Running head: Hippocampal pattern similarity in children

Children show adult-like hippocampal pattern similarity for familiar but not novel events

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Abstract

The ability to detect differences among similar events in our lives is a crucial aspect of successful episodic memory performance, which develops across early childhood. The neural substrate of this ability is supported by operations in the medial temporal lobe (MTL). Here, we used representational similarity analysis (RSA) to measure neural pattern similarity in hippocampus, perirhinal cortex, and parahippocampal cortex for 4- to 10-year-old children and adults during naturalistic viewing of clips from the same compared to different movies. Further, we assessed the role of prior exposure to individual movie clips on pattern similarity in the MTL. In both age groups, neural pattern similarity in hippocampus was lower for clips drawn from the same movies compared to those drawn from different movies, suggesting that related content activates processes focused on keeping representations with shared content distinct. However, children showed this only for movies with which they had prior exposures, whereas adults showed the effect regardless of any prior exposures to the movies. These findings suggest that children require repeated exposure to stimuli to show adult-like MTL functioning in distinguishing among similar events.

Keywords: representational similarity analysis, differentiation, hippocampus, cognitive development, episodic memory

Introduction

Young children do not remember events they have experienced as well as adults do. Emerging research suggests that this lack of memory refinement results from immaturity in the neural structures underlying episodic memory. The key brain region supporting episodic memory is the medial temporal lobe (MTL), which can be further divided into functional subregions. Prominent models propose that the hippocampus (HPC) and surrounding perirhinal cortex (PRC) and parahippocampal cortex (PHC) support contextual representations that can help differentiate highly similar events (Davachi, 2006; Eichenbaum et al., 2012), collectively allowing for the formation and retrieval of richly detailed episodic memories. However, retention of distinct episodic memories must overcome the problem of disentangling related information across episodes, as when two events share similar contexts. This kind of overlap necessitates keeping highly similar memories from interfering with one another, a process supported by the MTL (Kirwan & Stark, 2007). Keeping representations of naturalistic, multimodal stimuli such as movie clips separate in the face of overlapping elements requires neural operations to distinguish amongst similar events. While typically thought to be engaged during explicit memory encoding processes, they are also thought to be active during incidental, passive events such as movie watching.

Research on the development of episodic memory has shown that hippocampal subfields supporting episodic specificity show relatively late maturational profiles in both humans (e.g., Riggins et al., 2018; Keresztes et al., 2017) and nonhuman primates (Lavenex & Banta Lavenex, 2013), with relatively less research characterizing the development of nearby PRC and PHC. However, there is evidence that activation of PHC during encoding differs between children and adults (Ghetti, DeMaster, Yonelinas, & Bunge, 2010). PRC and PHC have been shown to work

in concert to support episodic memory in adults, but this interaction merits further investigation in developmental populations. With strong evidence for the protracted maturation of the hippocampus and some evidence for functional development of other MTL structures in early childhood, one would predict that memory processes supported by the MTL are not able to function maturely in early childhood, although they may begin to approach adult-like levels by middle or late childhood.

One important feature that may drive differences in MTL function across age groups is additional exposure to stimuli. In adults, both intraexperimental repeated exposures and pre-experimental prior exposures to stimuli improves memory performance for those stimuli (Poppenk et al., 2010); in children, repeated exposures to information enhances vocabulary learning and improves retention (Bloom, 2002; Horst et al., 2011; Koenig et al., 2020). Episodic memory is acquired through a single exposure, relies on the hippocampus (Tulving, 1972), and is fragile in childhood (Usher & Neisser, 1993; Wetzler & Sweeney, 1986). In children, whose hippocampi are still developing, repeated exposure may help them to recall details of their experiences that they might not have recalled after only a single encounter with a particular location, event, etc. because their hippocampi cannot yet support this one-shot process at adult levels. Additionally, episodic memory is scaffolded by prior general knowledge, including knowledge of schemas, which provide conceptual regularities that extend across multiple events, and understanding of which is still developing in childhood (Pudhiyidath, Roome, Coughlin, Nguyen, & Preston, 2019). Without the benefit of conceptual knowledge that helps adults quickly encode new information after only one exposure by providing, for example, names for items and expectations for experiences, children might need multiple encounters with a given item, location, experience, etc. to accurately recall it.

Understanding of narrative structures (Lynch et al., 2008) and scripts (Hudson, Fivush, & Kuebli, 1992) has also been shown to improve across development. Because of their greater experience with narratives and scripts, adults might be able to find connections between a pair of dynamic, realistic, temporally-unfolding stimuli, such as movie clips, without the benefit of prior exposure because of their understanding of how depicted scenarios tend to unfold, or how certain types of characters tend to interact. Children, on the other hand, might require repetitions to draw these same conclusions and recall the events presented in the stimuli. Thus, prior exposure likely benefits memory performance, especially in children whose episodic memory ability is still fragile and whose general knowledge is not yet robust, and thus will show more prominent differences in how the brain encodes information that is familiar versus information that is novel.

In the present study, we reanalyzed the KidVid dataset, which includes neuroimaging data obtained while participants viewed child-friendly naturalistic movies (Camacho et al., 2019; Karim & Perlman, 2017). We used it to investigate neural processes in the MTL in children compared to adults. Children (aged 4-10) and adults viewed video clips from popular, family-friendly movies, with two clips coming from each movie, which enabled the comparison of idiosyncratic experiences that shared content (i.e., within movie) or did not share content (i.e., across movies; Larocque et al., 2013). While we know much about age-related structural differences in HPC across development (Canada et al., 2020; Gogtay et al., 2006; Krogsrud et al., 2014; Lavenex & Banta Lavenex, 2013), understanding children's functional engagement while viewing naturalistic stimuli could inform how the MTL encodes real-world events, which are often much richer and more complex than stimuli employed in traditional memory tasks.

We used representational similarity analysis (RSA) to examine age-related differences in patterns of activation in three MTL regions—the HPC, PHC, and PRC—during viewing of

movie clips drawn from the same movie (i.e., within) or different movies (i.e., across), thus allowing us to investigate how these regions may represent events that share perceptual/conceptual content versus those that do not. RSA is a technique in which the multivoxel pattern responses of stimuli—obtained using similar methods to classification-based multivoxel pattern analysis (MVPA)—are compared to one another to provide a higher-order representation of the stimuli (Popal, Wang, & Olson, 2020). Studies using RSA of related and unrelated stimuli (e.g., Chanales et al., 2017; Favila et al., 2016) demonstrate that multivariate neuroimaging analyses can give insight into operations in the MTL that serve to represent related experiences distinctly in terms of neural signals. While there were no explicit task demands to encourage creating distinct representations of overlapping experiences in this study, we predicted that we would find pattern dissimilarity for more similar versus less similar events in the MTL, which would provide an index of making overlapping neural representations distinct. Further, given developmental data highlighting the importance of repeated exposure (Bloom, 2002; Horst et al., 2011; Koenig et al., 2020), we further assessed the role of prior exposure to the stimuli in our study, hypothesizing that prior exposure would allow for greater pattern dissimilarity in children, who might need more than a single exposure to show similar neural operations to adults.

Thus, the goal of this study was to arbitrate between two competing hypotheses. One hypothesis is that children will show dissimilar activation patterns compared to adults because developing MTL structures do not yet support mature mnemonic processing. This hypothesis would further suggest a relationship between age and neural pattern similarity within our child sample, as our age range spans a developmental window in which critical hippocampal changes and behavioral memory improvements are both taking place. Alternatively, children might show

similar patterns to adults only when they are familiar with the stimuli, with marked differences for more novel events. This hypothesis rests on prior findings showing increased memory performance in children when they are given increased exposure to memoranda (Horst et al., 2011; Koenig et al., 2020). In our study, this would be demonstrated by finding differences in pattern similarity for children that mirror those found in adults—but only for movies which they have previously viewed.

