for statistical analysis. We also repeated this procedure using idealized matrices for pixel-level information and Euclidean distance. For the pixel-based matrix, we measured the similarity between each pair of the six buildings by calculating the Pearson correlation between all pixels in the building pair (Fig. 4A).

Finally, to examine whether each ROI contained information about the overall layout of the town, we reconstructed the virtual town based on activity patterns in each ROI using MDS. Specifically, for each ROI, we first averaged the 6×6 correlation matrices across participants and normalized the values in the matrix between 0 and 1, converted the normalized matrix into a dissimilarity matrix by subtracting each value from 1, and finally applied MDS to the dissimilarity matrix. This produced a two-dimensional map that visualizes

how buildings were represented in each ROI relative to one another (Fig. 6B and C). To compare these neural maps to the actual layout of the town, we repeated this procedure using the Euclidean distance between the buildings, creating a two-dimensional map representing the actual layout of the town (i.e., ground truth). We then conducted Procrustes analysis to assess the distortion of each ROI's reconstructed map compared to the actual layout. Distortion of the reconstructed map was defined as the sum of squared errors between the reconstructed points and true locations after optimal linear alignment. To determine statistical significance, we performed a permutation test with 100,000 iterations. In each iteration, we randomly shuffled the correlation matrix and applied MDS to the shuffled matrix, generating a chance distribution for the level of distortion. This allowed us to assess whether the observed distortions were significantly lower than chance.

Data, Materials, and Software Availability. The datasets generated during the current study will be available at <https://osf.io/btk5c> (55).

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