Neural Correlates and Reinstatement of Recent and Remote Memory: A Comparison Between Children and Young Adults

Iryna Schommartz[a,i], Philip F. Lembcke[b,c], Javier Ortiz-Tudela[a], Martin Bauer[b], M., Angela M. Kaindl[c,d,e,f], Claudia Buss[b,h]*, and Yee Lee Shing[a,i]*

* Yee Lee Shing and Claudia Buss should be considered joint senior author.

[a]Department of Psychology, Goethe University Frankfurt, Frankfurt, Germany
[b]Charité – Universitätsmedizin Berlin, Department of Medical Psychology, Berlin, Germany
[c]Charité – Universitätsmedizin Berlin, Department of Pediatric Neurology, Berlin, Germany
[d]Charité – Universitätsmedizin Berlin, Center for Chronically Sick Children, Berlin, Germany
[e]Charité – Universitätsmedizin Berlin, Institute of Cell- and Neurobiology, Berlin, Germany
[f]Charité – Universitätsmedizin Berlin, Department of Pediatric Surgery, Berlin, Germany
[h]Development, Health and Disease Research Program, Department of Pediatrics, University of California Irvine, USA
[i]Center for Individual Development and Adaptive Education of Children at Risk (IDeA), Frankfurt, Germany

***Corresponding authors at:** Department of Psychology, Goethe University Frankfurt, Frankfurt, Germany, Theodor-W.-Adorno-Platz, 6, 60323

E-mail addresses: schommartz@psych.uni-frankfurt.de (I. Schommartz),
shing@psych.uni-frankfurt.de (Y.L. Shing)

RESEARCH HIGHLIGHTS

- Children showed less robust memory consolidation across short and long delay compared to young adults.
- From short to long delay, children show differential neural upregulation for remote versus recent memory compared to young adults.
- Over time, both children and young adults showed reduced scene-specific reinstatement of neural patterns.
- Children relied more on gist-like neural reinstatement in anterior hippocampal and medial prefrontal brain regions.

Abstract

Memory consolidation tends to be less robust in childhood than adulthood. However, little is known about the corresponding functional differences in the developing brain that may underlie age-related differences in retention of memories over time. This study examined system-level memory consolidation of object-scene associations after learning (immediate delay), one night of sleep (short delay), as well as two weeks (long delay) in 5-to-7-year-old children (n = 49) and in young adults (n = 39), as a reference group with mature consolidation systems. Particularly, we characterized how functional neural activation and reinstatement of neural patterns change over time, assessed by functional magnetic resonance imaging combined with representational similarity analysis (RSA). Our results showed that memory consolidation in children was less robust and strong (i.e., more forgetting) compared to young adults. Contrasting correctly retained remote versus recent memories across time delay, children showed less upregulation in posterior parahippocampal gyrus, lateral occipital cortex, and cerebellum than adults. In addition, both children and adults showed decrease in scene-specific neural reinstatement over time, indicating time-related decay of detailed differentiated memories. At the same time, we observed more generic gist-like neural reinstatement in medial-temporal and prefrontal brain regions uniquely in children, indicating qualitative difference in memory trace in children. Taken together, 5-to-7-year-old children, compared to young adults, show less robust memory consolidation, possibly due to difficulties in engaging in differentiated neural reinstatement in neocortical mnemonic regions during retrieval of remote memories, coupled with relying more on gist-like generic neural reinstatement.

Keywords: object-scene associations, memory consolidation, representational similarity analysis, neural reinstatement, drift diffusion modelling

INTRODUCTION

Every day we form new memories that may become long-lasting through memory consolidation, a complex process in flux between encoding and retrieval (Dudai, 2012; Josselyn et al., 2015; Moscovitch & Gilboa, 2022; Semon, 1921).During systems-level consolidation, memory representations and traces are reorganized across medial temporal lobe and neocortical brain networks (Ranganath & Ritchey, 2012; Ritchey & Cooper, 2020). These networks include brain regions that are involved both in initial encoding and in integration of new memories as time passes (Axmacher & Rasch, 2017; Dudai, 2012; Moscovitch & Gilboa, 2022; Squire et al., 2015). While decades of work have shed light on general neural mechanisms of memory consolidation in adults (Moscovitch & Gilboa, 2022; Sekeres et al., 2017a; Winocur & Moscovitch, 2011), much less is known about neural mechanisms that support memory consolidation in children – a knowledge gap that we aimed to address with the current study.

Neural correlates of memory consolidation

Learning through repeated activation and reinstatement is one way to rapidly stabilize memory traces and make them accessible upon retrieval (Dudai, 2004; Nader & Hardt, 2009; Teyler & Rudy, 2007). For instance, in young adults, repeated exposure to word-image pairs during encoding, compared to single exposure, was shown to accelerate memory consolidation. This is achieved through enhanced replay of repeated events in the retrosplenial cortex (RSC) and the medial prefrontal cortex (PFC), as well as via increased hippocampal (HC)-cortical replay that promotes the associative word-object memories (Yu et al., 2022). In another study by Brodt et al. (2016), it was found that during repeated spatial navigation in a virtual environment, activation in the posterior parietal cortex (PPC), especially the precuneus, increased and remained elevated after 24 hours, while HC activity and HC-PPC connectivity declined with repeated encoding rounds (Brodt et al., 2016). In addition, neocortical plasticity measured by diffusion-weighted magnetic resonance imaging in the PPC (Brodt et al., 2018) and the cerebellum (Stroukov et al., 2022) supported rapid cortical storage of memory traces for object-location associations after repeated exposure in young adults 1 hour and 12 hours post-learning. Taken together, these findings indicate that repeated learning in young adults promotes fast creation of neural memory representations, which can remain stable for at least 24 hours and predict behavioural mnemonic performance.

Memory consolidation of well-learnt information does not end with the last learning cycle, but undergoes further neural reorganizing and modification over time (Roüast & Schönauer, 2023; Sekeres et al., 2017). For example, during cued recall of face-location associations, young adults who were tested 24 hours after learning, compared to 15 minutes, showed increased activation in the precuneus, inferior frontal gyrus (IFG), and fusiform gyrus, whereas the hippocampus showed a decrease in activation (Takashima et al., 2009). Similarly, increased activation in the anterior temporal cortex during the retrieval of studied figure pairs eight weeks prior was observed, while increased activation in the HC was shown for pairs learned immediately before retrieval (Yamashita et al., 2009). Furthermore, delayed retrieval of naturalistic video clips after the delay of seven days in young adults was associated with the increased activation in the lateral and medial PFC and decrease in HC and parahippocampal (PHG) activation over time (Sekeres et al., 2021). This is convergent with the notion that the role of the prefrontal cortex increases during recollection as consolidation progresses over time (Milton et al., 2011). Moreover, subsequently recollected memories showed higher post-rest HC-lateral occipital cortex (LOC) connectivity specifically related to scene-related mnemonic content, indicating the role of LOC in associative memory consolidation (Tambini et al., 2010). On the other hand, HC activation has been reported to remain stable after seven days (Sekeres, Winocur, Moscovitch, et al., 2018) three months (Harand et al., 2012) or even years (Söderlund et al., 2012) for consistent episodic memories that retained contextual details.

To summarize, in alignment with the Multiple Trace Theory (Nadel et al., 2000; Nadel & Moscovitch, 1997), studies have shown that memories of well-learned information increasingly engage cortical regions over time. There regions include the prefrontal, parietal, occipital, and anterior temporal brain areas, supporting the retrieval of general and schematic memories, as well as complex associative information. In line with the Standard Consolidation Theory, some studies have demonstrated a decrease in the recruitment of the HC over time (Squire & Alvarez, 1995). Conversely, and converging with the Contextual Binding Theory (Yonelinas et al., 2019) and the Multiple Trace Theory, some studies have shown that hippocampal involvement lingers over time, particularly for detailed and contextual memories. However, most research has focused on only a selected delay window and solely on young adults.

Mnemonic transformation and reinstatement across consolidation

In addition to changes in neural activation during mnemonic retrieval over time, it is important to characterize the transformations and reinstatement of neural representations (i.e., distinctive pattern of neural activity generated by a specific memory; Averbeck et al., 2006; Kriegeskorte, 2008; Kriegeskorte & Kievit, 2013) because the multivariate activity pattern of memory may change over time. For example, memory for perceptual details may become worse over time, while memory for gist may be more likely to stay stable, indicating differential time-related transformational trajectories (Sekeres et al., 2016). According to the Fuzzy Trace Theory (Reyna & Brainerd, 1995, 1998), detailed and gist-like memories may be uniquely present or coexist, depending on the strength of formed memories. For instance, detailed memories may generally fade away over time, preserving however its specific accurate nature for correctly recalled memories (Diamond et al., 2020). In other instances, weaker detailed memories may be reorganized over time, with lingering specific memories and parallel creation of gist-like generic memories. Little is known about how the neural representation of well-learned memories at retrieval is transformed across the consolidation period (i.e., phenomenon, when similar patterns of neural activity may be reactivated when memory is retrieved again; Clarke et al., 2022; Deng et al., 2021).

Using representational similarity analysis (RSA; Kriegeskorte, 2008), Tompary & Davachi (2017) showed that a one-week delay led to differential memory reorganisation in HC and mPFC for memories with and without overlapping features. Specifically, after a one-week mnemonic representations became more similar for memories with overlapping features, indicating consolidation-related gist-like neural reorganization. Moreover, the authors showed memory-specific reinstatement of neural patterns for specific memories in the right HC, indicated by significant encoding-retrieval similarity for remote but not recent memories. Comparing neural reinstatement of visual clips during encoding, immediate, and delayed recall (after 1-week-period), Oedekoven et al. (2017) showed reliable reinstatement in core retrieval networks, including the precuneus, medial temporal gyrus, occipital gyrus, HC, and PHG among others. In contrast to Tompary and Davachi (2018), this study found no time-related differences in reinstatement effects. Therefore, the findings on memory reinstatement are mixed, and, to date, no study have directly tracked the neural representations of memory traces for perceptual together with more abstract, gist-like features (e.g., semantic categories).