Methods

Participants

Fifty-seven participants (21 adults and 36 children) with no history of psychiatric diagnosis were recruited from the University of Pittsburgh. After removing participants for excess head motion (see Methods: MRI data acquisition and pre-processing), our final sample consisted of 20 adults (9 female, 11 male; age 20-44, M_{age} = 26.65) and 25 children (14 female, 11 male; age 4-10, M_{age} = 7.36). Our child sample was distributed unevenly across the age range (see Figure 1), with few children under the age of 6 represented. This is important to keep in mind since the early childhood years represent a critical developmental window for memory—we address this in the following analyses by evaluating the relationship of reported effects by age within our child sample. Before participation began, adult participants and children's parents/guardians provided written consent and children provided assent.

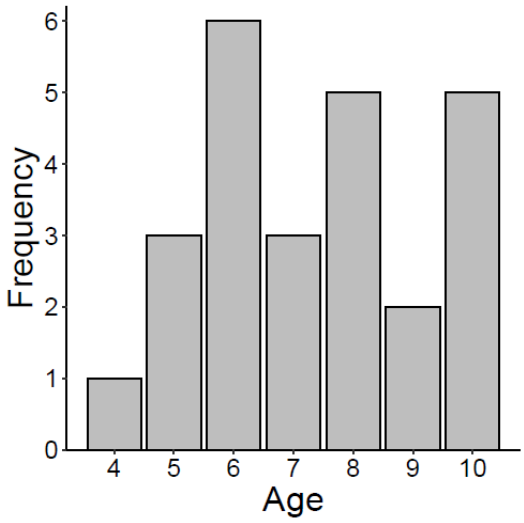

Figure 1 Distribution of children's ages.

Movie-viewing task

Participants watched 24 movie clips (see Figure 2A) while undergoing functional magnetic resonance imaging (fMRI). This task is explained in further detail in Karim & Perlman (2017) and Camacho, Karim, & Perlman (2019). In brief, clips ranged in length from 19-46 seconds (M = 31.1 seconds) with a jittered inter-stimulus interval (ISI) of 6-12 seconds, totaling 17 minutes of viewing time. The 24 clips were of positive, negative, or neutral affective valence (eight each). The positive and negative clips were taken from eight popular, child-friendly movies (e.g., *Lion King*, *Up*, etc.), with one positive and one negative clip taken from each movie; the neutral clips were taken from nature documentaries. Each clip was rated on a second-by-second basis for the valence of positive or negative affective content by an independent rater. Critically, there was no difference between positive and negative clips in duration ($t(7) = 0.24$, $p = .81$) or absolute value of emotional valence ($t(14) = 1.38$, $p = .19$; Karim & Perlman, 2017). For the purpose of the current work, we only looked at positive and negative clips, as they were the only stimuli for which there were two clips drawn from the same movie. The order of clips was randomized across three versions, which were randomly assigned to participants. Clips from

the same movie were never viewed in succession, and on average, clips from the same movie (*M* = 404.54 seconds) were viewed further apart than clips from different movies (*M* = 334.21 seconds; $t(1036.9) = 8.54$, $p < .001$). We explicitly control for this difference in timing of conditions across two subsequent control analyses (detailed in Methods: Main Analyses and Control Variables). Participants were simply instructed to lay in the scanner without moving while "[watching] the movies as they normally would" (Karim & Perlman, 2017). To ensure that participants were adequately attending to the task, a 16-question quiz was given following the scanning session in which participants were asked whether still frame images were taken from the clips they had watched—accuracy was near ceiling in both children and adults (Karim & Perlman, 2017). Additionally, adult participants and children's parents reported on their/their child's prior exposure to each movie on a scale of "never seen it", "seen only parts", "has seen it once or twice", or "watches often". Parents could ask their children if they were unsure. Importantly, the movies used in this study were all older films that were not recently released, therefore increasing the likelihood that adults and children would have equivalent exposure to the films, and decreasing the influence on prior knowledge of toys, games, etc. that tend to accompany newly-released movies. Adults and children did not differ in average level of prior exposure to the movies ($t(43) = -.40$, $p = .69$). For our analyses, we binned our data into no prior exposures ("never seen it") and prior exposures ("seen only parts", "has seen it once or twice", and "watches often"). For children, there were significantly more movies that were categorized as having prior exposures (*M* = 5.04, *SD* = 1.86) versus no prior exposures (*M* = 2.96, *SD* = 1.86; $t(24) = -2.80$, $p = .01$; see Table 1). In adults, there were also significantly more movies with prior exposures (*M* = 5.15, *SD* = .93) than no prior exposures (*M* = 2.85, *SD* = .93; $t(19) = -5.51$, $p < .001$; See Table 1 and Supplemental Figure 1). Although the sample sizes in each bin were

not equivalent, we grouped the data in this manner to understand how prior exposures influence representational similarity. However, to mitigate any confounds that might arise out of the significant difference in the number of movies in each category, we also conducted these exposure level analyses by binning our data into low familiarity ("never seen it" and "seen only parts") and high familiarity ("has seen it once or twice" and "watches often"). Here, there was no difference in the number of movies that were rated high (M = 4.32, SD = 2.04) versus low (M = 3.68, SD = 2.04) familiarity in children ($t(24) = -.79$, $p = .44$). Similarly, in adults there was no difference in the frequency of high (M = 4.25, SD = 1.16) and low (M = 3.75, SD = 1.16) familiarity ratings ($t(19) = -.96$, $p = .35$).

	Prior Exposures	**No Prior Exposures**
	Range *Mean (SD)*	*Range* *Mean (SD)*
Adults	4 - 7 5.15 (.93)	1 - 4 2.85 (.93)
Children	1 - 8 5.04 (1.86)	0 - 7 2.96 (1.86)

Table 1. Number of movies for which participants had prior exposures or no prior exposures for adults and children.

MRI data acquisition and pre-processing

MRI data was collected using a 3T Siemens Trio scanner with a 12-channel parallel transmit-receive head coil. Functional whole brain blood oxygen-level dependent (BOLD) images were collected in a sagittal acquisition (excluding part of the middle/superior temporal cortex from both hemispheres; TR = 2,000 ms, TE = 30 ms, flip angle = 90°, FOV = 256 mm, matrix size 64 x 64, voxel size 4 x 4 x 4 mm). Five hundred and ten brain volumes were

collected during this gradient echo EPI (echo-planar imaging) sequence, lasting 17 minutes and 6 seconds, collected in a single run.

