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Contextual features in the developing hippocampus: A representational similarity analysis

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Abstract

Functional divisions of labor in support of memory have been reported along the anterior–posterior axis of the hippocampus. However, little is known about how the developing hippocampus represents associative memories along this axis. The present research employed representational similarity analysis to ask whether developmental differences exist in the extent to which the anterior versus the posterior hippocampus represent features of the context and associative memories. Functional magnetic resonance imaging data were collected during the retrieval phase of an associative recognition task from 8-year-olds, 10-year-olds, and adults ($N = 58$). Participants were asked to retrieve pairs of items, which were presented either in the same location as during encoding or in a flipped location. In the anterior hippocampus and only for adults, pattern similarity between the two studied pair conditions was greater than pattern similarity between studied pairs presented in the same location and novel pairs. In contrast, this difference was not significant in the posterior hippocampus. Older, but not younger, children showed a similar, albeit attenuated, similarity pattern to that of adults, but measures of patterns similarity predicted associative recognition across ages. In addition, exploratory analyses showed that similarity patterns in the adult posterior, but not anterior, hippocampus tracked the order of the runs. Overall, the results suggest functional and developmental dissociations in processing different contextual features, with the anterior hippocampus responding to salient and rapid-changing features and the posterior hippocampus responding to slower-changing features of the context.

KEYWORDS
contextual binding theory, episodic memory, hippocampal subregions, memory development, representational similarity analysis

1 | INTRODUCTION

Episodic memory refers to the ability to remember events with their unique spatial–temporal features (Tulving, 2002). This ability improves substantially during the course of childhood and adolescence (Ghetti & Fandakova, 2020; Ngo, Lin, et al., 2019; Yim et al., 2013), due in part to changes in hippocampal structure and function (Lee et al., 2014; Riggins et al., 2015; Selmeczy et al., 2019) along its anterior–posterior axis (DeMaster et al., 2014; Lee et al., 2020). An open question remains about how unique processes implemented in the anterior versus posterior hippocampus support memory development. Previous research has underscored that developmental changes along the anterior–posterior axis may reflect the extent to which memory representations can be successfully cued and reinstated from variable and partial cues

(i.e., retrieval flexibility; Demaster et al., 2016). However, recent studies have additionally suggested that differences between anterior and posterior regions may have to do with the scales of event representation ranging from coarse to fine in the anterior versus posterior region, respectively (Brunec et al., 2018; Evensmoen et al., 2013). Accordingly, we examined whether data from a previous study investigating the effects of retrieval flexibility (Demaster et al., 2016) may reveal patterns of activation consistent with differences in representational scales/resolution. In the next paragraphs, we first revisit the rationale and results of the initial study and provide a conceptual and methodological justification for the current investigation using the same dataset.

Several studies have shown that the development of memory in childhood depends, at least in part, from gains in children's ability to reinstate episodic memories using a variety of cues (Ngo, Horner, et al., 2019; Paz-Alonso, 2009; Smith & Vela, 2001; Yim et al., 2013). Indeed, younger children find it more difficult to recognize or recall past events when elements of the context are missing or changed (Deák & Wiseheart, 2015; Demaster et al., 2016), suggesting stronger dependence on contextual reinstatement (Paz-Alonso, 2009; Smith & Vela, 2001). Previous research suggesting that the anterior hippocampus is particularly important for flexible episodic retrieval (Giovanello et al., 2009; Zeidman & Maguire, 2016) motivated the initial hypothesis that developmental dissociations would be observed: If the anterior hippocampus supports retrieval flexibility, then age-related differences in hippocampal contribution would be expected to be strongest in the anterior region.

To test this hypothesis, Demaster et al. (2016) had 8-year-olds, 10-year-olds, and young adults complete an associative recognition task in which participants were asked to recognize pairs of semantically unrelated objects. During the recognition phase, the objects of the studied pairs either were presented in their exact same location as during encoding (i.e., same-location) or exchanged locations with one another (i.e., flipped-location). Participants were asked to discriminate these pairs from new pairs, which either included studied objects rearranged into new pairs or pairs of completely new objects. Univariate fMRI analyses revealed that 8-year-old children were more likely to recruit the hippocampus when presented with same-location studied pairs compared to flipped-location studied pairs. In contrast, adults were more likely to recruit the hippocampus for flipped-location studied pairs. Interestingly, 10-year-old children showed similar hippocampal recruitment regardless of type of studied pairs, a pattern of activation that was intermediate to that of younger children and adults. Although these results suggested a developmental increase in hippocampal contribution to flexible retrieval, they did not reveal strong differences between the anterior and posterior hippocampus.

One possible explanation for the failure to observe these differences may be the use of univariate methods. Univariate methods compare mean activation levels across voxels, and thus they cannot reveal whether there are differences in the patterns and/or resolution of representation in the voxel-level activation across conditions and/or regions. Several studies have underscored that the examination of activation patterns afforded by multivariate methods including representational similarity analysis (RSA) (Kriegeskorte, 2008) may provide more sensitive assessments of functional contributions of the hippocampus (Diedrichsen & Kriegeskorte, 2017; Dimsdale-Zucker & Ranganath, 2018). Accordingly, we used RSA to investigate developmental differences in the pattern similarity associated with our experimental conditions (e.g., same-location pairs, flipped-location pairs, new pairs) within the anterior versus posterior hippocampus.

If the anterior hippocampus contributes more to flexible retrieval, in line with the hypothesis motivating the initial research, then it should respond more similarly to the identity of remembered pairs regardless of the location of individual objects belonging to the pairs. Thus, we should expect stronger similarity scores in this region between correctly recognized same-location and flipped-location studied pairs (reflecting common representational pattern indicative of intact pair memory across these conditions) compared to similarity scores between correctly recognized same-location studied pairs and completely novel pairs or forgotten same-location studied pairs. This pattern was expected to be attenuated in children. In contrast, if posterior hippocampal activation primarily reflects the degree of rigid reinstatement of the studied event, its similarity scores should be generally lower than those between same- and flipped-location studied pairs in the anterior hippocampus.

However, newer evidence of gradient granularity along the anterior–posterior axis of the hippocampus (Brunec et al., 2018; Evensmoen et al., 2013) supports a perhaps counterintuitive prediction. For the sake of clarity, we use the term *granularity* to refer to network density at the cellular level and we use the term *resolution* to describe density and/or scale of informational detail, which are represented in activation patterns (Evensmoen et al., 2015). Coarser granularity in the anterior hippocampus can support representations with lower resolution, which capture primarily the most salient and/or goal-relevant associative features of the event. In contrast, finer granularity in the posterior hippocampus can support representations with higher resolution including not only goal-relevant details, but also fine contextual features that may not be salient or goal-relevant. As an analogy, memory representations in the anterior hippocampus would be akin to the frames that may result from filming a night sky with an ordinary camera; this low-resolution camera could only capture the shiniest stars against a black background; small changes in the luminance of these stars across different frames would result in detectable changes against the dark background. In contrast, in the posterior hippocampus higher resolution of memory representations would be more akin to the images resulting from filming the same scene with a high-resolution camera, such as the Hubble telescope; the telescope gives very detailed frames with nuanced differences in luminance and detail. The same change in luminance of a particular star across frames would not be as noticeable as it would be in the image produced by a low-resolution camera, because most of the details would be similar across frames.