Neural correlates of memory consolidation and mnemonic transformation and reinstatement in middle childhood

Brain regions involved in memory consolidation show protracted developmental trajectories from early to late childhood (Badre & Wagner, 2007b; Ghetti & Bunge, 2012c; Gogtay et al., 2004; Keresztes et al., 2022; Lenroot & Giedd, 2006; Mills et al., 2016; Ofen et al., 2007; Shing et al., 2008), which could lead to differences in neural activity and/or patterns and subsequently mnemonic reinstatement between children and adults. For instance, univariate selectivity was reduced in children, while fine-grained neural representational similarity along the ventral visual stream was similar in 5-11 years old children and adults (Cohen et al., 2019; Golarai et al., 2015). Fandakova et al. (2019) also showed that the neural representational distinctiveness of information during encoding was similar in 8-to-15-year-old children and adults in the RSC, LOC and PHG. The fidelity of neural representations was also associated with subsequent memory in a similar way between children and adults. Overall, although these findings did not address the question of neural reinstatement directly in children, they suggest that mnemonic reinstatement may develop prior to univariate selectivity. However, it is yet to be investigated. Moreover, it is unclear whether the age-related differences in neural activation and reinstatement mentioned above are similar for memory consolidation. Specifically, to what extent does consolidation-related transformation of neural representations occur, and how does it impact neural reinstatement of mnemonic content in the developing brain?

In middle childhood, the trade-off between retaining vivid, detail-rich memories and their transformation into vague, gist-like memories due to delay may be more pronounced. Brainerd et al., (2002) demonstrated that, during development, specific memory and gist-memory for events emerge together. However, as children mature, they exhibit more false memories based on gist in the absence of exact memories for the events. On the other hand, Keresztes et al. (2018) postulated that younger children tend to rely more on generalization when forming new memories, while older children and adults use more specific detail-rich information, suggesting a shift from generalization to specificity as children mature. Hence, there are some inconsistencies in the theoretical postulations and findings regarding item-specific and gist-based memories that may impact memory consolidation in middle childhood. Investigation on the neural reinstatement patterns of item-specific and gist-like memories across time may add to the understanding of these inconsistencies in children.

Aim of the current study

In this study, we examined the univariate neural activation and multivariate neural reinstatement patterns of memories for object-location associations across a short delay (after one night of sleep) and a long delay (after a 2-week period), relative to recently consolidated memories (after 30 minutes). Children (5-to-7-year-old) were compared to young adults serving as a reference group with a mature memory consolidation system. We selected 5 to 7 years as the age range of interest because previous studies showed a large improvement in associative memory around this age (Sluzenski, Newcombe, & Kovacs, 2006). Practically, this is also the youngest age range in which MRI scanning coupled with active task execution could be applied relatively successfully. We hypothesized (i) according to the Multiple Trace Theory, an increasing involvement of prefrontal, parietal, cerebellar, occipital and PHG brain regions over time in adults in comparison to children, as these regions are still maturing in preschool and early school-aged children (Ghetti & Bunge, 2012b; Keresztes et al., 2022; Lebel et al., 2012; Shing et al., 2008, 2010a); (ii) according to the Contextual Binding Theory, the Multipe Trace Theory, and supported by the evidence from Sekeres, Winocur, & Moscovitch (2018), a stable involvement of HC over time in adults and children due to relative maturity of the HC in middle childhood and detailed contextual nature of the repeatedly learned information (Keresztes et al., 2017; Nadel et al., 2000; Sekeres, Winocur, Moscovitch, et al., 2018; Shing et al., 2008; Sluzenski et al., 2006; Yonelinas et al., 2019); (iii) a decreasing neural reinstatement in all ROIs over time, with this decrease being more pronounced in children compared to young adults (Cohen et al., 2019; Golarai et al., 2015); (iv) different contributions of category- and item-specific memories to neural reinstatement across age groups. Specifically, we expected more gist-like memory pattern reinstatement in children in comparison to more detailed item-specific neural pattern reinstatement in young adults over time due to differences in the strength of formed memories and differences in underlying associative and strategic components of memories (Reyna & Brainerd, 1995; Shing et al., 2008, 2010).This assumption aligns with the Fuzzy Trace Theory (Brainerd & Reyna, 2002) that verbatim memories can be created without the extraction of gist. Due to ongoing maturation of associative and strategic memory components and their underlying neural substrates, children may be more inclined to extract gist information at the expense of detailed or gist-like information.

RESULTS

Behavioural results

Final Learning Performance

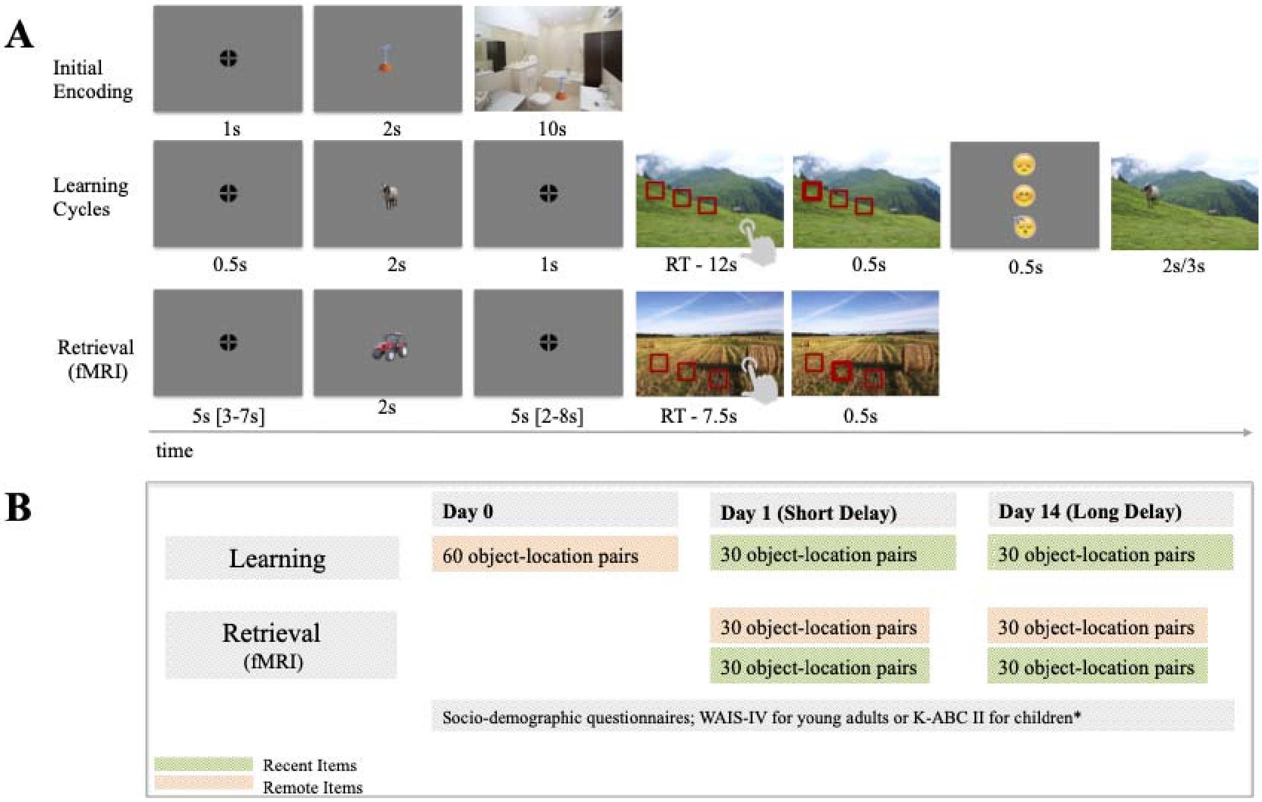
Unique sets of object-location association pairs were learned on Day 0, Day 1, and Day 14. During each initial encoding trial, participants were presented with an object within a congruent scene (e.g., a fox in a spring pine tree forest), and were asked to memorize the exact location on the object within the scene by creating a story and making “mental” pictures of the scene. The choices for locations varied across scenes while they remained constant across time within individuals. There were 18 unique key locations among which object could be distributed, resulting in a heterogenous set of locations for objects. We employed an adaptive, repetitive learning-to-criteria procedure to ensure initially strong memories (see Fig. 1A for the task overview and Fig. 1B for experimental procedure overview). Before learning began, participants were instructed to create stories to help them memorize the locations of the objects within the scenes. They practiced this strategy on two unique sets of five object-location associations. Subsequently, the learning began with the first encoding block. Following each encoding block, the repetitive learning-to-criteria started. During learning, participants were presented with the scenes again, but with three rectangles indicating possible locations for the previously learned objects. The choice options for the three alternative forced choice task (3AFC) were distributed variably: for some instances, the “correct” answer was the left option, for some instance – it was the middle option, and for other instances it was the right option. Therefore, the correct performance in the task required detailed and precise memory for locations. Moreover, the choice options were presented rather close together in the scene, requiring higher level of differentiation among the options. Participants were asked to choose one rectangle that corresponded to the correct location of the object within the scene (Fig 1A “Learning Cycles”). Regardless of accuracy, the object was shown again in the correct location. The learning procedure was repeated at least two times and maximally four times or until the response accuracy of 83% was reached within one cycle.