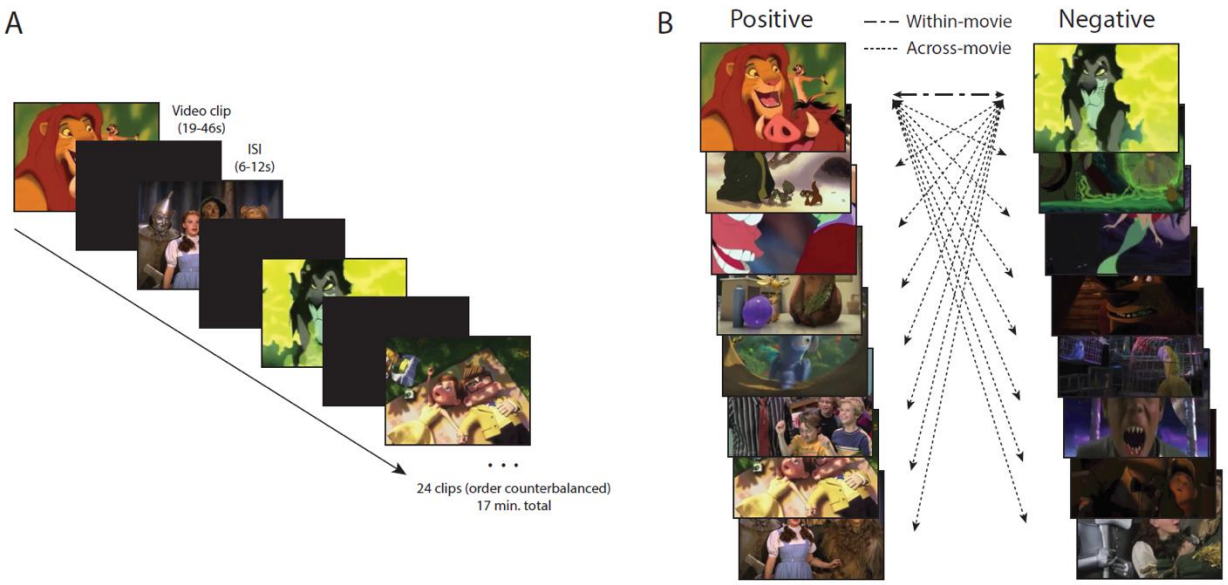

Figure 2 (A) Task schematic. Participants viewed movie clips while undergoing fMRI. (B) Depiction of within- and across-movie correlations to calculate pattern similarity for related and unrelated stimuli. Each movie had two clips drawn from it—one positive and one negative clip.

We preprocessed our data in a manner that would minimize the effects of head motion. This included preprocessing using FEAT (fMRI Expert Analysis Tool) with high-pass filtering, and skull stripping using BET (Brain Extraction Tool) in FSL version 5.0 (FMRIB Software Library; Jenkinson et al., 2012). Due to the slow nature of our task design, we used a high-pass filter with a relatively low frequency of 100s, which was unlikely to filter out signal related to our task. Functional data were then registered to the anatomical images and nonlinearly warped to MNI space. Head motion and noise-related factors were identified by calculating and thresholding metric values of how motion-affected each time point was using timeseries extracted from white matter and CSF, six head motion parameters, and their first derivatives. In addition to the listed nuisance regressors, we identified and regressed out individual TRs based

on excessive head motion. If greater than 15% of TRs were considered outliers, or if head motion values for any of the three rotations were greater than 1.5mm, the participant was removed from the analysis (participants removed: *n*=1 adult, *n*=11 children).

Analyses

Setting up the RSA

To investigate neural pattern similarity, for each participant we first estimated voxel-wise activation in response to each movie clip. We constructed a GLM with each individual movie clip modeled separately, including neutral clips not used in the current analyses, using a double-gamma hemodynamic response function (HRF) with the duration of the movie clip (19-46 sec). From these single-clip activation maps, we extracted the activation of each individual voxel from our regions of interest (ROIs). All ROIs were defined separately for each hemisphere. Our focus was on three MTL ROIs: HPC, PRC, and PHC. The HPC ROIs (right and left) were taken from the Harvard-Oxford subcortical atlas and thresholded at 50%. The left and right PRC and PHC ROIs were created from manually-segmented T1 images and thresholded at 50% (Ritchey, Montchal, Yonelinas, & Ranganath, 2015). We also selected V1 as a control region because we expected this region to show a response to visual stimuli, but not to show sensitivity to differences in mnemonic content across movies. The V1 ROIs were taken from the Juelich histological atlas and thresholded at 50%. All ROIs were defined at the group level in MNI space and transformed into subject native space using non-linear estimation (FNIRT) and visually inspected for accuracy.

We used representational similarity analysis (RSA), a technique commonly used to measure neural pattern similarity by computing correlations between comparisons of interest (Popal et al., 2019), to compare pattern similarity in each of our ROIs within and across movie

clips, including only the positive and negative clips (Figure 2B). We did not include neutral clips because they were all drawn from different movies, so there was no opportunity to compare clips from the same movie, which was a central feature of our analysis. Within-movie correlations were defined as the Fisher-transformed correlation between the *t*-statistics across individual voxels within a region of interest for two clips from the same movie (e.g., *Lion King* positive-valence to *Lion King* negative-valence). With one correlation per movie, each participant had eight within-movie correlations total. Across-movie correlations mirrored the within-movie in that each comparison of every positive clip to every negative clip and every negative clip to every positive clip—critically excluding the clip from the same movie—was captured and Fisher-transformed (e.g., *Lion King* positive to *Little Mermaid* negative, *Lion King* negative to *Little Mermaid* positive, *Little Mermaid* positive to *Open Season* negative, etc.) This negative-positive comparison for the across-movie clips was done to reflect the same type of cross-valence comparisons that were inherent in the within-movie correlations. There is naturally a larger number of correlations being computed for the across-movie comparisons (56) than for the within-movie comparisons (8) for each participant, leading to wider and more variable within-movie distributions. Rather than sampling a subset of across-movie correlations to match the availability of within-movie data, we opted to use all of the data available to provide a more accurate depiction and reduce the variability in this metric.

Main Analyses and Control Variables

For all of our ROIs, to determine if shared versus discrete contexts significantly influenced pattern similarity, we submitted our RSA values to a mixed effects model in which subject and video identity were defined as random effects and laterality, head motion, univariate activation, and time between the clips were included as control terms. To determine significance,

we ran model comparisons in which one model contained the fixed effect of interest (e.g., within- versus across-movie correlation in HPC) and the other model excluded that effect with everything else remaining.

Before conducting our main analysis of interest, we tested whether there were any effects of laterality within each ROI (i.e., HPC, PRC, and PHC) and age group (children, adults). Specifically, we ruled out laterality effects by separately running a two-way analysis of variance (ANOVA) for children and adults with pattern similarity predicted by correlation type (within-movie versus across-movie) and laterality. No significant laterality differences were seen in any of these regions (all p's > .07). Thus, laterality was only included as a control term in subsequent analyses. Additionally, to make certain that subject-level differences in head motion did not influence our results, we included the total number of TRs considered outliers as a control variable in each of our analyses.

Theoretically, pattern similarity is orthogonal to activation level, and pattern similarity can be present even when there are no differences in univariate activation level (Popal, Wang & Olson, 2019). However, given that overall activation level can bias pattern similarity results (Freund, Etzel, & Braver, 2021), we wanted to control for this factor beyond including it as a covariate in our models. For both within- and across-movie univariate activation, we took the mean signal between the two clips from each movie in the comparison (e.g., *Lion King* positive and *Lion King* negative for within-movie and *Lion King* positive and *Little Mermaid* negative for across-movie). To mirror the correlations we obtained for similarity, we calculated univariate activation within and across movies separately, again deriving 8 within-movie and 56 across-movie activations. We then included this univariate activation metric as a covariate in each model to control for overall activity differences.

Finally, given the importance of autocorrelation between nearby trials, and that our task took place in a single run, we wanted to consider any timing- and order-related variables that could confound our results. For instance, the two clips in a within-movie comparison always contain the "first" and "second" presentation of a video clip drawn from the same movie, whereas trials for the across-movie comparison may contain two "first" or two "second" presentations. To account for this, we ran an analysis on a subset of the data where only across-movie comparisons that contained one "first" and one "second" presentation of the movies were included. Another potential confound is that clips from the within-movie comparisons on average may have been viewed farther apart in time than those drawn from across-movie comparisons since it was experimentally manipulated that clips from the same movie were never viewed in succession. In an additional control analysis to address this, for each movie, we only included the two across-movie trials that were viewed most similarly in temporal distance from its respective within video. For example, if Lion King positive was viewed 350 seconds away from Lion King negative, we would use both the *Lion King* positive to any other negative clip and *Lion King* negative to any other positive clip whose temporal distance was closest to 350 seconds. With this analysis, each participant had eight within-movie comparisons and 16 across-movie comparisons—two values for each movie. We then include the distance (in seconds) between each pair of clips as a covariate in all of our mixed effects models (see Supplemental Figure 2) as well as an additional analysis with clips matched in temporal distance across conditions. These measures were taken to ensure that dissimilarity in within- versus across-movie comparisons was driven by differences in the clips themselves, rather than due to the simple adjacency or order of presentation of certain clips.