Overall, then, patterns of similarity in the anterior hippocampus across types of trials may be more distinguishable than those in the posterior hippocampus where levels of similarity may be high across trials because they might capture common elements across experiences. In other words, lower resolution memory representations in the anterior hippocampus should be associated with lower autocorrelation and higher cross-voxel correlations compared to high resolution memory-representations in the posterior hippocampus. Consistent with this idea, Brunec et al. (2018) found lower cross-voxel correlation

in the posterior compared to the anterior hippocampus regardless of whether participants were engaged in a navigation task or were resting. In the only developmental study examining this distinction, Callaghan et al. (2021) found age-related decreases in cross-voxel correlations in the activity of the posterior hippocampus during a memory task consistent with the developmental improvements in the granularity of memory representations in this sub-region. This resolution gradient account is consistent with contextual binding theory (Yonelinas et al., 2019) proposing that hippocampal activation may capture all aspects of context including slow-changing features that are not directly relevant or manipulated in the experimental setting, but belong instead to the background. From this perspective, anterior hippocampal regions may support the retrieval of associative information based on currently salient task goals (e.g., which two items have been presented together), whereas more posterior hippocampal regions may support a more detailed representation of contextual features that may be common across items (e.g., the same monitor and screen background, or environmental details such as being in the same room). Therefore, as participants undergo the experiment, the hippocampus may not only bind the manipulated and intended features of the experimental items, but also these additional environmental features that are common across events. Consistent with contextual binding theory, Reagh and Ranganath (2018) found that the posterior hippocampus supports the ability to distinguish events based on their slow-changing overall temporal context (i.e., event boundaries). Based on this literature, the posterior hippocampus may be predicted to exhibit higher levels of representational similarity scores than the anterior hippocampus overall, due to the strong overlap of slowly changing contextual features across all trials. If this is the case, we could also expect these pattern similarity scores to differ as a function of temporal context. We thus explored whether pattern similarity observed for trials closer in time (i.e., similarity between first and second run of the experiment) were greater than those for trials further in time (i.e., similarity between first and third run of the experiment) in the posterior hippocampus. This pattern is expected to be absent in the anterior hippocampus based on the hypothesis that this region responds mainly to salient features (i.e., fast-changing elements). These hypothesized effects are expected to be attenuated in children.

2 | METHODS

2.1 | Participants

Participants included 58 individuals across three age groups: 14 8-year-olds (age: $M = 8.42$, $SD = 0.52$; 8 females), 21 10-year-olds (age: $M = 10.48$, $SD = 0.60$; 9 females), and 23 young adults (age: $M = 19.80$, $SD = 1.80$; 11 females). Participants were allowed to stop their participation at any point. Only participants with at least two full runs were included in the final sample. An additional 12 children and 2 adults were excluded because they did not complete at least two runs of the retrieval task, which we considered critical for conducting RSA analysis. Finally, one additional child and two adults were excluded from the analyses because their score on the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) was 1 *SD* below the mean. All participants were right-handed and had no documented history of a neurological or psychiatric disorder. Among participants retained for this report, 10 children completed only 2 runs, 17 children and 9 adults completed 3 runs, and 8 children and 14 adults completed all 4 runs.

Participants' race was distributed as White ($N = 36$), Asian ($N = 5$), African American ($N = 1$), other ($N = 2$), mixed race ($N = 6$), and not reported ($N = 8$). Twelve participants reported being Hispanic or Latino. Family reported income was distributed as follows: 8% between $15,000 and $25,000, 15% between $25,000 and $40,000, 9% between $40,000 and $60,000, 38% between $60,000 and $90,000, and 30% more than $90.000. Participant demographics conformed to those of the local community.

2.2 | Tasks and procedures

We used the dataset utilized in Demaster et al. (2016). Adult participants or children's parents/guardians signed an informed consent and completed an MRI safety screening form. Then, all participants practiced remaining still in a mock scanner while they listened to the scanner noises and looked at a screen. This practice was followed by completion of the Vocabulary and Matrix Reasoning subtests from the WASI (Wechsler, 1999) which yields a full-scale IQ score. Finally, participants completed the scanned memory task.

2.3 | Memory task

Before starting the scanned version of the task, participants completed practice trials for both encoding and retrieval phases. During the encoding practice, participants viewed pairs of vertically shown colorful pictures of everyday objects on the screen (as represented in Figure 1a), and were asked to determine which of the two items was heavier. Vertical presentation prevented left item selection bias which was identified during piloting. Based on pilot data, relative-weight judgments were performed accurately across age groups during the allotted trial time. Once the encoding practice was completed, participants completed a retrieval practice in which they were presented with 14 trials, and were instructed to determine which pair of items had been previously presented together (i.e., same pairs) regardless of whether they were presented in the same location. Participants were informed that some of the pairs would be rearranged to include presented items from different pairs (see Figure 1b). Participants indicated their responses by pressing a "together" or "not together" button on a response pad.

After practice, participants completed the memory task involving four encoding-retrieval scanning runs. Each encoding run (Figure 1a) included 84 trials of unique pair of objects, each presented on the screen for 1500 ms, interleaved by a fixation screen (i.e., a white cross in the middle of a black screen) with a jitter ranging between 1500 and 7500 ms. Each retrieval run (Figure 1b) included 96 trials. These trials included: 1) 21 unique old pairs presented in the same location as during encoding