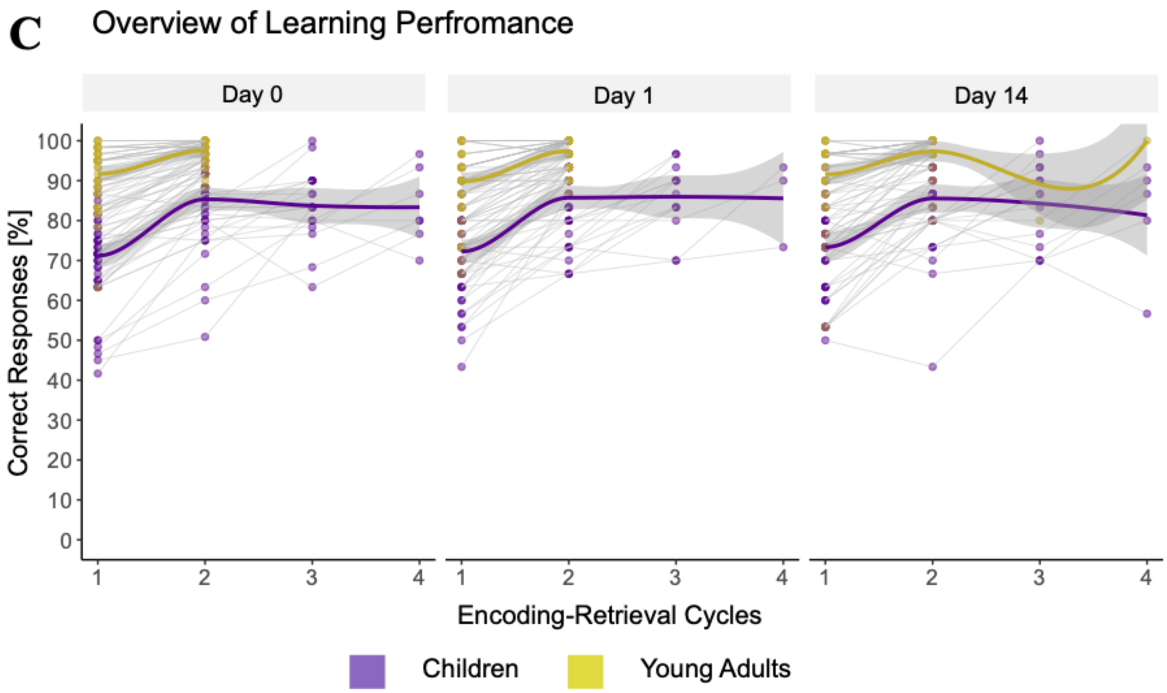
Concerning number of learning cycles, the linear mixed effects (LME) model revealed a significant *Group* effect, $F_{(1,563)} = 7.09$, p $.008$, $w^2 = .01$, with children needing more learning cycles to reach the learning criteria in comparison to adults, $b = -.43$, $t_{(563)} = -2.66$, $p = .008$. On average, children needed between two to four learning-retrieval cycles to reach the criterion of

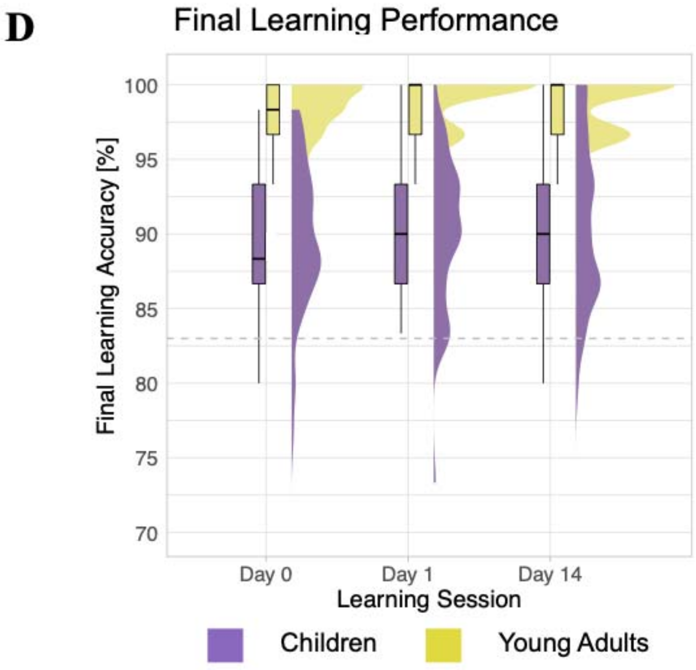
83% correct responses, while young adults required on average two cycles (Fig. 1C). The number of learning cycles did not differ between sessions as revealed by non-significant *Session* effect and *Group x Session* interaction (all p > .40).

For final learning accuracy, operationalized as percentage of correctly identified locations relative to the total number of locations, the LME model revealed a significant effect of *Group*, $F_{(1,79)} = 94.31$, $p < .001$, $w^2 = .53$, showing higher overall final accuracy in young adults in comparison to children $t_{(185)} = 7.55$, $p < .001$ (Fig. 1D). No *Session* effect (p = .79) or *Session x Group* interaction was significant (p = .96), indicating a stable level of final learning accuracy in each age group across sessions with different stimuli sets. Although the learning procedure was adaptive, the memory performance of children was inferior to that of young adults at the end of learning.

Figure 1







(A) Trial Structures in the Experimental Task. (i) In the *Initial Encoding* phase, participants were instructed to remember object-location pairs by creating a story or making a "mental photo" of the scene, memorizing the exact location of each object within the scene. (ii) In the *Learning Phase*, participants chose one location out of three choices and received feedback for their response. The feedback was given in the form of a smiley face, with a happy face denoting a correct answer, a sad face denoting an incorrect answer, and a sleeping face denoting a missed response. After receiving feedback, the correct object-location association was shown again. (iii) In the *Retrieval Phase* participants chose the location of the object in the scene out of three options without feedback. The retrieval phase took place in the MR scanner. **(B) Experimental Procedure**. The testing took place across three days. On Day 0, participants learned 60 object-location associations (remote items). On Day 1, participants learned 30 new object-location associations (recent items). For retrieval (short delay), 30 remote pairs learned on Day 0 and 30 recent pairs learned on Day 1 were retrieved. A similar procedure was followed on Day 14 (long delay), with another 30 new object-location associations. Across all testing days, participants also completed socio-demographic questionnaires and other psychometric tests, which were distributed across sessions. *Note*: RT – reaction time; s – second, fMRI – functional magnetic resonance imaging. **(C) Overview of Learning Performance**. Children needed on average between two to four learning-retrieval cycles to reach the criterion of 83% correct responses, while young adults needed on average two cycles. **(D) Final Learning Performance.** Final learning accuracy is calculated as the percentage of correct responses during the last learning cycle for both children and young adults. Final learning accuracy was significantly higher in young adults compared to children across all sessions. Grey dashed line indicates the criteria of 83% correctly learned items.

Memory Retention Across Time

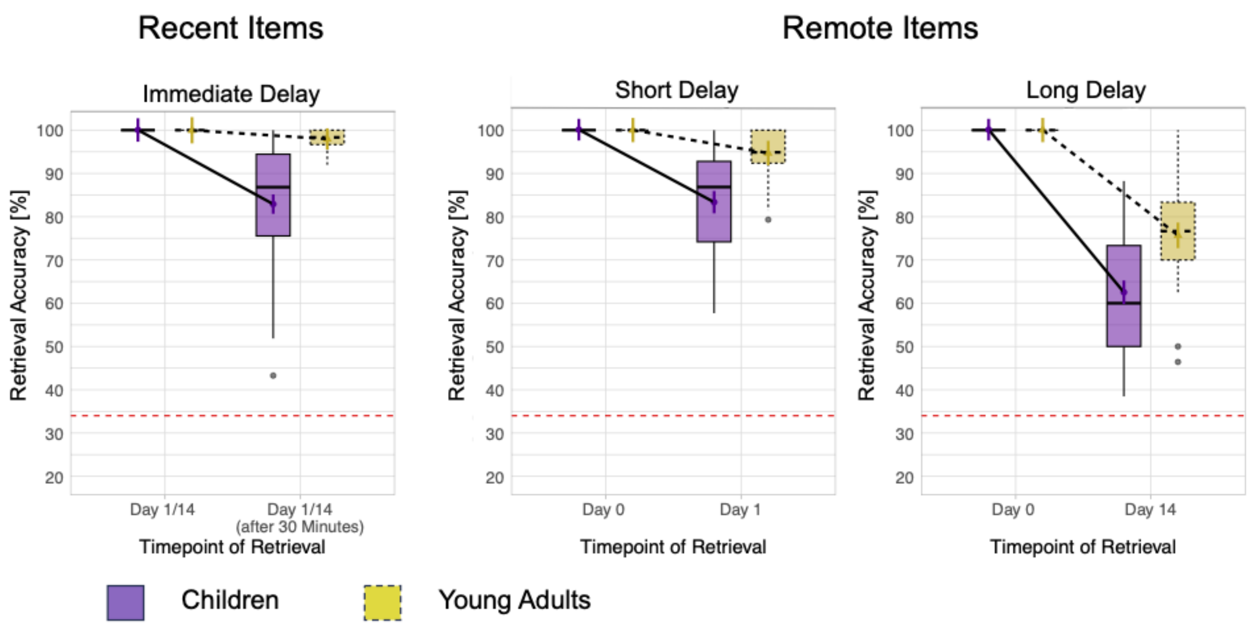
Change in memory retention was investigated during the retrieval part of the memory task (Fig. 1A “Retrieval (fMRI)”). Participants were cued with the object and were instructed to recall as vividly as possible the associated scene and location of the object within the scene during the fixation time window, where no visual input was presented on the screen. After that the associated scene with three choice options was presented and participants had to choose one rectangle denoting the correct location of the object in the scene (see Methods for more details).

First, we investigated whether retention rates for recent items initially correctly learned on Day 1 and Day 14 differed between sessions in children and adults. We observed no significant *Session x Group* interaction, $F_{(1,75)} = 1.77$, $p = .187$, $w^2 = .001$, indicating that the difference between retention rates for recent items on Day 1 and Day 14 for initially correctly learned items did not significantly differ between children and young adults. Based on that, we collapsed recent retention rates across sessions in each group for the further analysis.