Examining Differences by Age Group

In additional to our primary analysis looking at within- vs. across-movie pattern similarity differences within each group, we also asked if there was a difference in pattern similarity across correlation type between children and adults by calculating a difference score (within – across) for each participant. To do this, we needed one within- and one across-movie score for each movie for each participant. The eight within-movie comparisons for each participant remained the same as in the previous analysis, in which the within-movie value is the correlation between the two clips from each movie (i.e., *Lion King* negative to *Lion King* positive). For the across-movie comparisons, we took the average of all correlations for each video (i.e., *Lion King* negative to *Little Mermaid* positive, *Lion King* positive to *Little Mermaid* negative, *Lion King* negative to *Open Season* positive, etc.) to yield 8 total across-movie values, one for each movie. We then took the difference between the within-movie and across-movie values for each movie, resulting in eight values for each participant.

Examining Differences by Level of Prior Exposure

In our last series of analyses, we tested whether having prior exposures to the movies would explain any differences in neural pattern similarity between the within- and across-movie correlations. We planned to conduct this analysis only in regions where both children and adults showed robust pattern similarity differences, because our hypotheses reflect that children may show pattern similarity differences by level of exposure, given that prior exposures to the movies may be required for children to notice the shared content between clips from the same movie. We conducted this analysis in a similar manner to the analyses comparing similarity differences between age groups using the collapsed data, in that we kept all eight within-movie comparisons and labeled each movie with its respective level of exposure (prior exposures versus no prior

exposures) for each participant. For the across-movie comparisons, we again wanted eight values—one for each movie—in order to label its associated exposure level. For the across-movie comparisons, we took the average of all correlations for each video (i.e., *Lion King* negative to *Little Mermaid* positive, *Lion King* positive to *Little Mermaid* negative, *Lion King* negative to *Open Season* positive, *Lion King* positive to *Open Season* negative, etc.), so that for each participant, we were left with one across-movie value for each movie. The exposure level was then labeled for each movie for each participant. The subsequent exposure analyses were conducted at the video-level as opposed to the subject-level, resulting in large degrees of freedom.

Results

Hippocampus (HPC)

Pattern Similarity Within Groups

We began by examining pattern similarity differences within- versus across-movie in hippocampus (HPC). By comparing our mixed effects models (see Methods), we asked whether adults and children, separately, show different levels of hippocampal pattern similarity when viewing clips from the same compared to different movies. In adults, we found a significant effect of correlation type (i.e., within- versus across-movie), such that within-movie comparisons showed lower pattern similarity than across-movie comparisons ($\chi^2 = 15.55$, $p < .001$; Figure 3A – Supplemental Figure 3A for subject-level). Like adults, children also showed the same pattern of lower similarity between clips from the same movie compared to clips from different movies ($\chi^2 = 6.49$, $p = .01$; Figure 3B – Supplemental Figure 3B for subject-level). This result suggests that greater pattern dissimilarity arises when clips are from the same movie (within) compared to

when the clips in question are from different movies (across). Because two clips drawn from the same movie are likely to be more similar than those drawn from different movies, greater dissimilarity might be required to distinguish among these overlapping representations, although we only propose this as a theory for the function of pattern dissimilarity since we do not have behavioral memory data with which to fully investigate this proposition.

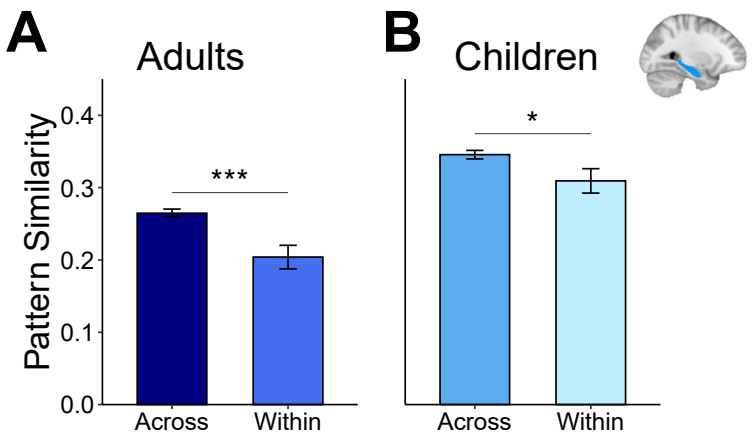

Figure 3. RSA effects in hippocampus. Mixed-effect models conducted separately for (A) adults and (B) children investigating differences in pattern similarity within- and across-movies. *** p < .001, * p < .05

Accounting for Potential Confounds

We next ran a series of control analyses addressing several factors that were not related to our predictors of interest that could potentially confound the above results, the first being potential order effects in the presentation of the clips, i.e. whether a given clip was a "first" or "second" presentation of a given movie. The structure of the model was identical to our initial mixed effects model described above, maintaining all the aforementioned control variables, but only included a subset of trials on which presentation order was matched (see Methods). Similar to the model with all trials included, adults ($\chi^2 = 10.81$, $p < .01$) and children ($\chi^2 = 4.67$, $p = .03$) both showed lower pattern similarity to clips from the same relative to different movies in HPC.

In our main analyses, we included the temporal distance between each clip in our models. However, to further address this potentially confounding variable, we also ran a subset analysis to match the temporal distance between clips for our within- and across-movie comparisons. Again maintaining the same covariates as in the prior models, the results mirrored the main analysis such that adults (χ^2 = 14.06, p < .001) and children (χ^2 = 5.22, p = .02) both showed lower pattern similarity for within- versus across-movie clips.

Group Differences

Lastly, we examined group differences using a difference score of within – across for each participant (see Methods). A mixed effect model included laterality and level of prior exposure to each movie as covariates, and a subject identifier and video identity as random effects. Univariate activation was left out because the model did not converge when this factor was included. This analysis revealed no significant difference between children and adults (χ^2 = 1.08, p = .30) in terms of the within – across movie pattern similarity differences. Since we did not find support for an effect of age on pattern similarity differences, we ran a Bayesian analysis and found moderate evidence for the null hypothesis (BF_{01} = 6.07). For all of our Bayesian statistics, we used established criteria for determining the robustness of our null findings based on our calculated Bayes Factors, ranging from no evidence for the null (BF_{01} = 1), to strong evidence (BF_{01} = 10-30), to extreme evidence (BF_{01} = >100; Lee & Wagenmakers 2014). Because both age groups showed similar differences in pattern similarity for within-movie comparisons versus across-movie comparisons in HPC, our null result is not surprising.

Age Effects in Children

Finally, because our sample included children spanning ages 4-10 years, we predicted that there might be variation in similarity patterns within the child group, as substantial neural

development takes place across this age range. Thus, to examine whether children's pattern similarity profile would more closely resemble that of adults with increasing age, we tested whether age was related to the within-across difference score in children only, using a similar mixed effects model to the previous analysis, but with age as the predictor variable, and found no significant relationship (χ^2 = .01, p = .93) A Bayesian analysis suggested moderate evidence for the null hypothesis (BF_{01} = 9.46).

Perirhinal Cortex (PRC)

Pattern Similarity Within Groups

Next, we asked whether adults and children show pattern similarity differences in response to overlapping and non-overlapping content in PRC. Using the full trial-level model described for HPC with laterality, univariate activation, head motion, and distance between clips included as covariates, we found that adults again showed significantly lower pattern similarity for within- than across-movie comparisons (χ^2 = 14.37, p < .001; Figure 4A – Supplemental Figure 4A for subject-level), whereas children showed no difference (χ^2 = 0.52, p = .47; Figure 4B – Supplemental Figure 4B for subject-level), with the Bayes Factor (BF_{01} = 13.79) suggesting strong evidence for the null hypothesis.