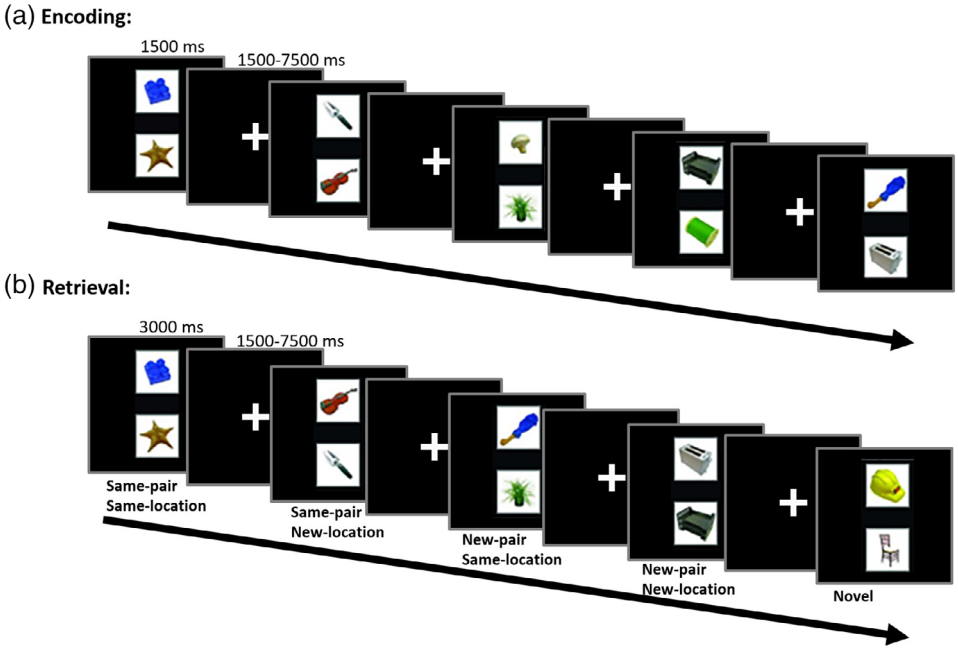

FIGURE 1 Experimental paradigm. The experimental paradigm included four successive encoding and retrieval runs. During encoding (a), participants were asked to select the heavier object within each pair of stimuli presented on screen for 1500 ms interleaved by a jittered a fixation screen between 1500 and 7500 ms. During retrieval (b), participants were asked to report whether pairs of objects had been previously presented together regardless of whether they were presented in the same location. Each pair presented on screen for 3000 ms interleaved by a jittered fixation between 1500 and 7500 ms. Five different trial types were presented in a random order across each retrieval run. Here, trial types are shown in a progression from most similar to novel

(Same-pair-Same-location); 2) 21 unique old pairs presented in new, flipped locations compared to encoding (Same-pair-New-location); 3) 21 unique rearranged pairs consisting of one item drawn from each of two different encoding pairs presented in their same location as during encoding (New-pair-Same-location); 4) 21 rearranged pairs presented in new, flipped locations compared to encoding (New-pair-New-location); and 5) 12 completely novel pairs (novel). Images of individual objects were presented once during encoding as parts of a pair and once during the retrieval only in one of the four non-novel trial types. Stimuli were presented on the screen for 3000 ms, interleaved by the fixation screen jittered between 1500 and 7500 ms. Unique items were used within each run. Accordingly, 768 unique objects were presented in 4 runs (672 items were presented twice, once during encoding and once during retrieval, and 48 items were presented once during retrievals in the novel trials). The instructions were the same as those provided during the practice phases.

Participants were provided with a 5-min break after the second retrieval run (approximately halfway through the scanning session) to reduce fatigue. During the break, participants were removed from the scanner and engaged in a light stretching exercise outside the scanning room.

2.3.1 | Behavioral data analysis

We reported hit rates which were defined as the rate of recognized pairs among studied pairs, separately for each type of studied pairs (i.e., Same-pair-Same-location and Same-pair-New-location). We also reported false alarms which were defined as the rate of false recognition of non-studied pairs separately for rearranged pairs (i.e., new pair same location and new pair new location) and completely novel pairs. To investigate behavioral performance from the perspective of signal detection theory, we computed d-prime index separately for Same-pair-Same-location and Same-pair-New-location conditions (i.e., z-transformed hit rates of Same-pair-Same-location and Same-pair-New-location conditions *minus* z-transformed false alarm rates of completely novel trials) (Macmillan & Creelman, 2005). We also calculated memory discrimination indices for the most challenging discrimination (i.e., hit rate on Same-pair-Same-location trials *minus* false alarm rate on New-pair-Same-location trials) and the least challenging discrimination (i.e., hit rate on Same-pair-Same-location trials *minus* completely novel trials) to investigate the relation between behavioral performance and similarity scores between activation patterns of corresponding trial types.

2.3.2 | fMRI data acquisition and analysis

A Siemens 3 T Skyra scanner was used for image acquisition. A gradient echo EPI sequence (TR = 1500 ms, TE = 25 ms, no inter-slice gap, flip angle = 90°, and FOV = 204) was used to acquire the functional data. Each volume included 37 axial slices with 3-mm thickness. A high-resolution MPRAGE anatomical scan was acquired at the end of the session. A short break was provided between each scan.

We used SPM12 for pre-processing. Functional EPI images were corrected for slice acquisition timing and were realigned to the first image. High-resolution structural images were co-registered to the functional images and spatially normalized to the template in SPM. All functional images were also normalized with these normalization parameters, and smoothed with a 6-mm full-width half-maximum isotropic Gaussian kernel. ArtRepair was used to detect and replace interpolated volumes with volumes showing more than 1-mm motion or 2% signal change. Overall, 4.78% of the data were interpolated.

Structurally defined region of interest (ROI) analyses was performed using the same regional boundaries explained in Demaster et al. (2016), with the exceptions that the body and the tail regions were combined in a posterior hippocampal region and the anterior and posterior regions were separated by one voxel margin in coronal plane removed from the anterior portion of the body region to fully eliminate overlap. We used the smoothed version of the functional images. Voxel-wise patterns of activation were extracted from each ROI from the beta images computed at the condition level for each participant for each run. Run-wise beta images for each condition give more stable similarity patterns compared to single trial beta images (Allefeld & Haynes, 2014). Moreover, we adopted the run-wise approach because we were interested in comparing pattern similarities in hippocampal subregions as a function of retrieval processes as opposed to as a function of type of individual memoranda. We deemed this choice appropriate because pattern similarity resulting from low-level or semantic features of individual studied items, which were changing trial by trial, was not the focus on this research and was not expected to vary as a function of type of retrieval trial (Dimsdale-Zucker & Ranganath, 2018). As a result, pattern similarity scores were expected to reflect associative processes pertaining to retaining the relation among studied pairs and retaining elements of the broader context. Returning to our night sky scene metaphor, we reasoned that our use of beta images averaged across conditions would be optimal to capture processes that are involved in recalling which stars were consistently visible when other, task irrelevant, elements (i.e., frame by frame changes), such as an airplane or a comet, crossed the sky. An individual item analytical approach would be more reasonable if we had been more interested in similarities among stars, airplanes or comets. Pattern similarity scores were extracted using a customized version of the RSA toolbox (Nili et al., 2014). We calculated correlations (Pearson's *r*) between the patterns of activity within each retrieval condition separately for each ROI, participant, and run. Z-transformed values of PS scores were used for all statistical tests (Dimsdale-Zucker & Ranganath, 2018). Mixed analysis of variance (ANOVA) and post hoc *t* tests were conducted in R using rstatix and ez packages (R Core Team, 2020). We also conducted a linear mixed effect model for the effect of runs using IBM SPSS, and *F* test results for the fixed effects are reported.