Second, we examined change in memory retention rates for items that were initially correctly learned (i.e., initially strong memories) particularly testing for group differences in recent and remote (short- and long-delay) memory retention in relation to baseline of 100% (see Fig. 2, Supplementary Table S1 for a full overview). The linear mixed-effects model for retrieval accuracies of learned object-location pairs explained a significant amount of variance, $R^2 = .77$, 95% CI [.73 – .81]. We observed a significant main effects of *Item Type*, $F_{(3,250)} = 229.18$, $p < .001$, $w^2 = .73$, indicating overall no difference between recent memory retention compared to short delay remote memory retention, $b = 1.49$, $t_{(259)} = 1.26$, $p = .754$, but higher recent memory retention compared to long delay remote memory retention, $b = 21.36$, $t_{(259)} = 17.59$, $p < .001$, and higher short delay remote memory retention compared to long delay remote memory retention, b = 19.88, $t_{(260)} = 16.16$, $p < .00$. Further, we observed a significant main effect of *Group*, $F_{(1,85)} = 55.00$, $p <.001$, $w^2 = .38$, indicating overall lower memory retention in children compared to young adults, b = -11.1, $t_{(91)} = -7.20$, $p < .001$. Additionally, we observed a significant *Item Type* x *Group* interaction, $F_{(3,250)} = 17.35$, $p < .001$, $w^2 = .16$. Model-based Sidak post hoc comparisons revealed that in children group there was a significant decline in memory retention rates for correctly learned recent items, b = 17.18, $t_{(254)} = 11.09$, $p < .001$, short delay remote items, b = 16.74, $t_{(255)} = 10.60$, $p < .001$, and long delay remote items, b = 37.45, $t_{(260)} = 22.87$, $p < .001$. In young adults' group, there was no significant decline in memory retention rates for correctly learned recent items, b = 1.91, $t_{(254)} = 1.10$, $p = .983$, but for short delay remote items, b = 5.32, $t_{(254)} = 3.05$, $p = .033$, and long delay remote items, b = 24.37, $t_{(258)} = 13.58$, $p < .001$. Additionally, the slope of memory retention decline was significantly steeper in children compared to adults for recent items, b = 15.26, $t_{(254)} = 6.56$, $p < .001$, for short delay remote items, b = 11.41, $t_{(255)} = 4.84$, $p < .001$, and for long delay remote items, b = 13.08, $t_{(258)} = 5.38$, $p < .001$. Furthermore, we observed that memory retention rates significantly increased with age in the child group for recent items, b = .89, t = 2.62, $p = .016_{\text{(FDR-corrected)}}$, for short delay remote items, b = .91, t = 2.67, $p = .016_{\text{(FDR-corrected)}}$, but not for long delay remote items, b = .15, t = .326, $p = .747_{\text{(FDR-corrected)}}$.

Taken together, both age groups showed a decline in memory performance over time. However, compared to young adults, children showed a steeper slope of memory decline for both immediate recent and remote short and long delay memories. In sum, the results showed that children had overall worse memory retention rates compared young adults, indicating less robust memory consolidation in children.

Figure 2



Retention rates for initially correctly learned items. Memory accuracy is operationalized as the percentage of correct responses in the retrieval task conducted during the MRI scanning sessions for items that were initially correctly learned, indicating initially strong memories. Memory accuracy for recently consolidated items did not differ between sessions in young adults and children and was collapsed across recent memory accuracy on Day 1 was higher than on Day 14. Memory accuracy for remotely consolidated items differed between sessions in both young adults and children, showing higher remote memory accuracy on Day 1 than on Day 14. All tests used Sidak correction for multiple comparisons. Red dashed line indicates the threshold for random performance. *p < .05; **p < .01; ***p < .001(significant difference); non-significant differences were not specifically highlighted. Error bars indicate standard error based on the underlying LME-model.

fMRI Results

Mean activation for remote > recent memory in ROIs.

To investigate the change in the neural activation for correctly recalled memories from short to long delay, we analysed the difference in neural activation for the contrast remote > recent across age groups and sessions during the object presentation time window. We controlled for sex, handedness, general intelligence score, and mean reaction time. In the following section, the results of the univariate analysis of the selected ROIs based on the object presentation time window (Fig. 1A "Retrieval fMRI) are summarized, with a full statistical report on LME-model in Supplementary Table S6. Results for the whole-brain analyses are available in Supplementary Tables S3-5. All main and interaction effects are adjusted for multiple comparisons with False Discovery Rate (FDR). All post hoc tests were Sidak-corrected.

Our results showed that for the **anterior and posterior HC** (Fig. 3A) as well as for the **anterior PHG** (Fig. 3B)**,** the mean signal difference for the contrast of remote > recent remained similar across age groups and across sessions (all $p > .430_{\text{FDR-adjusted}}$), indicating similarly elevated mean blood oxygen level-dependent (BOLD) signal intensity for recent and remote memories across time in both age groups. An additional analysis conducted for recent and remote neural activation measures (for more detailed results refer to Fig. S2 and Table S7) revealed that all activations measures in both age groups we significantly higher than zero (all $p < .028_{\text{FDR-adjusted}}$) other than for recent Day1 posterior hippocampus in children ($p = .14_{\text{FDR-adjusted}}$).

For the **posterior PHG** (Fig. 3B), we observed a significant *Session x Group* interaction, $F_{(1,83)} = 9.54$, $p = .020_{\text{FDR-adjusted}}$, $w^2 = .09$, indicating more pronounced increase in remote > recent mean signal difference from Day 1 to Day 14 in young adults compared to children, $b = .11$, $t_{(83)} = 3.09$, $p = .003$. Similarly, also in the ***cerebellum*** (Fig. 3C) a significant *Session x Group* interaction, $F_{(1,161)} = 7.68$, $p = .020_{\text{FDR-adjusted}}$, $w^2 = .04$, indicated stronger increase in remote > recent mean signal difference from Day 1 to Day 14 in young adults compared to children, $b = .09$, $t_{(160)} = 2.77$, $p = .006$.

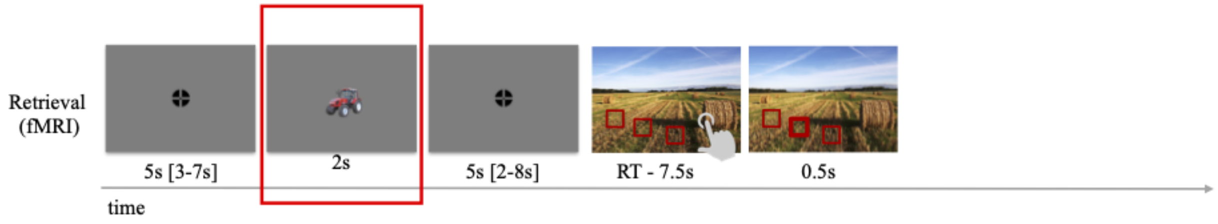
For the ***mPFC*** (Fig. 3D), there was a significant main effect of *Group*, $F_{(1,86)} = 7.61$, $p = .023_{\text{FDR-adjusted}}$, $w^2 = .07$, denoting lower remote > recent mean signal difference in young adults compared to children, $b = -.10$, $t_{(86)} = -2.76$, $p = .007$. In the ***vlPFC*** (Fig. 3E), a significant main effect of *Group*, $F_{(1,82)} = 31.35$, $p = <.001_{\text{FDR-adjusted}}$, $w^2 = .13$, highlighted lower remote > recent mean signal difference in children compared to young adults, $b = -.125$, $t_{(108)} = -3.91$, $p < .001$. In addition, in the **vlPFC** (Fig. 3E), we observed a significant main effect of *Session*, $F_{(1,99)} = 10.68$, $p = .005_{\text{FDR-adjusted}}$, $w^2 = .09$, pointing out that remote > recent mean signal difference was higher on Day 14 compared to Day 1, $b = .08$, $t_{(99)} = 3.27$, $p = .001$.

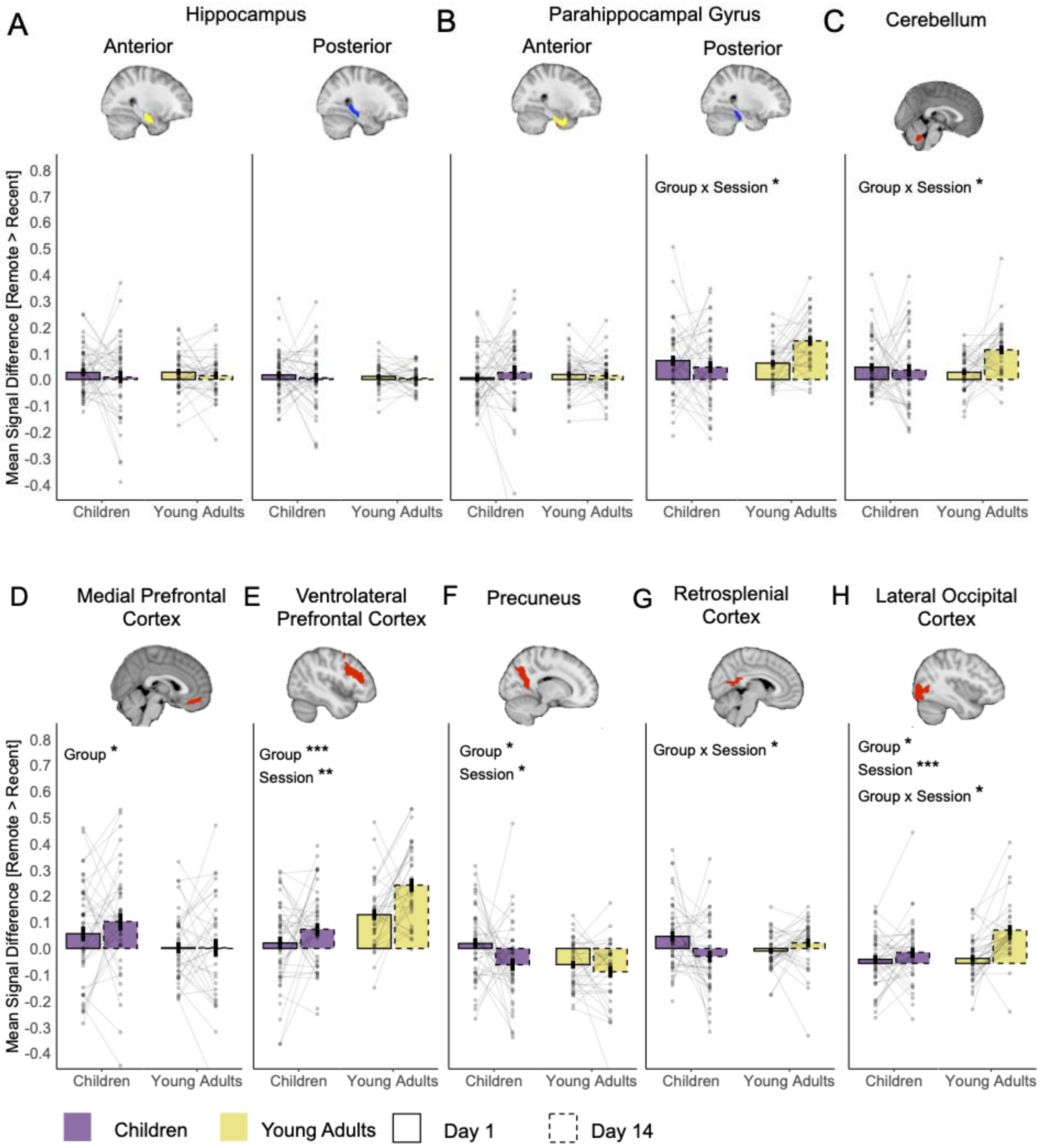
In the ***precuneus*** (Fig. 3F), a significant main effects were observed for both *Group*, $F_{(1,161)} = 5.09$, $p = .027_{\text{FDR-adjusted}}$, $w^2 = .02$, and *Session*, $F_{(1,161)} = 6.50$, $p = .036_{\text{FDR-adjusted}}$, $w^2 = .03$. There was a lower remote > recent mean signal difference in adults compared to children, $b = -.05$, $t_{(160)} = -2.26$, $p = .025$, and for Day 14 compared to Day 1, $b = -.05$, $t_{(160)} = -2.55$, $p = .012$. For the ***RSC*** (Fig. 3G), a significant *Session x Group* interaction, $F_{(1,161)} = 8.56$, $p = .020_{\text{FDR-adjusted}}$, $w^2 = .04$, showed a greater decrease in remote > recent mean signal difference from Day 1 to Day 14 in children than in young adults, $b = -.10$, $t_{(160)} = -2.93$, $p = .004$. In the