Accounting for Potential Confounds

These results remain consistent in both adults (χ^2 = 12.97, p < .001) and children (χ^2 = 0.45, p = .50, BF_{01} = 12.99) when subsetting the across-movie data to match the "first" and "second" presentation nature of the within-movie comparisons, with strong Bayesian evidence for the null in children. Similarly, adults still show less within- than across-movie similarity when matching the timing of across-movie trials to that of within (χ^2 = 16.50, p < .001), whereas children still do not show a significant difference (χ^2 = 0.16, p = .69, BF_{01} = 14.90), with the Bayes Factor again

demonstrating strong evidence for the null hypothesis. These data suggest that in children, PRC may not be sensitive to differences between similar content presented in a context-rich naturalistic format such as a movie.

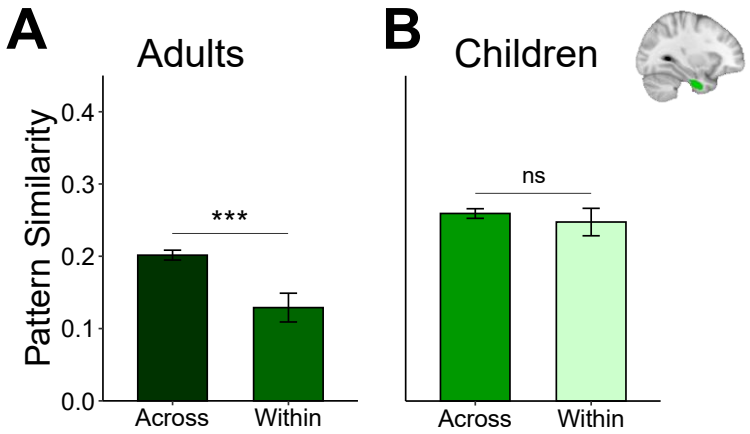

Figure 4. RSA effects in perirhinal cortex. Mixed-effect models conducted separately for (A) adults and (B) children investigating differences in pattern similarity within- and across-movies. *** $p < .001$, ns $p > .05$

Group Differences and Age Effects in Children

We again wanted to test whether PRC pattern similarity differed between children and adults. There was a significant difference in the pattern similarity difference scores (within – across) between the age groups ($\chi^2 = 3.90$, $p = .048$), suggesting that children's pattern similarity for within- versus across-movie comparisons in PRC differs from that of adults. When looking at just the children, age was not a significant predictor in explaining within- versus across-movie differences ($\chi^2 = .43$, $p = .51$); as in HPC, there was moderate evidence for the null hypothesis ($BF_{01} = 6.80$).

Parahippocampal Cortex (PHC)

Pattern Similarity Within Groups

We then tested how PHC responds to clips from the same versus different movies in adults and children. In the full trial-level model including all comparisons as well as all covariates mentioned above, both adults (χ^2 = 15.46, p < .001; Figure 5A – Supplemental Figure 5A for subject-level) and children (χ^2 = 4.11, p = .04; Figure 5B – Supplemental Figure 5B for subject-level) displayed lower pattern similarity to clips from the same versus different movies, similar to the effects found in HPC.

Accounting for Potential Confounds

This effect remained true in adults in both subset control analyses: the model including only comparisons that contained one "first" and one "second" presentation of a movie (χ^2 = 12.65, p < .001), and the model including timing between within- and across-movie comparisons (χ^2 = 12.17, p < .001). However, in children, this pattern was not robust to the presentation (χ^2 = 3.21, p = .07) and timing (χ^2 = 2.57, p = .11) control analyses—with the Bayes Factor for presentation offering only anecdotal evidence for the null (BF_{01} = 3.94), but timing showing moderate evidence (BF_{01} = 7.33). Because these results did not hold for children after controlling for critical confounds, we suggest that in children, PHC may not be sensitive to contextual overlap within the same movie like it is for adults. These results mirror the findings in PRC, where adults showed significant pattern similarity differences within versus across movies and children did not.

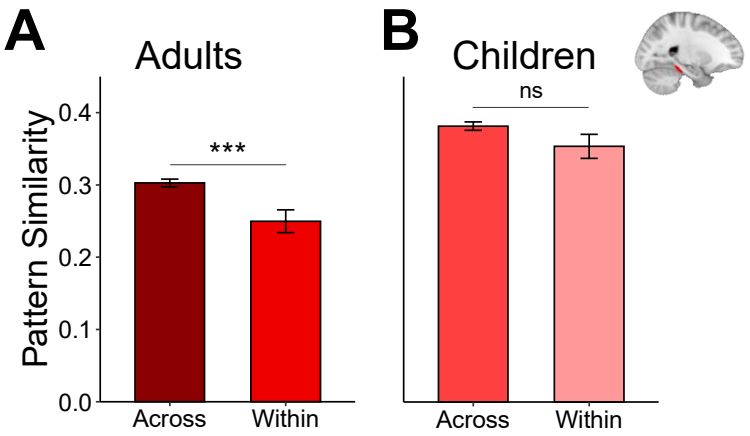

Figure 5. RSA effects in parahippocampal cortex. Mixed-effect models conducted separately for (A) adults and (B) children investigating differences in pattern similarity within- and across-movies. *** $p < .001$, ns $p > .05$

Group Differences and Age Effects in Children

Unlike in PRC, there was no significant difference in pattern similarity between children and adults ($\chi^2 = 1.17$, $p = .28$), with moderate evidence for the null hypothesis ($BF_{01} = 4.73$). Given the inconsistencies in the within- versus across-movie differences in children for PHC, it is not surprising that we were not able to detect a significant difference between the age groups. We again asked whether there was a change in pattern similarity with age in children and found that age was not a significant predictor in explaining within- versus across-movie differences ($\chi^2 = .07$, $p = .80$), and Bayes Factors revealed moderate evidence for the null hypothesis ($BF_{01} = 9.55$).

Visual Cortex (V1)

Pattern Similarity Within Groups

As a control, we conducted the same analyses as above in V1, to ensure that our findings were specific to MTL regions, and not purely driven by perceptual differences in the clips, which would be expected in V1. Specifically, we chose V1 as a control region because we believed it would be sensitive to visual stimuli but would not show differences in activation patterns for clips that did versus did not contain shared mnemonic content. Our full model indicated that

neither adults (χ^2 = 1.98, p = .16) nor children (χ^2 = .06, p = .81) showed a difference in within- versus across-movie pattern similarity in V1, with evidence for the null being moderate for adults (BF_{01} = 6.18) and strong for children (BF_{01} = 11.80).

Accounting for Potential Confounds

Again, these results held true for both adults (χ^2 = 1.05, p = .31) and children (χ^2 = .01, p = .93) in the control analysis, in which only across-movie comparisons that included one "first" and one "second" presentation of a movie were used. Bayes Factors again revealing moderate evidence for the null in adults (BF_{01} = 7.24) and strong evidence in children (BF_{01} = 11.21). Similarly, neither adults (χ^2 = 1.41, p = .24) nor children (χ^2 = .05, p = .82) showed significant effects when matching the timing of clips in the across-movie comparisons to the temporal distance of within-movie comparisons, with the same pattern of null results determined by Bayesian analysis for adults (BF_{01} = 6.86) and children (BF_{01} = 10.51).

Group Differences and Age Effects in Children

There was no difference between the age groups in the within—across difference score (χ^2 = 1.33, p = .25, BF_{01} = 5.00). Finally, age did not significantly explain any differences in within- versus across-movie pattern similarity in children (χ^2 = .13, p = .72, BF_{01} = 5.92). Bayes Factors showed moderate evidence for the null hypothesis in both of these cases. In all, this suggests that our pattern similarity effects are not simply whole-brain effects.