3 | RESULTS

3.1 | Behavioral results

To confirm the age differences in behavioral performance reported in Demaster et al. (2016) within the current sample, we conducted a 3 (age group: 8-year-olds, 10-year-olds, and adults) × 5 (trial type: Same-pair-Same-location, Same-pair-New-location, New-pair-Same-location, New-pair-New-location, and novel) mixed ANOVA, with the latter variable varied within participants. We are reporting this analysis again because, for the current study purposes, our sample includes fewer participants due to eliminating participants who contributed only one retrieval run.

Results showed a main effect of trial type, $F_{4,220} = 89.96$, $p < .001$, $\eta_p^2 = 0.62$, such that the average hit rate for Same-pair-Same-location trials was significantly higher ($M = .62$, $SD = .13$) than the average hit rate for Same-pair-New-location trials ($M = 0.59$, $SD = 0.14$), $t(57) = 4.06$, $p < .001$, 95% CI = [0.02, 0.06]. In addition, Same-pair-New-location hit rate was in turn significantly higher than the false alarm rate for New-pair-Same-location trials ($M = 0.45$, $SD = 0.12$), $t(57) = 6.75$, $p < .001$, 95% CI = [0.01, 0.17]. Thus, participants were overall better at recognizing old pairs presented in the same location compared to those with flipped location, and they were overall more likely to recognize studied pairs compared to mistakenly recognize rearranged pairs. The main effect of trial type was further qualified by an interaction with age, $F_{8,220} = 2.73$, $p = .007$, $\eta_p^2 = 0.09$, such that 8-year-olds had a significantly reduced hit rate for Same-pair-New-location trials ($M = 0.49$, $SD = 0.12$) compared to Same-pair-Same-location trials ($M = 0.57$, $SD = 0.13$), $t(13) = 5.96$, $p < .001$, 95% CI = [0.12, 0.06]; in contrast, 10-year-olds and adults showed no significant differences between their hit rates (Same-pair-Same-location vs. Same-pair-New-location) (*p*s > .356). Moreover 8-year-olds showed no significant differences between hit rate for Same-pair-New-location and false alarm rate for New-pair-Same-location ($p = .346$), while both 10-year-olds and adults could make this distinction, *p*s ≤ .002 (see Table 1).

We also conducted a 3 (age group: 8-year-olds, 10-year-olds, and adults) × 2 (condition: Same-pair-Same-location, Same-pair-New-location) mixed ANOVA on d-prime scores. Results showed a main effect of condition, $F_{1,55} = 22.80$, $p < .001$, $\eta_p^2 = 0.29$, such that the average d-prime score for Same-pair-Same-location condition ($M = 1.16$, $SD = 0.85$) was significantly higher than the average d-prime score for Same-pair-New-location condition ($M = 1.06$, $SD = 0.84$), $t(57) = 3.94$, $p < .001$, 95% CI = [0.05, 0.16]. This effect was also qualified by a significant interaction with age $F_{1,55} = 5.51$, $p = .007$, $\eta_p^2 = 0.17$ such that a significant reduction of d-prime index in Same-pair-New-location condition was observed in both 8-year-olds ($M = 0.72$, $SD = 0.27$) and 10-year-olds ($M = 0.96$, $SD = 0.90$) compared to Same-pair-Same-location condition, ($M = 0.95$, $SD = 0.33$), $t(13) = 5.74$, $p < .001$, 95% CI = [0.15, 0.32], and ($M = 1.08$, $SD = 0.93$), $t(20) = 3.02$, $p = .006$, 95% CI = [0.04, 0.22], respectively; this was not the case for adults ($p = .734$) (see Table 1). This result suggests that only children, regardless of age, were sensitive to the location violation (i.e., it is harder for them to identify old pairs when they were presented in flipped location compared to the encoding).

3.2 | fMRI results

The univariate analyses of these data are reported elsewhere (Demaster et al., 2016). For the current report, we conducted RSA

analyses and compared Z-transformed similarity scores for correctly recognized studied items (Same-pair-Same-location and Same-pair-New-location, the arguably most similar trials) to the most different trials (i.e., Same-pair-Same-location vs. correctly identified novel pairs) and their inaccurate counterparts (correctly recognized Same-pair-Same-location vs. forgotten Same-pair-Same-location pairs which will be denoted as Missed-Same-pair-Same-location).

Thus, we conducted a 3 (age group: 8-year-olds, 10-year-olds, and adults) × 2 (ROI: anterior hippocampus and posterior hippocampus) × 3 (condition: Same-pair-Same-location—Same-pair-New-location, Same-pair-Same-location—Novel, Same-pair-Same-location—Missed-Same-pair-Same-location) mixed ANOVA on pattern similarity scores. Average of the pattern similarities in different age groups as a function of ROI and condition are depicted in Figure 2. We found a significant effect of trial type, $F_{2,110} = 6.84$, $p = .002$, $\eta_p^2 = 0.11$, such that average pattern similarity of Same-pair-Same-location—Same-pair-New-location ($M = 0.55$, $SD = 0.25$) was significantly higher than that of Same-pair-Same-location—Novel ($M = 0.49$, $SD = 0.30$), $t(115) = 2.21$, $p = .029$, 95% CI = [0.01, 0.11], which in turn was significantly higher than that of Same-pair-Same-location—Missed-Same-pair-Same-location ($M = 0.41$, $SD = 0.23$), $t(115) = 2.82$, $p = .006$, 95% CI = [0.03, 0.14]. These effects were qualified by a significant interaction effect between condition and ROI, $F_{2,110} = 6.00$, $p = .003$, $\eta_p^2 = 0.10$. In the anterior hippocampus, similarity scores for Same-pair-Same-location—Same-pair-New-location ($M = 0.54$, $SD = 0.25$) were significantly higher than those of both Same-pair-Same-location—Novel ($M = 0.46$, $SD = 0.31$), $t(57) = 2.27$, $p = .027$, 95% CI = [0.01, 0.17] and Same-pair-Same-location—Missed-Same-pair-Same-location ($M = 0.44$, $SD = 0.24$), $t(57) = 3.15$, $p = .003$, 95% CI = [0.04, 0.17], with no significant difference between Same-pair-Same-location—Novel and Same-pair-Same-location—Missed-Same-pair-Same-location ($p = .693$). In contrast, in the posterior hippocampus, similarity scores for Same-pair-Same-location—Same-pair-New-location ($M = 0.55$, $SD = 0.25$) and Same-pair-New-location—Novel ($M = 0.53$, $SD = 0.28$) were not significantly different from each other ($p = .478$), but each was significantly higher than those for Same-pair-Same-location—Missed-Same-pair-Same-location ($M = 0.38$, $SD = 0.22$), $t(57) = 4.94$, $p < .001$, 95% CI = [0.10, 0.24] and $t(57) = 3.82$, $p < .001$, 95% CI = [0.07, 0.23], respectively. We also note that in the posterior hippocampus, both 10-year-olds and adults had significantly higher similarity score in both Same-pair-Same-location—Same-pair-New-location and Same-pair-New-location—Novel compared to Same-pair-Same-location—Missed-Same-pair-Same-location (*ps* < .002), but not 8-year-olds ($p > .799$).