LOC (Fig. 3H), a significant main effect of *Group*, $F_{(1,82)} = 9.12$, $p = .015_{\text{FDR-adjusted}}$, $w^2 = .09$, indicated a higher remote > recent mean signal difference in young adults compared to children, $b = .07$, $t_{(82)} = 3.02$, $p = .003$. Additionally, a significant main effect of *Session*, $F_{(1,97)} = 16.76$, $p = <.001_{\text{FDR-adjusted}}$, $w^2 = .14$, showed an increase in remote > recent mean signal difference on Day 14 compared Day 1 across age groups, $b = .07$, $t_{(97)} = 4.10$, $p = <.001$. Furthermore, a significant *Session x Group* interaction, $F_{(1,81)} = 6.42$, $p = .032_{\text{FDR-adjusted}}$, $w^2 = .06$, demonstrated higher increase in remote > recent mean signal difference from Day 1 to Day 14 in adults compared to children, $b = .09$, $t_{(81)} = 2.53$, $p = .013$.

In summary, our findings revealed distinct consolidation-related neural upregulation for remote memory between children and adults. From Day 1 to Day 14, adults showed higher increase in remote > recent signal difference for remembered items in the posterior PHG, LOC, and cerebellum than children. Adults showed overall higher remote > recent difference in the vlPFC than children, while children showed overall higher remote > recent difference in the mPFC than adults. Furthermore, we observed a constant activation of anterior and posterior HC and anterior PHG in memory retrieval across age groups irrespective of memory type or delay.

Figure 3





Mean Signal Differences Between Correct Remote and Recent Memories.

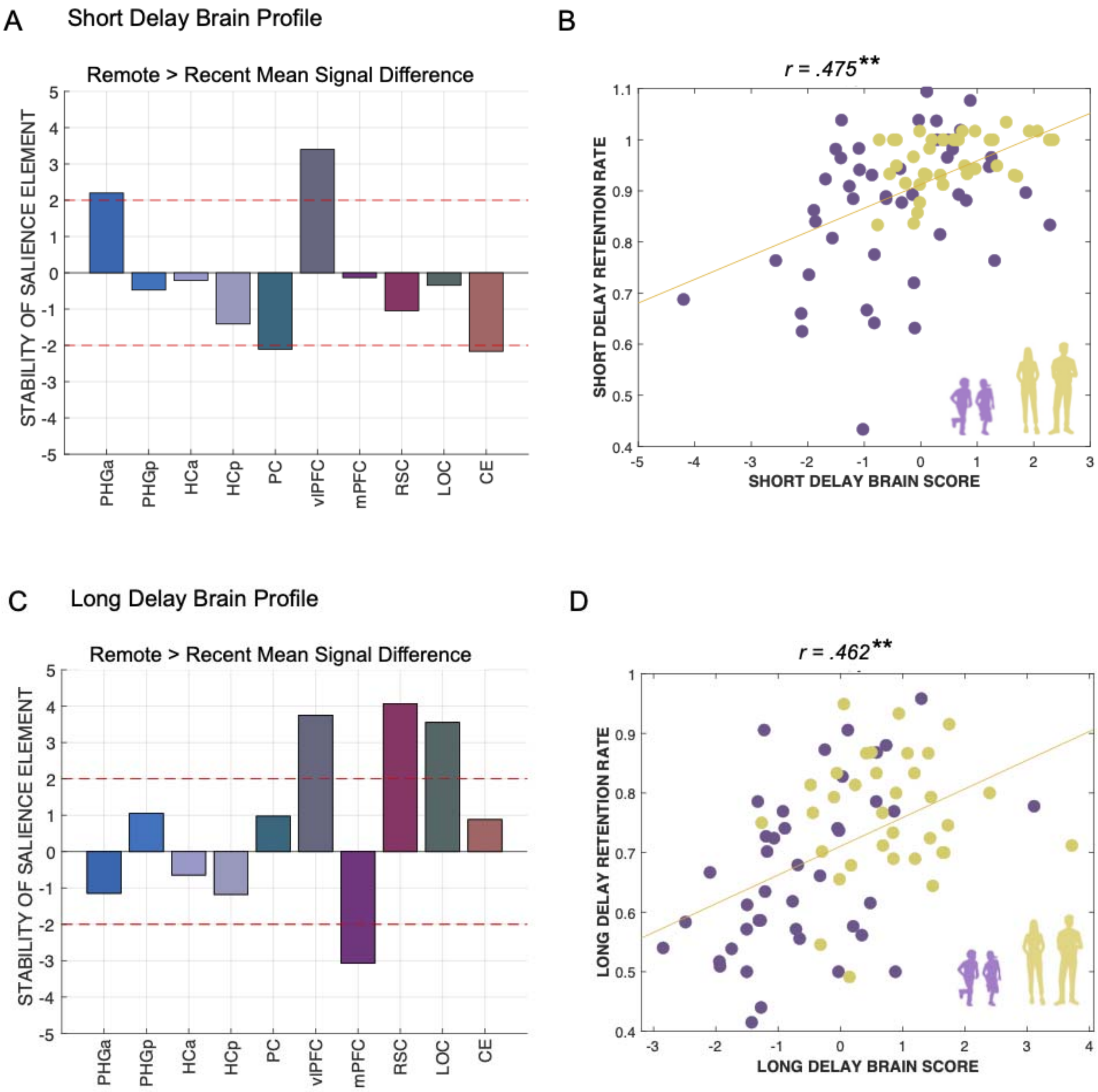
The figure presents mean signal difference for remote > recent memories on Day 1 and Day 14 in children and adults during the object presentation time window in **(A)** anterior and posterior hippocampus; (**B**) anterior and posterior parahippocampal gyrus; **(C)** cerebellum; **(D)** medial prefrontal cortex; **(E)**ventrolateral prefrontal cortex; cerebellum; **(F)** precuneus; **(G)** retrosplenial cortex; **(H)** lateral occipital cortex. *Note:* Bars represent the average signal difference. The colour indicated the age groups: purple for children and khaki yellow for young adults. Solid-lined bars represent data from Day 1, while dashed-lined bars depict data from Day 14. Across all panels, mean of individual subject data are shown with transparent points. The connecting faint lines reflect within-subject differences across sessions. Error bars indicate standard error of the mean. **p* < .05; ***p* < .01; ****p* < .001(significant difference); non-significant differences were not specifically highlighted. Significance main and interaction effects are highlighted by the corresponding asterisks. All main and interactions p-values were FDR-adjusted for multiple comparisons.

Neural-behavioural Correlation

We further investigated whether neural upregulation (i.e., remote > recent univariate signal difference) is related to memory performance. Specifically, considering all ROIs simultaneously and differential directionality of remote > recent signal differences, we investigated whether any specific profile of ROI constellation of neural upregulation is related to variations in memory performance. For this purpose, we employed the partial least square correlation analysis (PLSC; Abdi, 2010; Abdi & Williams, 2013). With regard to the interconnectedness of the predefined ROIs, the PLSC is a well-suited method to address multivariate associations between neural measures and memory measures. Consequently, latent variables that represent differential profiles of ROI's neural upregulations with robust relation with either short- or long-delay variations in memory performance were extracted (for more detailed description of the PLSC method, refer to Method section). In addition, we derived for each subject a value that denotes a within-person robust expression of either short- or long-delay brain profile.

For each delay, the permutation test of significance resulted in a single latent variable that reliably and optimally represents across age groups (i) the associations of short delay ROI neural upregulations with variations in short-delay memory accuracy (Fig. 4A; r = .536, p = .0026); and (ii) the associations of long delay ROI neural upregulations with variations in long-delay memory accuracy (Fig. 4C; r = .542, p = .0024). With further bootstrapping, we identified Z-scores estimates of robustness (larger/smaller than ± _1.96 (a < 0.05)) of the components within the multivariate brain profiles across all participants. Thus, for short delay, we observed that higher memory accuracy was robustly associated with greater neural upregulations in the anterior PHG (Z-score = 2.161, r = .347) and vlPFC (Z-score = 3.457, r = .640), as well as with lesser neural upregulation in precuneus (Z-score = -2.133, r = -.323) and cerebellum (Z-score = -2.166, r = -.371) across age groups. In contrast, for long delay, we observed that higher memory accuracy was robustly associated with greater neural upregulation in the vlPFC (Z-score = 3.702, r = .492), RSC (Z-score = 4.048, r = .524), and LOC (Z-score = 3.568, r = .455), and with lesser neural upregulation in mPFC (Z-score = -2.958, r = -.394) across age groups. The identified latent variables indicate that substantial amount of variance (short delay: r = .536 and long delay: r = .542) in either short- or long-delay memory performance was accounted by the identified differential functional profiles of brain regions.