Prior Exposure

Finally, we examined the role of prior exposure in pattern similarity differences between within- versus across-movie correlations. We did so only in HPC, as it was the only ROI in which both children and adults showed robust pattern similarity differences. This analysis was conducted similarly to that comparing the age groups using the collapsed data, in that we kept all

eight within-movie comparisons and labeled each movie with its respective level of exposure (prior exposures versus no prior exposures) for each participant. Bonferroni-corrected planned *t*-tests revealed that adults had lower hippocampal pattern similarity for within-movie comparisons than across-movie comparisons, both when they had seen all or part of the movie before ($t(205) = 2.80$, $p = .01$) and when they had never seen the movie ($t(113) = 3.46$, $p = .002$; Figure 6A – Supplemental Figure 6A for subject-level). Interestingly, this pattern was only evident in children when they had been exposed to the movie before ($t(251) = 2.89$, $p = .008$), but not when they had never seen it ($t(147) = .55$, $p = .58$; Figure 6B – Supplemental Figure 6B for subject-level); there was moderate evidence for the null hypothesis for movies with no prior exposure ($BF_{01} = 8.33$) in children.

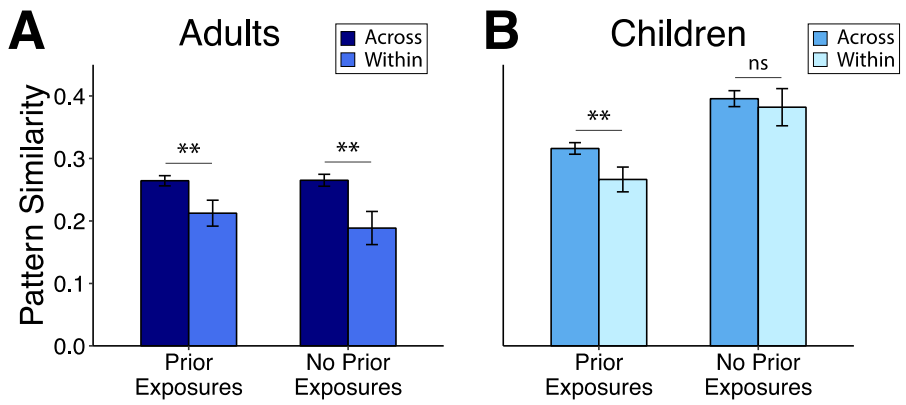

Figure 6. Prior exposure effects in hippocampus. Mixed-effect models conducted separately for (A) adults and (B) children investigating differences in pattern similarity within- and across-movies based on whether participants had prior exposures to the movies. ** $p < .01$, ns $p > .05$

Re-binning by Familiarity

Since there was an uneven distribution in the number of movies participants had been exposed to or not, we conducted the same analyses as above, but instead grouped exposure level into low familiarity ("never seen it" and "seen it at all") and high familiarity ("has seen it once or twice" and "watches often") to roughly equate the sample sizes in each familiarity level.

Grouped this way, there was no difference in the number of movies in each bin for either age group (all p's > .35). With this method, we found the same pattern of results: for movies with which adults were familiar, lower hippocampal pattern similarity was evident for clips from the same compared to different movies ($t(169) = 2.39$, $p = .04$), and the same was true when their familiarity with the movie was low ($t(149) = 3.88$, $p < .001$). Again, children only showed lower pattern similarity to clips from the same movie when they were familiar with the movie ($t(215) = 3.32$, $p = .002$), but not when they were less familiar with the movie ($t(183) = .25$, $p = .80$).

Differences by Age Group

Next, we returned to our original method of measuring exposure level (i.e., binning "never seen it" versus "seen only parts", "has seen it once or twice", and "watches often"). Using a difference score calculated as within – across movie correlations, we compared the level of prior exposure with the movies in each age group and found that there was no difference between the conditions in adults ($t(257.54) = -.85$, $p = .40$), with a Bayes Factor suggesting moderate evidence for the null ($BF_{01} = 5.56$). Similarly in children, the difference between within and across-movie comparisons did not differ by level of prior exposure ($t(284.5) = 1.20$, $p = .23$); however, this effect was marginally significant when binning by low and high familiarity (i.e., including "seen only parts" with "never seen it"; $t(383.08) = 2.02$, $p = .09$). We then asked if, among the clips with which participants had no prior exposure, there was a difference in within versus across comparisons by age group. We saw a marginally significant interaction between a model including only main effects of age group and correlation type and a model with their interaction term ($\chi^2 = 2.89$, $p = .09$)—a t-test revealed that adults' within-movie pattern similarity was significantly lower than that among children for clips to which they had no prior exposure ($t(259.88) = -4.85$, $p < .001$). While interpreting with caution given the marginal interactions,

this supports the idea that greater pattern dissimilarity—which we propose might help distinguish clips from the same movie—is taking place for adults in HPC even when they haven't seen the movie before, but only for children when they had prior exposure.

Child Group Age Effects

Finally, we tested whether there was a relationship in children between age and the difference between within- and across-movie similarity for movies with no prior exposure. There was no correlation between age and pattern similarity for movies that were unfamiliar to children (r = .002, p = .88), and there was moderate evidence for the null hypothesis (BF_{01} = 8.33). In all, this suggests that children do show hippocampal pattern similarity differences for shared vs. dissimilar content that are similar to adults', but perhaps only for information with which they have had previous exposures.

Discussion

We characterized the neural development of operations that distinguish between events that share many overlapping elements compared with those that do not across childhood and in adulthood. Our results demonstrate that both children and adults showed lower pattern similarity for related compared to unrelated video clips in HPC. Although participants in our study were not required to distinguish between similar stimuli as part of a behavioral task, we suggest that the neural dissimilarity for passively watching movies with overlapping content shown here is akin to previously reported processes from other research groups. These prior studies highlight a role for the HPC in generating dissimilar neural representations for related events in memory (Chanales et al., 2017; Favila et al., 2016). In our study, we showed that PRC and PHC (after controlling for potential confounds), pattern similarity differences between within- versus across-

movie comparisons were present only in adults. We speculate that perhaps children are not yet able to detect overlap between stimuli at the level of specific item and contextual details, although we cannot be certain what is driving these results since behavioral data was not collected. Further, the difference in within- versus across-movie similarity by level of prior exposure showed a marginally-significant interaction with age group in HPC; that is, children only showed differences in pattern similarity for overlapping versus distinct clips for movies they had seen prior to the study, while adults showed this effect regardless of exposure. This pattern of results suggests that prior or repeated exposures, which are known to benefit memory, may also boost neural operations supporting representational dissimilarity of mnemonic content in early childhood, although we can only speculate about the behavioral implications of our neural findings.