TABLE 1 Means and *SD*s (in parentheses) for hit rates, false alarm rates, and d-prime scores as a function of age

	8-year-old	10-year-old	Adults
SPSL hit rate	0.57 (0.13)	0.63 (0.15)	0.65 (0.11)
SPNL hit rate	0.49 (0.12)	0.58 (0.15)	0.65 (0.12)
NPSL false alarm	0.47 (0.13)	0.48 (0.10)	0.42 (0.12)
NPNL false alarm	0.41 (0.13)	0.45 (0.14)	0.40 (0.14)
Novel false alarm	0.24 (0.11)	0.28 (0.20)	0.22 (0.25)
SPSL d-prime	0.95 (0.33)	1.08 (0.93)	1.37 (0.97)
SPNL d-prime	0.72 (0.27)	0.96 (0.90)	1.35 (0.94)

Abbreviations: Novel, completely novel items; NPNL, New-pair-New-location; NPSL, New-pair-Same-location; SPNL: Same-pair-New-location; SPSL, Same-pair-Same-location.

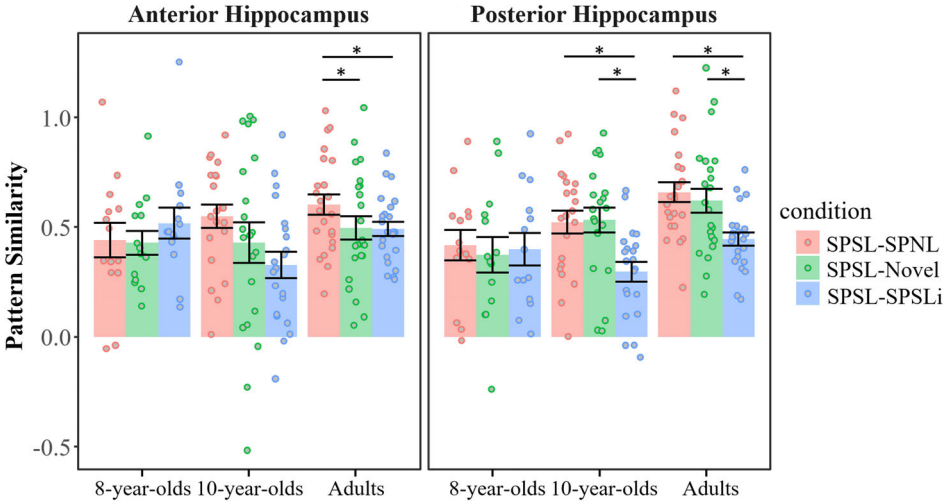

FIGURE 2 Pattern similarity scores in the developing hippocampus. Anterior hippocampus responds to goal-related conditions differently only in adults (highest similarity for SPSL-SPNL). Developmental effect across accurate trials observed in the posterior hippocampus (highest for adults). Pattern similarity scores as a function of age, hippocampal region and three experimental conditions (SPSL: Same-pair-Same-location correctly recognized as an old pair, SPNL: Same-pair-New-location correctly recognized as an old pair, Novel: Completely novel items correctly recognized as a new pair, SPSLi: Same-pair-Same-location incorrectly recognized as new pair). Bar heights are the mean values within conditions and error bars are ±1 *SEM*. *$p < .05$

In addition, we found a significant interaction between age group and condition, $F_{4,110} = 2.92$, $p = .024$, $\eta_p^2 = 0.10$, such that 8-year-olds showed no significant difference between the conditions ($p > .367$); 10-year-olds showed higher similarity for both Same-pair-Same-location—Same-pair-New-location ($M = 0.54$, $SD = 0.24$) and Same-pair-Same-location—Novel ($M = 0.48$, $SD = 0.35$) compared to Same-pair-Same-location—Missed-Same-pair-Same-location ($M = 0.31$, $SD = 0.24$), $t(41) = 5.73$, $p < .001$, 95% CI = [0.15, 0.30] and $t(41) = 3.20$, $p = .003$, 95% CI = [0.06, 0.28], respectively; and, in adults similarity scores for Same-pair-Same-location—Same-pair-New-location ($M = 0.63$, $SD = 0.22$) were significantly higher than Same-pair-Same-location—Novel ($M = 0.56$, $SD = 0.26$), $t(45) = 3.06$, $p = .004$, 95% CI = [0.03, 0.12], which in turn were significantly higher than Same-pair-Same-location—Missed-Same-pair-Same-location ($M = 0.47$, $SD = 0.15$), $t(45) = 2.45$, $p = .019$, 95% CI = [0.02, 0.16].

To investigate whether patterns of similarity were relevant for behavioral performance, we assessed the correlation between levels of pattern similarity in the anterior and posterior hippocampus for Same-pair-Same-location—Same-pair-New-location and Same-pair-Same-location—Novel and memory accuracy (i.e., the ability to discriminate between studied and unstudied pairs). For the sake of limiting the number of correlations examined, we focused on the indices reflecting the most challenging memory discrimination in the task and the least challenging memory discrimination. Since age was significantly associated with memory accuracy ($r = .31$, $p = .018$), we conducted a partial correlation analysis across the entire sample accounting for age. We found that pattern similarity for Same-pair-Same-location—Same-pair-New-location (i.e., the most similar conditions) in the anterior hippocampus was significantly associated with the ability to discriminate between studied pairs presented in the same location (Same-pair-Same-location) and rearranged pairs presented in the same location (New-pair-Same-location) (partial $r(56) = .30$, $p = .025$); the same analysis in the posterior hippocampus failed to reach conventional levels of statistical significance (partial $r(56) = .25$, $p = .059$), although the magnitude of the correlations was similar in both regions (see Figure 3a,b). In addition, we found that pattern similarity for Same-pair-Same-location—Novel (i.e., the least similar conditions) was significantly correlated with the ability to discriminate between old (Same-pair-Same-location) and completely novel pairs in both the anterior (partial $r(56) = .37$, $p = .005$) and posterior hippocampus (partial $r(56) = .47$, $p < .001$) (see Figure 3c,d).