Figure 4



Multivariate short- and long-delay brain profiles of neural upregulation (remote versus recent neural activation differences) are associated with variations in memory accuracy. A) *Short Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite short-delay brain profile. Stability of salience elements is defined by Z-scores (depicted as red line: a value larger/smaller than ± _1.96 is treated as reliably robust at (a <0.05). B) *Association between Short Delay Retention Rate and Short Delay*

Brain Score. Within-participant short delay brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against short delay memory retention rates defined as percentage of correctly recalled items on Day 1 relative to Day 0. C) *Long Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite long-delay brain profile. D) *Association between Long Delay Retention Rate and Long Delay Brain Score*. Within-participant long delay brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against long delay memory retention rates defined as percentage of correctly recalled items on Day 14 relative to Day 0. *Note:* PHGa – anterior parahippocampal gyrus; PHGp – posterior parahippocampal gyrus; HCa – anterior hippocampus ; HCp – posterior hippocampus; PC– precuneous; vlPFC – ventrolateral prefrontal cortex; mPFC – medial prefrontal cortex; RSC – retrosplenial cortex; LOC – lateral occipital cortex; CE – cerebellum; r – Spearman's rank order correlation index.

Identified brain profiles across groups suggest shared patterns between neural mean signal differences in differential sets of ROIs and memory accuracy are consistent across children and adults. However, the strength of this relationship may still differ. To investigate this, we examined with linear regression whether brain score (i.e., weights of the latent variable) predict memory retention rates differentially in the two groups. The results revealed that this relationship was similar between both age groups, as highlighted by non-significant *Brain Score x Group* interactions for both short delay, $F = .52$ $p = .473$, $w^2 = .00$, and for long delay, $F = 3.67$ $p = .059$, $w^2 = .03$. Based on this, we ran Spearman's rank-order correlation analyses across both age groups to identify the strength of the relationship. For short delay, we observed that the stronger expression of brain score was moderately associated with higher memory performance (Fig. 4B), $r = .456$, $p < .001_{\text{FDR-adjusted}}$. Furthermore, for long delay, the results showed that stronger expression of brain score was also moderately associated with higher long-delay memory performance (Fig. 4D), $r_{(76)} = .473$, $p < .001_{\text{FDR-adjusted}}$.

Taken together, differential short- and long-delay brain profiles of neural upregulation were related to variations in memory accuracy. Despite age-related differences in the derived brain scores, higher expression of within-participant brain score was associated with higher memory retention rates in short and long delay similarly in children and young adults.

Representational similarity results.

In addition to distinct univariate neural upregulation for recent and remote memories, children and adults may exhibit differences in neural representations of these memories. Over time, these representations could also undergo consolidation-related transformations. To address this further, we investigated both more differentiated detailed scene-specific and more generic gist-like neural representations in children and adult.

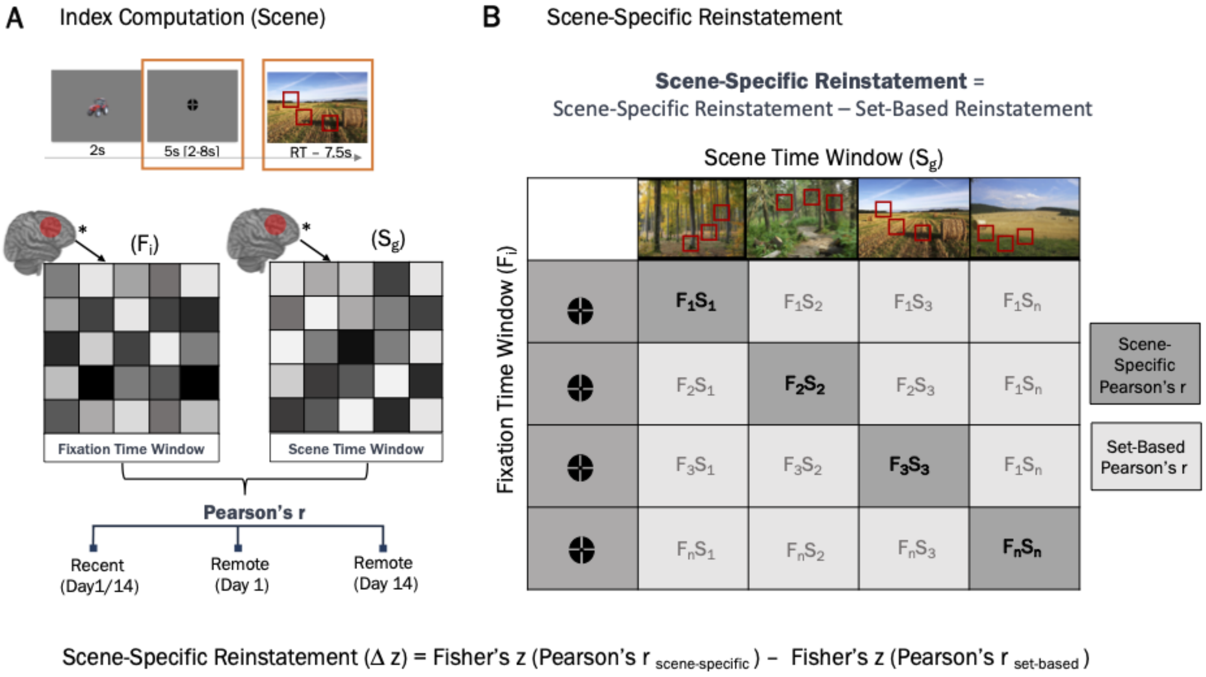
3.2.2.1 *Corrected scene-specific reinstatement.*

To measure how scene-specific reinstatement at retrieval during fixation time window (after short cue by object presentation; see Fig 1A (Retrieval) and Fig. 5A) changes over time as memories decay, we computed a *scene-specific reinstatement index* for each neural RSM. We hypothesized that neural patterns evoked by reinstatement of a specific scene without any visual input during fixation time window would be similar to neural patterns evoked by actual presentation of the scene during the scene time window. Therefore, the scene time window was used as a template against which the fixation period can be compared to. Participants were explicitly instructed to recall and visualize the scene and location of the object during fixation time window after being cued by the object. Since the locations were contextually bound to the scene and each object had a unique location in each scene, the location of the object was always embedded in the specific scene context.

To investigate how successful scene-specific reinstatement changes over time with memory consolidation, all analyses were restricted to correctly remembered items (Fig. 5). For each specific scene, the correlation between neural patterns during fixation "*fixation period*" and neural patterns when viewing the scene "*scene period*" was conducted (Fisher-transformed Pearson's r; Fig. 5B). A *set-based reinstatement index* was calculated as an average distance between "*fixation*" and "*scene period*" for a scene and every other scene within the stimuli set (Deng et al., 2021; Ritchey et al., 2013; Wing et al., 2015). The set-based reinstatement index reflects the baseline level of non-specific neural activation patterns during reinstatement. We then calculated the *corrected scene-specific reinstatement index* as the difference between set-based and scene-specific Fisher-transformed Pearson's r (Deng et al., 2021; Ritchey et al., 2013; Wing et al., 2015). Given the temporal proximity of the fixation and scene time window, we refrain from interpreting the absolute values of the observed scene-specific reinstatement index. However, given that the retrieval procedure is the same over time and presumably similarly influenced by the temporal autocorrelations, we focus primarily on the changes in reinstatement index for correctly retrieved memories across immediate, short, and long delays. In other words, the focus in the following analysis lies on the time-related change in the scene-specific reinstatement index.

First, we combined the scene-specific reinstatement indices for recent items across sessions, as there were no significant differences between sessions in ROIs in children (all $p > .999$) and adults ($p > .999$). To investigate time-dependent change in scene-specific reinstatement in children and young adults in the predefined ROIs, we conducted a LMER model, with delay (recent, remote short and remote long delays), group (children and young adults) for each ROI, controlling for ROI BOLD activation (Varga et al., 2023) during corresponding sessions. All main and interaction effects were FDR-adjusted and all post hoc tests were Sidak-corrected for multiple comparisons.