Research on non-human primates shows that the HPC continues to develop across childhood (Lavenex & Banta Lavenex, 2013) and prior behavioral work has demonstrated that the ability to retain specific aspects of episodes is still developing in early childhood (Benear et al., 2021; Ngo et al., 2018; Ngo, Lin et al., 2019) and is worse in children compared to adults (e.g. Keresztes et al., 2017; Ngo et al., 2018; Ngo, Newcombe, et al., 2019; Rollins & Cloude, 2018). In contrast to this prior work, we found that the neural patterns in HPC that may subserve pattern dissimilarity between related representations of encoded information are similar across age groups. These results may seem at odds, especially since the movies contained many related elements across contexts, but the findings dovetail well with prior literature when considering the moderating effects of prior exposure we found in children. Our results suggest that children may need more exposures to any given stimulus than adults to build robust knowledge of that stimulus, then leading them to show differences in representations for similar versus dissimilar

stimuli in HPC. Prior research has shown that young children often require multiple repetitions and exposures to retain information (Horst et al., 2011) and their general knowledge and schematic understanding of the world is still developing (Hudson, Fivush, & Kuebli, 1992; Pudhiyidath, Roome, Coughlin, Nguyen, & Preston, 2019). In light of this previous work, one possibility is that prior exposures to the movies might have provided children with a scaffold for recalling specifics of that movie in the face of lesser general knowledge when compared to adults. This in turn could allow them to show pattern similarity differences for clips from the same movie that share overlapping content. Following this line of reasoning, a single presentation might be sufficient for an adult to recall enough detail to distinguish between two similar stimuli because adults have superior episodic memory and greater schematic and general knowledge of the world than children. However, a single exposure may not be sufficient for children whose episodic memory abilities are not yet fully refined and whose general knowledge stores are still accruing. Overall, while behavioral investigations show that complex mnemonic abilities such as context binding are not at adult-like levels in children before age 6 (Benear et al., 2021; Newcombe, Lloyd, & Ratliff, 2007; Ngo et al., 2018), our results suggest the underlying neural machinery for these abilities exists before the behavior is fully developed and can be bolstered by prior knowledge. Future work could support these results by directly examining the role of operations that support representational dissimilarity in memory performance based on differing, experimentally manipulated levels of prior exposure to naturalistic stimuli in adults compared to children.

We also saw pattern similarity differences only for adults in PRC and PHC after accounting for potential confounds such as temporal autocorrelation. Because the results in PHC for children were not robust to accounting for effects of distance between clips or order of clip

presentation, we remain cautious about interpreting effects in PHC for children. The lack of significant effects in PRC and PHC for children suggest these two regions may become relevant to representational dissimilarity operations later in development. While HPC provides holistic representations of mnemonic content, PRC and PHC are regions important to the encoding of object and contextual details (Davachi, 2006; Eichenbaum et al., 2012), which young children are often not yet skilled at detecting in a single exposure when stimuli are unfamiliar and share many overlapping elements with other stimuli (e.g., Ngo, Lin, Newcombe, & Olson, 2019). The age-related differences we found in these two MTL regions underscore the importance of future work specifically investigating the structural and functional development of these regions and their association with memory performance in children, as they have been relatively understudied in the memory development literature. The fact that we found effects for adults in PHC and PRC as well as in HPC—the structure most commonly associated with neural dissimilarity among competing representations—was surprising given prior literature, and may be due to the nature of our experimental design. Specifically, the ability to dissimilarly represent scenes drawn from the same movies emphasizes picking up on individual characters or contextual details to distinguish between clips. Rather than encoding experimentally-designed, explicit images to later be recalled in a behavioral memory task (Chanales et al., 2017; Favila et al., 2016), participants in our study were simply passively watching naturalistic movie clips, so the difference in task design might have influenced our neural findings. The PHC has been shown to be sensitive to contextual novelty (Aminoff, Kveraga, & Bar, 2013) and recollection effects (Diana, Yonelinas, & Ranganath, 2012), so it is not necessarily surprising that we found similar results in this region as we did in HPC, since both are often engaged during encoding of contextually rich stimuli. Similarly, the PRC is known to participate in the coding of

semantically rich information, which is embedded in naturalistic stimuli such as video clips, and pattern similarity differences for these stimuli in PRC in adults may reflect nuanced differences in semantic information (Henson & Gagnepain, 2010). However, we note that the interpretation of these PHC and PRC findings are quite speculative, especially since we do not have mnemonic data to support our conclusions. Future work should address what is driving the pattern similarity differences in these cortical MTL regions for overlapping versus non-overlapping content in adults, which would provide insight into interpreting the ramifications for child development.

Further, our findings extend work in adults showing that prior exposure enhances pattern similarity differences in HPC by showing—with some caveats—the same phenomenon occurs in children with dynamic, naturalistic stimuli, which may better reflect real-world events than previously used stimuli. Taxing participants' memorization of static images is a commonly used paradigm in neuroimaging studies of human memory. However, the dynamically-unfolding videos used in our study more closely resemble how one experiences events in daily life, in which we do not expect to later be tested on what we experience, but it may nevertheless be adaptive to distinguish one event from another. Research looking at differences in pattern similarity for naturalistic stimuli in children that later tests their memory is needed to determine the nature of both operations that promote separation of neural signals and prior exposure effects in children and how they relate to memory performance.

An important limitation of our study is the small number of total trials used in both the within- and across-movie comparisons. However, our stimuli were movie clips ranging in length from 19-46 seconds, which results in capturing brain activation that is more similar to a blocked design response rather than a single trial estimate. Thus, we are likely getting robust responses to each of our individual videos. Additionally, given that data was collected from a developmental

population, scan times had to remain short to obtain usable data. Therefore, the small number of trials may be an intrinsic problem with the field of developmental cognitive neuroscience rather than our study in isolation.

Although we provide evidence that children as young as 4 years old show adult-like neural activation patterns in HPC, the younger children in our study were under-sampled. Thus, the absence of an age effect within our child group may be due to under-representation of the younger ages, which is particularly relevant given the developmental gains in episodic mnemonic performance that occur between the ages of 4 and 6 (Benear et al., 2021; Newcombe, Lloyd, & Ratliff, 2007; Ngo et al., 2018). Since many of the children in our sample were 6 years old or older, perhaps their memory systems were more mature, allowing for neural activation patterns that more closely resembled those of adults. Our results would be bolstered by future work examining pattern similarity in MTL regions in young children with behavioral memory measures and a larger sample size.

The present work demonstrates that children indeed show neural patterns in HPC in response to encoding of naturalistic stimuli that are like those of adults, although patterns in PRC and PHC demonstrate differences across the age groups, with effects present only in adults. Prior exposures to the stimuli influences the level of pattern similarity differences in HPC for shared versus distinct content in children, demonstrating that while adults may be able to orthogonalize related mnemonic representations after a single encounter with a set of stimuli, children may require multiple exposures in order to show adequate neural signatures of representational dissimilarity operations between similar representations. This work sets the foundation for indicating how structural integrity of the MTL may not completely predict the functional

operations of these systems and highlights the need to integrate across multiple levels of analysis to better understand the development of episodic memory.

Acknowledgements

This work was supported in part by National Institute of Health grants to V. Murty [R21 DA043568, K01 MH111991], S. Perlman [K01 MH094467, R01 MH107540], I. Olson [R01 MH091113] and I. Olson and N. Newcombe [R21 HD098509; R01 HD099165], and by a National Science Foundation Graduate Research Fellowship to M.C. Camacho [DGE-1745038]. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health or National Science Foundation.