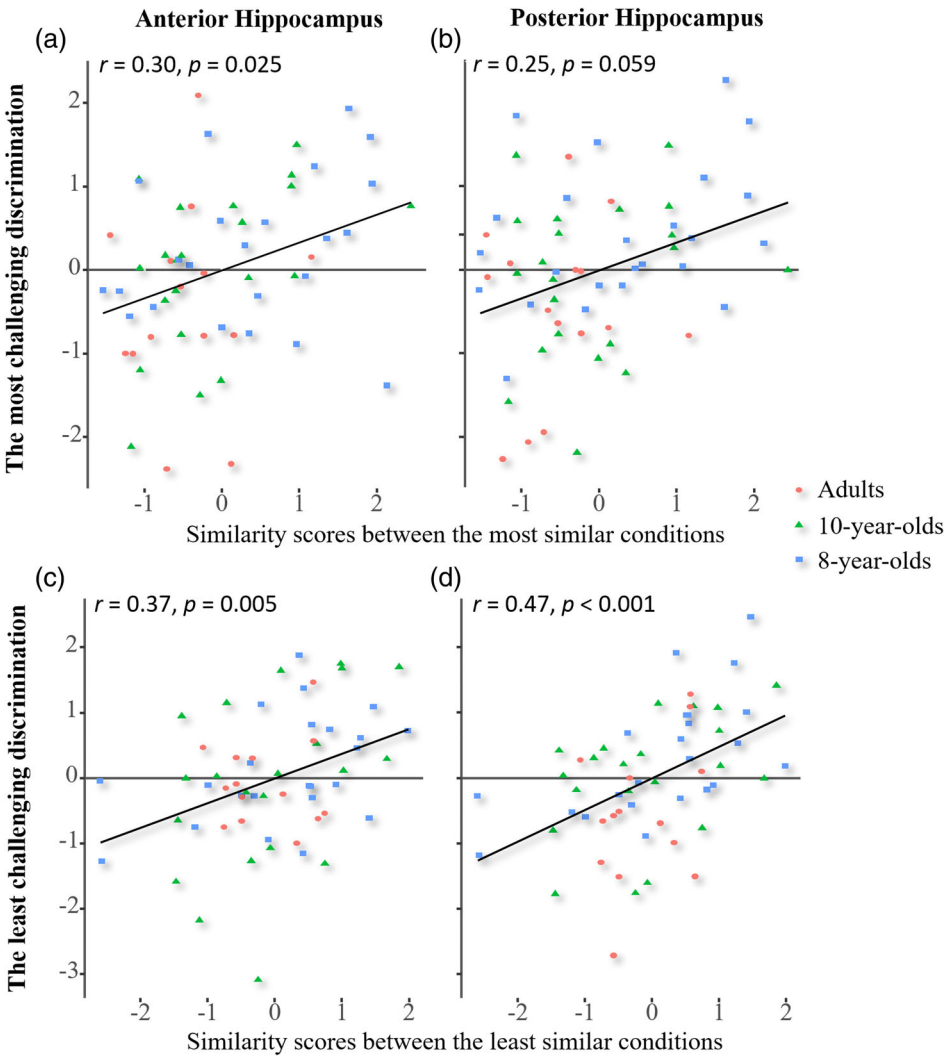

FIGURE 3 Partial correlations between pattern similarity scores and memory performance. Positive correlation was observed across all regions. In the top half of the figure, are partial correlations between the most challenging discrimination (i.e., hit rate on Same-pair-Same-location trials minus false alarm rate on New-pair-Same-location trials) and pattern similarity score for the most similar conditions (i.e., Same-pair-Same-location and Same-pair-New-location trials) in anterior (a) and posterior (b) hippocampal regions. In the bottom half, are partial correlations between the least challenging discrimination (i.e., hit rate on Same-pair-Same-location trials minus completely novel trials) and pattern similarity score for the least similar conditions (i.e., Same-pair-Same-location and Novel trials) in anterior (c) and posterior (d) hippocampal region. Solid lines are the standardized residuals corrected for age. Each age group is identified with a different color and shape, red circles for adults, green triangles for 10-year-old children, and blue rectangles for 8-year-old children

Given the general positive associations across conditions, hippocampal regions and memory accuracy indices, it is difficult to differentiate any unique role of anterior or posterior hippocampus. To explore this question further, we re-examined the correlations of each behavioral index with one subregion of the hippocampus controlling for the other subregion (in addition to age). When we did so, all of the correlations with performance were no longer significant (partial $rs < .19$, $ps > .09$ across all of these partial correlations) with the exception of the correlation between memory discrimination between old and completely novel pairs in the posterior hippocampus (partial $r(54) = .32$, $p = .016$).

3.2.1 | Exploratory analyses

The absence of a significant difference in similarity between Same-pair-Same-location—Same-pair-New-location and Same-pair-Same-location—Novel in the posterior hippocampus in both older children and adults (matched increased similarity for both Same-pair-Same-location—Same-pair-New-location and Same-pair-Same-location—Novel trials compared to similarity between Same-pair-Same-location—Missed-Same-pair-Same-location) is consistent with the idea that the posterior hippocampus may capture features that are common among all trials (e.g., elements of the overall retrieval context and background). Although the positive association with similarity in the posterior hippocampus and memory performance supports this possibility, it is difficult to interpret a null difference between experimental conditions. We thus explored whether the posterior hippocampus would track other slow-changing features of the context. We recognize that this study was not designed to explore this possibility. However, examining the extent to which separate retrieval runs show different degrees of similarity as a function of their temporal proximity could provide new and relevant insight. For the sake of simplicity, we combined Same-pair-Same-location with Same-pair-New-location trials to create a general old pair condition and we combined New-pair-Same-location with New-pair-New-location to create a rearranged pair condition. Thus, we were able to examine the effect of run across old pairs and rearranged pairs as a function of run in the posterior hippocampus (and in comparison, to the anterior hippocampus).

We considered the first run as the reference. Thus, we compared the degree to which each condition in the first run was similar to the same condition in subsequent runs. However, we had an unbalanced number of observations. Respectively, in the second, third and fourth runs, children (across both 8-year-olds and 10-year-olds) contributed 35, 25, and 8 data points, and adults contributed 23, 23, and 14 data points per condition per ROI. Accordingly, considering both 8-year-olds and 10-year-olds as children group, we fit a linear mixed effect model which does not use list-wise deletion but utilizes all data points in order to examine the effects of age (children vs. adults), ROI (anterior vs. posterior hippocampus), run (Run1-Run2 vs. Run1-Run3 vs. Run1-Run4) and condition (old pairs vs. rearranged pairs) as fixed effects, and participants as the random effect. We did not expect an effect of condition, but we were interested in examining whether the effects of run generalized across conditions.