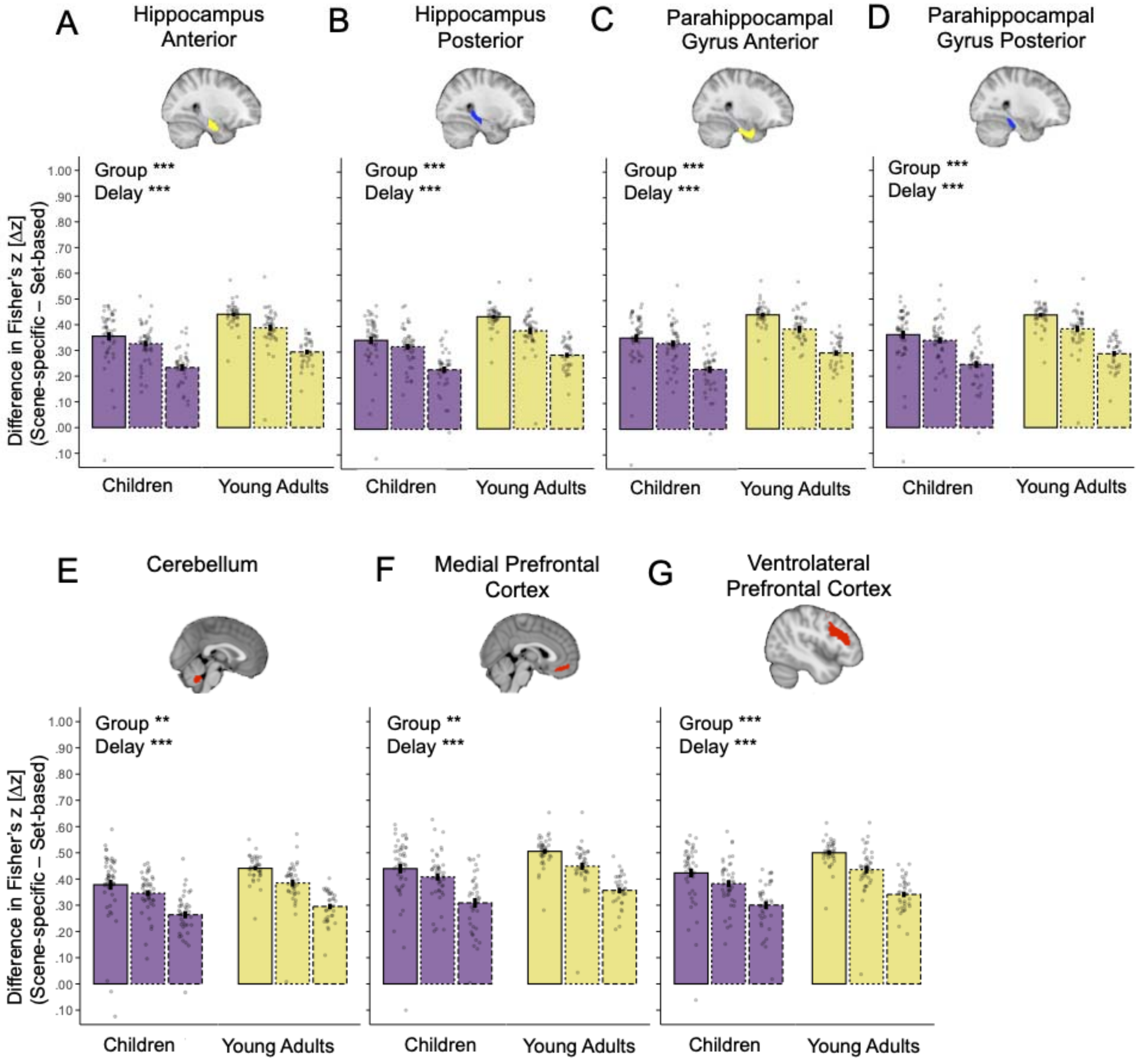
Figure 5

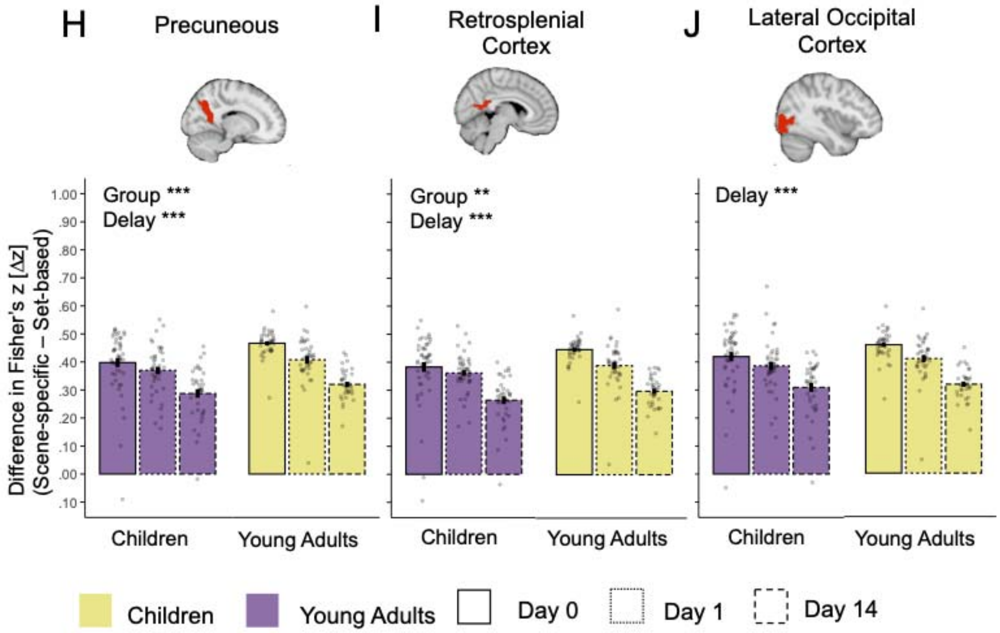


Representational Similarity Analysis.
(A) Index Computation (Scene). A representational similarity index was computed by assessing the average similarity between fixation and scene time window separately for recent, remote (Day 1), and remote (Day 14) scenes. **(B) Scene-Specific Reinstatement**. A corrected scene-specific reinstatement index was computed by assessing the average similarity in fixation and scene time window within each trial and subtracting from it the average set similarity between the fixation and scene time window across trials. S – scene time window; F – fixation time window; r – Pearson's correlation index; Δz – difference between two Fisher transformed r values. * - Activation patterns.

Generally, in all predefined ROIs, we observed a significant main effect of Session (all $p < .001_{\text{FDR-adjusted}}$) in all ROIs and a significant effect of Group in all ROI (all $p < .004_{\text{FDR-adjusted}}$), except for the LOC, $F_{(1,100)} = 1.23$, $p = .271$, $\omega^2 = .002$ (Fig. 6). The pattern of time-related decline was similar across age groups, as indicated by not significant Session x Group interactions in all ROIs (all p > .159). There was no significant effect of BOLD activation (all p > .136). The full statistical report on the LME-model is in Supplementary Material in Table S8. A more detailed overview of the observed main effects and their Sidak-corrected post-hoc tests are summarized in the Table 2.

Figure 6





Corrected scene-specific neural reinstatement.

Scene-specific neural reinstatement defined as the difference between Fisher-transformed scene-specific and set-specific representational similarity. (**A**) Hippocampus Anterior; (**B**) Hippocampus Posterior; (**C**) Parahippocampal Gyrus Anterior; (**D**) Parahippocampal Gyrus Posterior; (**E**) Cerebellum; (**F**) Medial Prefrontal Cortex; (**G**) Ventrolateral Prefrontal Cortex; (**H**) Precuneus; (**I**) Retrosplenial Cortex; (**J)** Lateral Occipital Cortex. *$p < .05$; **$p < .01$; ***$p < .001$(significant difference). Error bars indicate standard error. Δ z – difference between two Fisher transformed r values.

Table 2

Statistical overview of LME-model based Sidak corrected post hoc comparisons for scene-specific reinstatement analysis (based on LME-model described in Table S8).

	*Model-based post hoc comparisons**								
		YC > YA			Recent > Remote Day1			Remote Day 1 > Day 14	
ROI	*b*	$t_{(DF)}$	*p*	*b*	$t_{(DF)}$	*p*	*b*	$t_{(DF)}$	*p*
HCa	-.071	$-5.15_{(89)}$	**<.001**	.040	$4.35_{(162)}$	**<.001**	.095	$9.60_{(167)}$	**<.001**
HCp	-.068	$-5.14_{(91)}$	**<.001**	.040	$4.29_{(162)}$	**<.001**	.094	$9.45_{(168)}$	**<.001**
PHGa	-.069	$-4.75_{(90)}$	**<.001**	.039	$4.05_{(162)}$	**<.001**	.098	$9.62_{(167)}$	**<.001**
PHGp	-.055	$-3.91_{(90)}$	**<.001**	.040	$3.77_{(178)}$	**<.001**	.096	$9.07_{(172)}$	**<.001**
mPFC	-.049	$-2.94_{(92)}$	**.004**	.045	$4.16_{(162)}$	**<.001**	.093	$7.91_{(169)}$	**<.001**
vlPFC	-.058	$-3.84_{(93)}$	**<.001**	.053	$4.55_{(179)}$	**<.001**	.089	$7.79_{(169)}$	**<.001**
CE	-.044	$-3.05_{(89)}$	**.003**	.046	$3.97_{(166)}$	**<.001**	.086	$7.19_{(170)}$	**<.001**
RSC	-.041	$-2.99_{(90)}$	**.003**	.039	$3.72_{(162)}$	**<.001**	.094	$8.56_{(169)}$	**<.001**
PC	-.047	$-3.33_{(89)}$	**.001**	.044	$4.15_{(165)}$	**<.001**	.086	$7.89_{(168)}$	**<.001**

LOC	-.017	$-1.09_{(103)}$	.279	.045	$3.97_{(173)}$	**<.001**	.083	$7.07_{(174)}$	**<.001**

Notes. Degrees of freedom were adjusted based on Kenward-Roger methods. P-values were adjusted based on Sidak adjustment. YA – young adults; CH – children; ROI – region of interest; HCa – anterior hippocampus ; HCp – posterior hippocampus; PHGa – anterior parahippocampal gyrus; PHGp – posterior parahippocampal gyrus; mPFC – medial prefrontal cortex; vlPFC – ventrolateral prefrontal cortex; CE – cerebellum; RSC – retrosplenial cortex; PC– precuneous; LOC – lateral occipital cortex; b – Beta values; t – t-value; DF – degrees of freedom; p – p-value; CI – confidence interval; *p < .05; ** <.01, ***<.001 (significant difference).

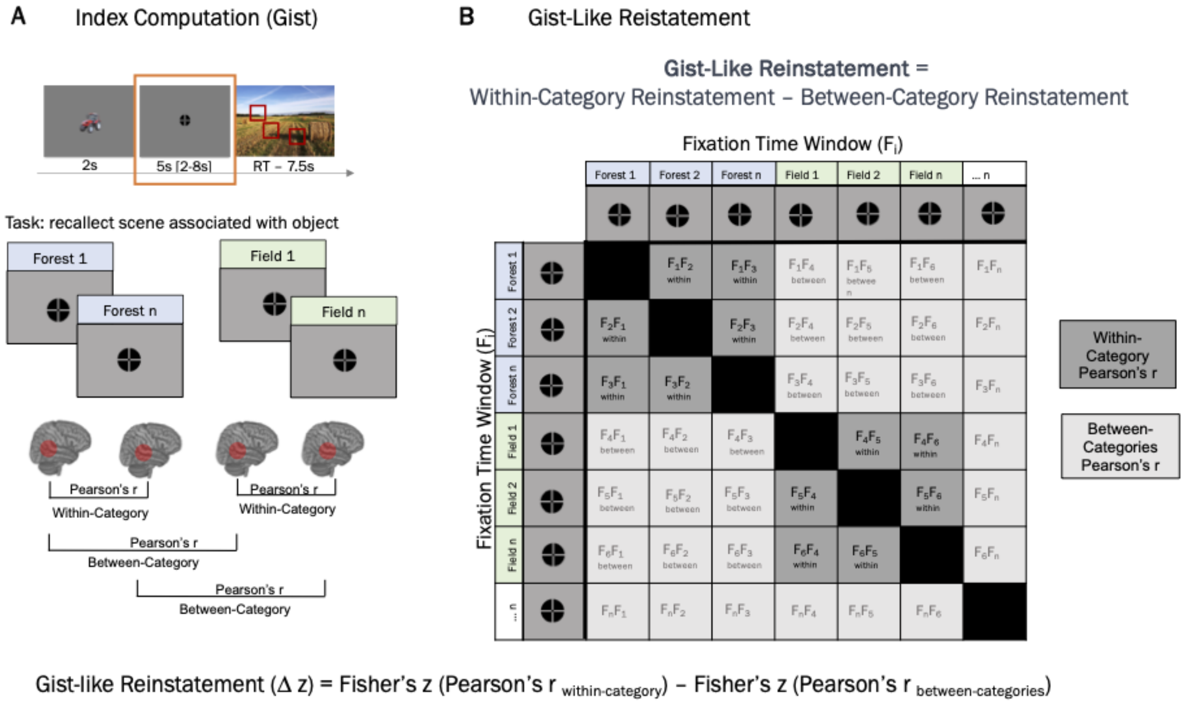
Taken together, we observed more attenuated scene-specific neural reinstatement in children compared to young adults. Scene-specific reinstatement declined significantly for overnight old memories compared to immediate memories declined further after a 2-week-period for all ROIs. These results indicate that the main decrease in scene-specific neural reinstatement for successfully consolidated memories occurs already after a short overnight delay and proceeds further after longer fortnight delay.