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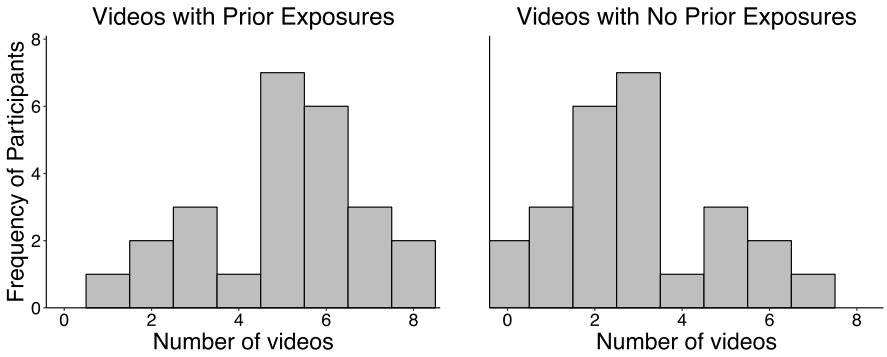
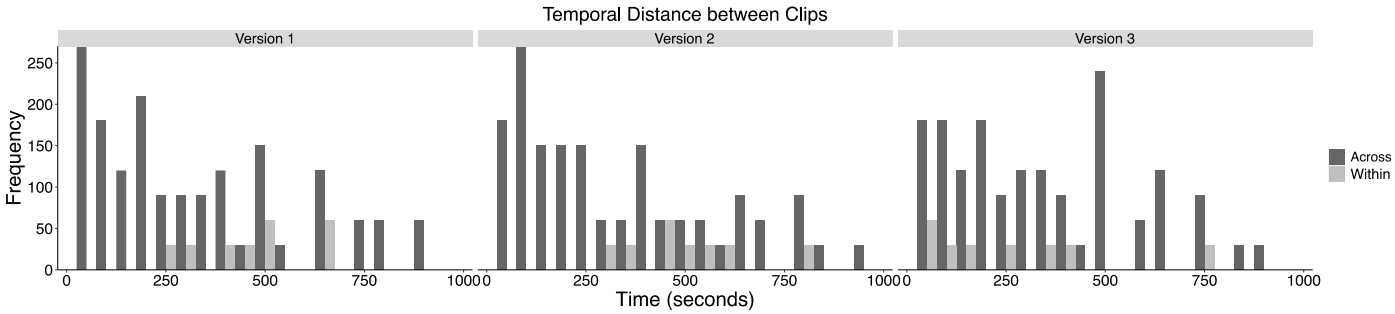
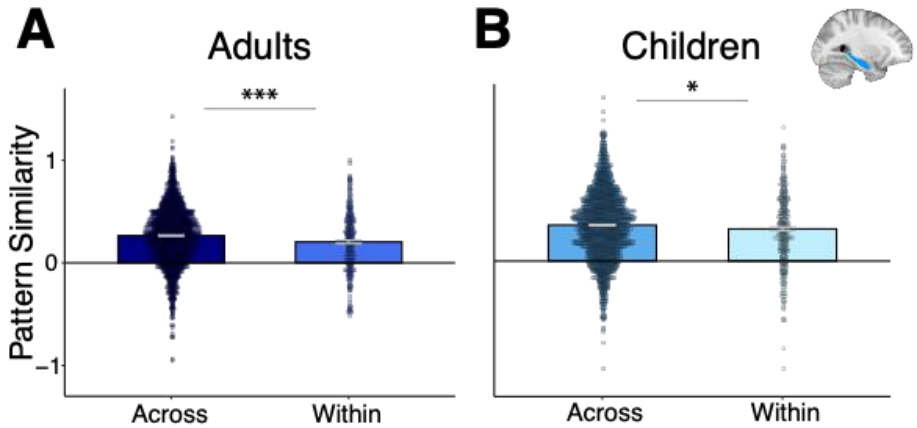
Supplemental Materials



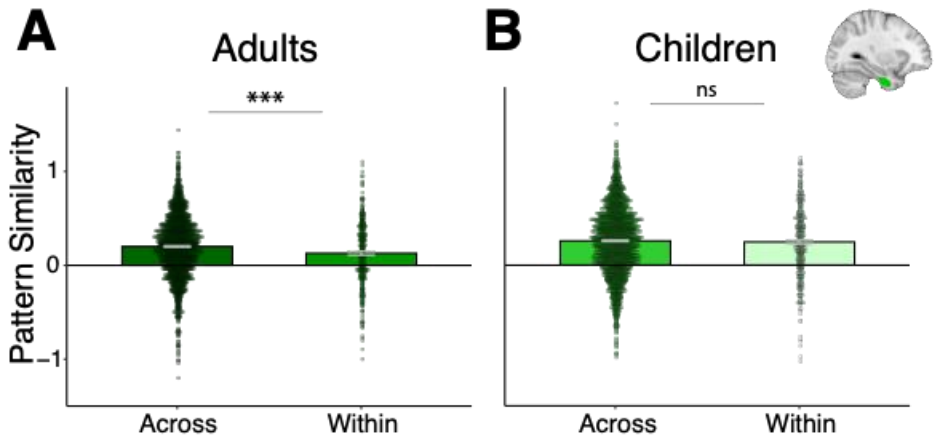
Supplemental Figure 1. Distribution of participants who rated videos as having prior exposures ('seen only parts', 'has seen it once or twice', or 'watches often') vs. no prior exposures ('never seen it').



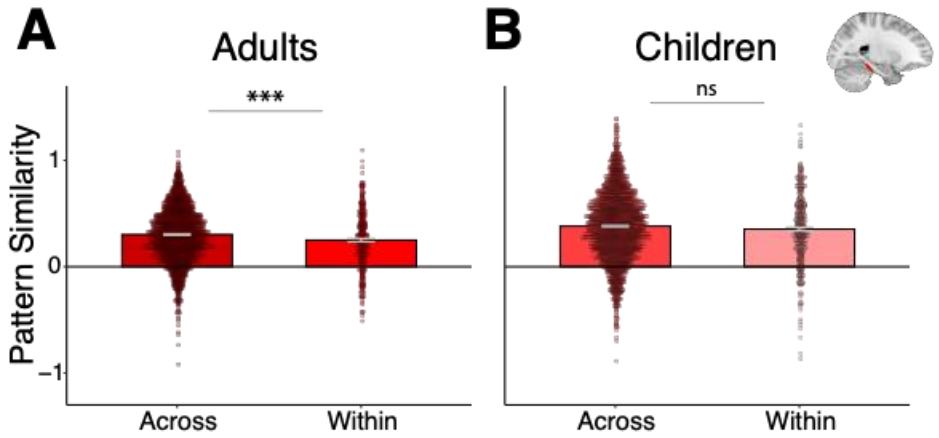
Supplemental Figure 2. Time in seconds between clips. Frequency represents the number of times each distance is present across movie comparisons across all participants The dark bars represent the average time between clips from different movies (i.e., across-movie) and the light bars represent the time between clips from the same movie (i.e., within-movie).



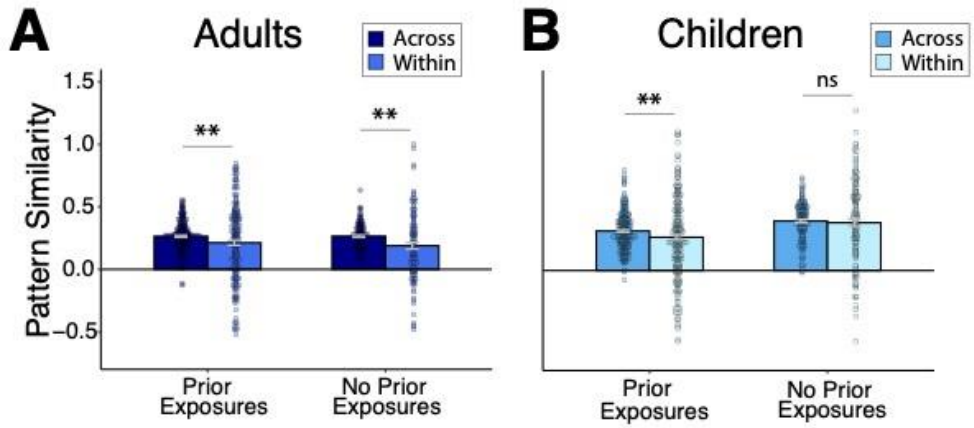
Supplemental Figure 3. RSA effects in hippocampus with subject-level dots overlaid on group-level bars.



Supplemental Figure 4. RSA effects in perirhinal cortex with subject-level dots overlaid on group-level bars.



Supplemental Figure 5. RSA effects in parahippocampal cortex with subject-level dots overlaid on group-level bars.



Supplemental Figure 6. Prior exposure effects in hippocampus with subject-level dots overlaid on group-level bars.