We observed a main effect of run, $F_{2,162} = 3.89$, $p = .022$, such that average pattern similarity for Run1-Run2 ($M = 0.12$, $SD = 0.36$) was significantly higher than Run1-Run3 ($M = 0.06$, $SD = 0.32$), $t(191) = 2.63$, $p = .009$, 95% CI = [0.02, 0.16]. Pattern similarity for Run1-Run3 was also significantly lower than that for Run1-Run4 ($M = 0.17$, $SD = 0.41$, $t(87) = 2.27$, $p = .026$, 95% CI = [0.02, 0.28]). Also, there was a main effect of ROI, $F_{1,153} = 4.81$, $p = .030$. Pattern similarity was higher in the posterior hippocampus ($M = 0.14$, $SD = 0.36$) than in the anterior hippocampus ($M = 0.07$, $SD = 0.34$, $t(225) = 2.5$, $p = .013$, 95% CI = [0.01, 0.11]). Critically, there was a significant interaction between age group and run, $F_{2,162} = 3.96$, $p = .021$, such that the pattern described above was found for adults

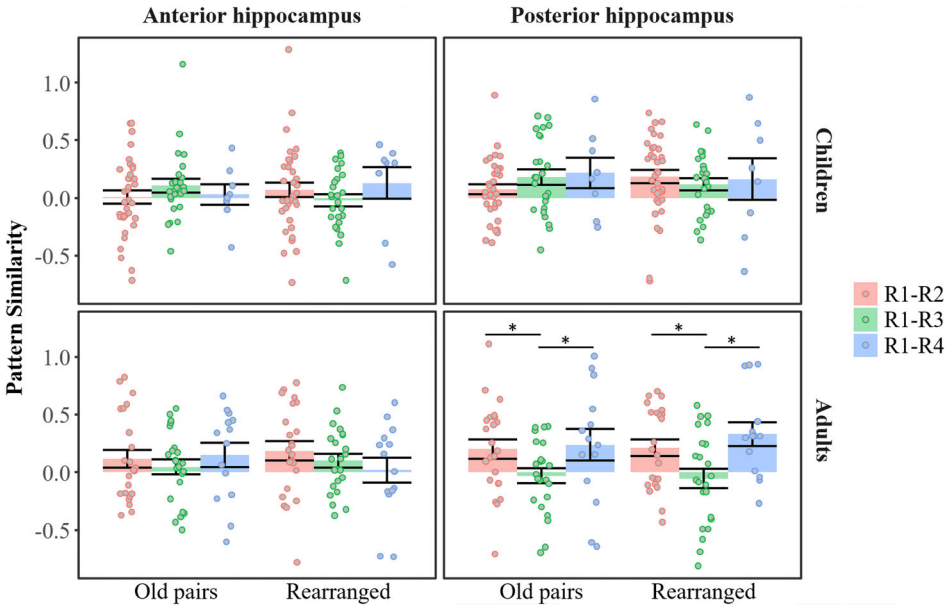

FIGURE 4 Patterns of similarity as a function of age, type of stimulus, and run. Higher similarity between successive runs (R1-R2) compared to farther runs (R1-R3) and event boundary effect (R1-R4) only observed in adults' posterior hippocampus. Same-pair-Same-location and Same-pair-New-location trials were collapsed into old pairs; New-pair-Same-location and New-pair-New-location trials were collapsed into rearranged pairs. Bar height are the mean values within conditions and error bars are ±1 *SEM*

(see Figure 4). Children did not show any significant differences in any of the comparisons (*p*s > .23). However, adults showed a significant interaction between ROI and run, $F_{2,105} = 3.58$, $p = .031$, such that in the anterior hippocampus there were no significant difference between runs (*p*s > .398), whereas in the posterior hippocampus average pattern similarity for Run1-Run2 ($M = 0.21$, $SD = 0.35$) was significantly higher than Run1-Run3 ($M = -0.04$, $SD = 0.32$), $t(43) = 2.50$, $p = .016$, 95% CI = [0.05, 0.45] which in turn was significantly lower than that for Run1-Run4 ($M = 0.28$, $SD = 0.40$, $t(23) = 2.58$, $p = .017$, 95% CI = [0.06, 0.59]). There was no main effect nor any interactions with condition (*p*s > .181).

To rule out the possibility that the order effects reported here depended on the effect of run (i.e., fatigue) on behavioral performance, we first verified whether the there was such an effect. Thus, we fit a linear mixed effect model with the effects of age (children vs. adults) and run (Run1 vs. Run2 vs. Run3 vs. Run4) as fixed effects, and participants as the random effect. The results showed a main effect of run $F_{3,92} = 2.84$, $p = .042$, such that d-prime scores in both Run1 ($M = 0.51$, $SD = 0.43$) and Run2 ($M = 0.48$, $SD = 0.50$) were significantly higher than Run4 ($M = 0.33$, $SD = 0.43$), $t(42) = 2.42$, $p = .020$, and $t(42) = 2.74$, $p = .009$, respectively; but not different from Run3 ($M = 0.42$, $SD = 0.42$), *p*s > .197. Critically, there were no interaction effect of run (*p*s > .229). Thus, the effect of run was similar across age groups. Consistent with the previously reported behavioral findings, we found a significant main effect of age, $F_{1,199} = 33.56$, $p < .001$, such that d-prime score for adults ($M = 0.63$, $SD = 0.49$) was significantly higher than that for children ($M = 0.31$, $SD = 0.36$), $t(36) = 3.21$, $p = .003$, 95% CI = [0.12, 0.52].

Although the effect of run on performance was not unique to children, we conducted a final control analysis. Specifically, we included declines in d-prime between the runs as an additional predictor to the initial linear mixed model such that the effects of age (children vs. adults), ROI (anterior vs. posterior hippocampus), run (Run1-Run2 vs. Run1-Run3 vs. Run1-Run4) and condition (old pairs vs. rearranged pairs) were included as fixed effects, and indices of performance change (Run1-Run2, Run1-Run3, and Run1-Run4) were included as covariates. The effects of run on similarity scores also persisted in this model as a significant main effect $F_{2,162} = 3.65$, $p = .028$ and a significant interaction with age $F_{2,162} = 3.67$, $p = .028$. Thus, the effects of order on pattern similarity did not depend on differences in behavioral performance.

4 | DISCUSSION

The main goal of this study was to investigate the contribution of anterior and posterior hippocampal regions to the development of episodic retrieval. Univariate analyses on the same dataset showed developmental differences in the extent of hippocampal recruitment as a function of flexibility operationalized as whether studied pairs were presented in the same or flipped locations (Demaster et al., 2016). However, Demaster et al. (2016) reported little evidence of a differentiation along the anterior–posterior hippocampal axis, which may be attributable to the use of univariate analyses. In this study, we used RSA to compare activation patterns between experimental conditions. Using this analytic approach, we found evidence that anterior and posterior hippocampal regions respond to different types of information during retrieval.

Our results showed that adults exhibited the highest similarity between types of studied pairs (i.e., between Same-pair-Same-location stimuli and Same-pair-New-location stimuli) compared to the other conditions only in the anterior hippocampus. In the posterior hippocampus, levels of pattern similarity between types of studied pairs were not different from those between studied pairs and novels pairs suggesting that this subregion might respond to not only the salient features of the task but also common features shared between studied and novel pairs such as the context and background. From this perspective, the anterior hippocampus may specifically represent more readily task-relevant features (Zeidman & Maguire, 2016). This division of labor across the longitudinal axis of the hippocampus is also supported by evidence that granularity increases from anterior to posterior regions of the hippocampus across a variety of tasks including spatial and nonspatial (Brunec et al., 2018; Callaghan et al., 2021) underscoring the hippocampus as key to processing cognitive maps in spatial tasks and relational memories in nonspatial tasks by representation of both types of information in the same network (Whittington et al., 2020). Accordingly, lower resolution of representations can be supported in the anterior hippocampus which might be critically used for retaining the task features that are more relevant to the current goals. In contrast, finer granularity in the posterior region is capable of supporting representations with higher resolution (see also Yonelinas et al., 2019). Importantly, age-related differences in the overall level of pattern similarity were observed in the posterior hippocampus, which is consistent with recent findings suggesting an age-related increase in the granularity of this region (Callaghan et al., 2021). Critically, older children showed the same effect as adults in the posterior hippocampus but not the anterior region, suggesting earlier development of posterior regions compared to the anterior hippocampus. Other research has also hinted at earlier development of posterior regions (DeMaster & Ghetti, 2013; Tang et al., 2020).

Despite these differences, the examination of associations between levels of pattern similarity and behavioral performance suggested that the entire hippocampus plays a similar role in supporting episodic retrieval, consistent with dominant accounts of the hippocampal role in supporting various forms of relational processes (Ranganath, 2010; Yonelinas et al., 2019). This may be expected given the sizeable correlation of activation patterns between anterior and posterior regions. However, when we examined the correlations with behavioral performance in one subregion while controlling for pattern similarity in the other region, the only correlation, which retained statistical significance was that pertaining pattern similarity between same-location old pairs and completely novel pairs in the posterior hippocampus and memory accuracy when discriminating those same two conditions.

At the surface, this finding may seem to contradict the intuitive expectation of a negative correlation between the ability to

discriminate between old and novel pairs and a lack of discrimination between old and novel pairs (i.e., higher pattern similarity) in the posterior hippocampus. However, these results suggest that the posterior hippocampus may respond to associative information that is common across all trials, such as slow-changing information about the experimental context (e.g., the room, the screen, etc.). If representing the common contextual features of the experiment is the source of similarity between the old and novel pairs, then this positive correlation may reflect an advantage of representing these features. Moreover, the rejection of novel pairs may be supported by retrieval of general features of the study context, enabling the discrimination between old and new items by computing contextual mismatch signals in the hippocampus (Ranganath & Rainer, 2003; Schomaker & Meeter, 2015). Thus, better detection of novel pairs may be partly correlated with representing and/or reactivating the familiar/old context. Furthermore, having the similar role for flexible demand stimuli (hit rate for Same-pair—Same-location minus false alarm rate for New-pair—Same-location) across the entire hippocampus suggest that efficient flexible retrieval may require an effective binding of both goal-relevant features (in the anterior hippocampal regions) and contextual detailed features (in the posterior hippocampal regions). Future research should examine the developmental dynamics between processing of both goal-relevant features and detailed contextual features in supporting memory gains during development.

4.1 | Exploration of pattern similarity as a function of temporal order

The failure to detect trial effects in the posterior hippocampus motivated an exploratory analysis of temporal order. We reasoned that if this subregion tracks low-changing features, it might respond to the temporal order of the runs with similarity being greater between successive runs or runs at the boundaries of events. According to contextual binding theory (Yonelinas et al., 2019), memory interference and representational overlap between similar events may be supported by representations of slow-changing features which may serve as markers of broader, situational changes. Recently, Reagh and Ranganath (2018) reported a role of the posterior hippocampus in supporting event boundaries. We also found higher similarity in successive runs (between the first and second run) compared to farther ones (between the first and third run) in the posterior hippocampus. This pattern was consistent across trial types which supports the idea that slow-changing contextual features determine this similarity independent of fast-changing elements such as item pairs. This idea is also supported by studies highlighting the role of the hippocampus in event order processing (Davachi & DuBrow, 2015). However, we also observed comparable levels of similarity between the same trial types in the first and last runs. This finding seemingly contradicts the idea that the posterior hippocampus tracks temporal contiguity. This finding highlights instead the possibility that this region may also track commonalities between event boundaries—that is, moments that mark the beginning or the end of an event or experience as a whole (e.g., Yonelinas et al., 2019). Participants were informed when the experiment started and also notified of its impending end at the beginning of the last run, procedures that potentially highlighted the boundaries of the broader event. Importantly, we ruled out the possibility that run-related behavioral differences could account for these patterns of similarity.

Children showed the same level of similarity between runs across all conditions. One possible explanation is that relational processes supporting the retention of temporal features are late developing (Lee et al., 2016). Accordingly, temporal features that are common across successive runs and different between farther ones are not presented in children's hippocampal activation patterns to the same degree as adults. In addition, children may encounter difficulties responding to the temporal changes of an experience (Lamotte et al., 2012). However, these results may also reflect overall developmental differences in hippocampal contribution to processing contextual features, be they goal-related or more general. Future research should manipulate temporal proximity and event boundaries within the same experiment to provide direct evidence that the posterior hippocampus may respond to both variables.

This study has several limitations that should be addressed in future research. First, our experimental manipulation was limited, in its ability to formally dissociate, the effect of goal driven or contextual details in the similarity scores between these New-pair-Same-location and New-pair-New-location, and other conditions. Second, as we acknowledged earlier, this experimental paradigm was not specifically designed to investigate the effect of temporally slow-changing feature of the context. Third, we had limited number of data points for the fourth run in children, likely because of fatigue. Future designs should include manipulation of temporal contiguity using several shorter runs.

In conclusion, we used a multivariate approach to investigate representation of the contextual features in the developing hippocampus and observed functional and developmental dissociations between the anterior and posterior hippocampus. These findings contribute to shedding light on the heterogeneity of hippocampal structure and functions and its contribution to episodic memory in children and adults.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Behavioral and fMRI data used in this study are available in open science framework at https://osf.io/5dcqs/.

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