Gist-like neural reinstatement.

To assess the quality of reinstatement of the scenes belonging to the same category (e.g., field, forest, etc.) during the fixation time window following the object cueing (see Fig. 1A (Retrieval) and Fig. 7), we computed the gist-like reinstatement index. The distribution of within-category items across runs was similar and balanced. Additionally, their presentations within runs were randomised without close temporal proximity. First, a within-category similarity indices were computed based on fixation time window of correctly remembered items belonging to the same category (i.e., field, water, housing, forest, infrastructure, indoor, farming), excluding the similarity computation for the fixation time windows with itself. A between-category similarity indices were computed based on fixation time window of correctly remembered items belonging to different categories. A gist-like reinstatement index was computed by subtracting between-categories from within-categories Fischer-transformed distances ([within $\text{category}_{\text{recent}}$ r – between $\text{category}_{\text{recent}}$ r] and [within $\text{category}_{\text{remote}}$ r – between $\text{category}_{\text{remote}}$ r] for each session, Fig. 7) . Therefore, the gist-like reinstatement gives us a measure of the preactivation of the whole category of scenes (i.e., forests).

The non-zero values in this index reflect gist-like *reinstatement*, as the similarity distance would be higher for pairs of trials within the same category, indicating more generic reinstatement (e.g., during reinstatement of scenes belonging to a category "forest", participants may tend to recall a generic image of some forest without any specific details). In other words, the reinstatement of a more generic, gist-like image of a forest across multiple trials should yield more similar neural activation patterns. Not significant gist-like reinstatement would indicate that even within the same category, reinstatement of specific scenes is sufficiently differential and rich in details, rendering them dissimilar (e.g., participants may tend to recall detailed image of forests: fall forest with yellow trees, dark pike-tree forest, light summer forest with young birch trees, etc.).

Figure 7

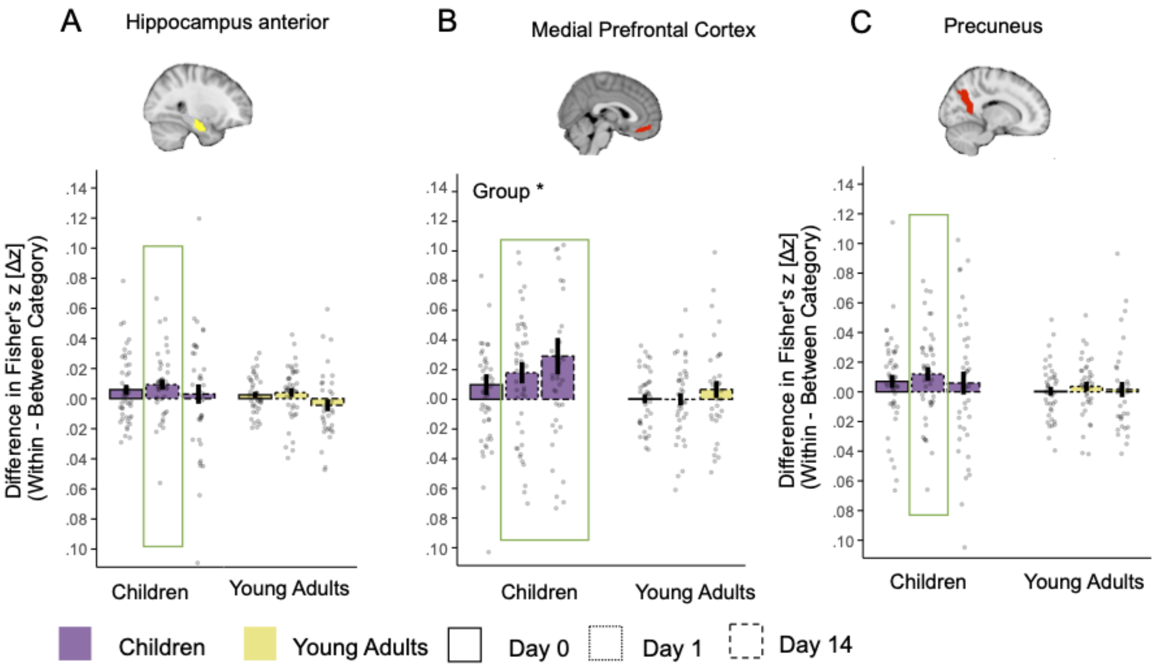


	Forest 1	Forest 2	Forest n	Field 1	Field 2	Field n	... n
Forest 1		F_1F_2 within	F_1F_3 within	F_1F_4 between	F_1F_5 between	F_1F_6 between	F_1F_n
Forest 2	F_2F_1 within		F_2F_3 within	F_2F_4 between	F_2F_5 between	F_2F_6 between	F_2F_n
Forest n	F_3F_1 within	F_3F_2 within		F_3F_4 between	F_3F_5 between	F_3F_6 between	F_3F_n
Field 1	F_4F_1 between	F_4F_2 between	F_4F_3 between		F_4F_5 within	F_4F_6 within	F_4F_n
Field 2	F_5F_1 between	F_5F_2 between	F_5F_3 between	F_5F_4 within		F_5F_6 within	F_5F_n
Field n	F_6F_1 between	F_6F_2 between	F_6F_3 between	F_6F_4 within	F_6F_5 within		F_6F_n
... n	F_nF_1	F_nF_2	F_nF_3	F_nF_4	F_nF_5	F_nF_6	

Representational Similarity Analysis.
(A) Index Computation (Gist). A representational similarity index was computed by assessing the average similarity for fixation time window for within-category and between-category scenes separately for recent, remote (Day 1), and remote (Day 14) scenes. The diagonal (similarity of fixation time window with itself) was excluded from the analysis. **(B) Gist-like Reinstatement**. A gist-like reinstatement index was computed by assessing the average similarity in fixation time window for the same-category pairs and subtracting from it the any-other-category pairs. S – scene time window; F – fixation time window; r – Pearson's correlation index. Δ z – difference between two Fisher transformed r values.

First, we aggregated the gist-like reinstatement indices for recent items on Day 1 and Day 14, as there were no significant differences between sessions in ROIs in children (all p > .95) and adults (p > .99). Then we applied a one-sample permutation t-test to test for significance of all gist-like indices against zero in each ROI (for full overview see Table S10, Figure S4). FDR-corrected values revealed that young adults did not show any category-based reinstatement (all p > .127), while significant gist-like reinstatement was observed in children in the mPFC, Precuneus, and anterior HC (all p < .042). Following this, we conducted a final LME model, separately for each ROI that showed significant gist-like reinstatement, with *Subject* as the random factor and *Delay* (recent, remote Day 1, remote Day 14) and *Group* (children, young adults) as fixed factors, controlling for the BOLD mean activation in each ROI during corresponding sessions.

Figure 8



Gist-like Reinstatement.

Gist-like reinstatement is reflected by the difference in Fisher's z (Δ z) between within-category and between-category representational similarity during fixation time window, where participants were instructed to reinstate the scene associated with the learned object before the actual scenes were shown. Higher values mean higher gist-like reinstatement. The index was tested for significance against zero and all results were FDR corrected for multiple comparisons. Significant reinstatement of gist-like information is highlighted by a green rectangle (**A**) Hippocampus Anterior; (**B**) Medial Prefrontal Cortex; (**C**) Precuneus; **p* < .05; ***p* < .01; ****p* < .001(significant difference); non-significant difference was not specifically highlighted. Error bars indicate standard error.

Second, we investigated the time-dependent change in gist-like reinstatement in ROIs that showed significant gist-like reinstatement. We observed a significant main effect of *Group* in the mPFC, $F_{(1,75)} = 6.77_{\text{FDR-adjusted}}$, p = .011, $\omega^2 = .03$ (Fig. 8B), indicating significantly higher gist-like reinstatement in the mPFC in children compared to young adult, b = .02, $t_{(83)} = 2.52$, p = .013, 95% CI [.004 – .036]. Neither anterior HC nor precuneous showed any significant main or interaction effects (all $p > .111$; Fig. 8A and 8C; detailed overview in Table S11). Taken together, only the child group showed gist-like reinstatement in the medial-temporal, medial prefrontal, and parietal brain regions. We observed a significantly higher overall gist-like reinstatement in medial prefrontal cortex region in children compared to young adults, indicating a higher level of gist-like representations in children.

Neural-behavioural Correlations

Further, we also explored whether over time, short- and long-delay scene-specific and gist-like reinstatement is beneficial or detrimental for memory performance by correlating the indices with memory retention rates. We derived, with a PLSC analysis, latent brain pattern across implicated ROIs for reinstatement indices that share the most variance with either short-delay or long-delay variations in memory accuracy.

For gist-like reinstatement, we included only those ROIs that showed significant reinstatement (i.e., only in children; mPFC, anterior HC and PC for short delay; mPFC for long delay). For the scene-specific reinstatement also all predefined ROIs in both age groups were included. Finally, we examined how scene-specific and gist-like reinstatement brain profiles are related to memory performance for both children and young adults, correlating these values with memory accuracy for respective delays.

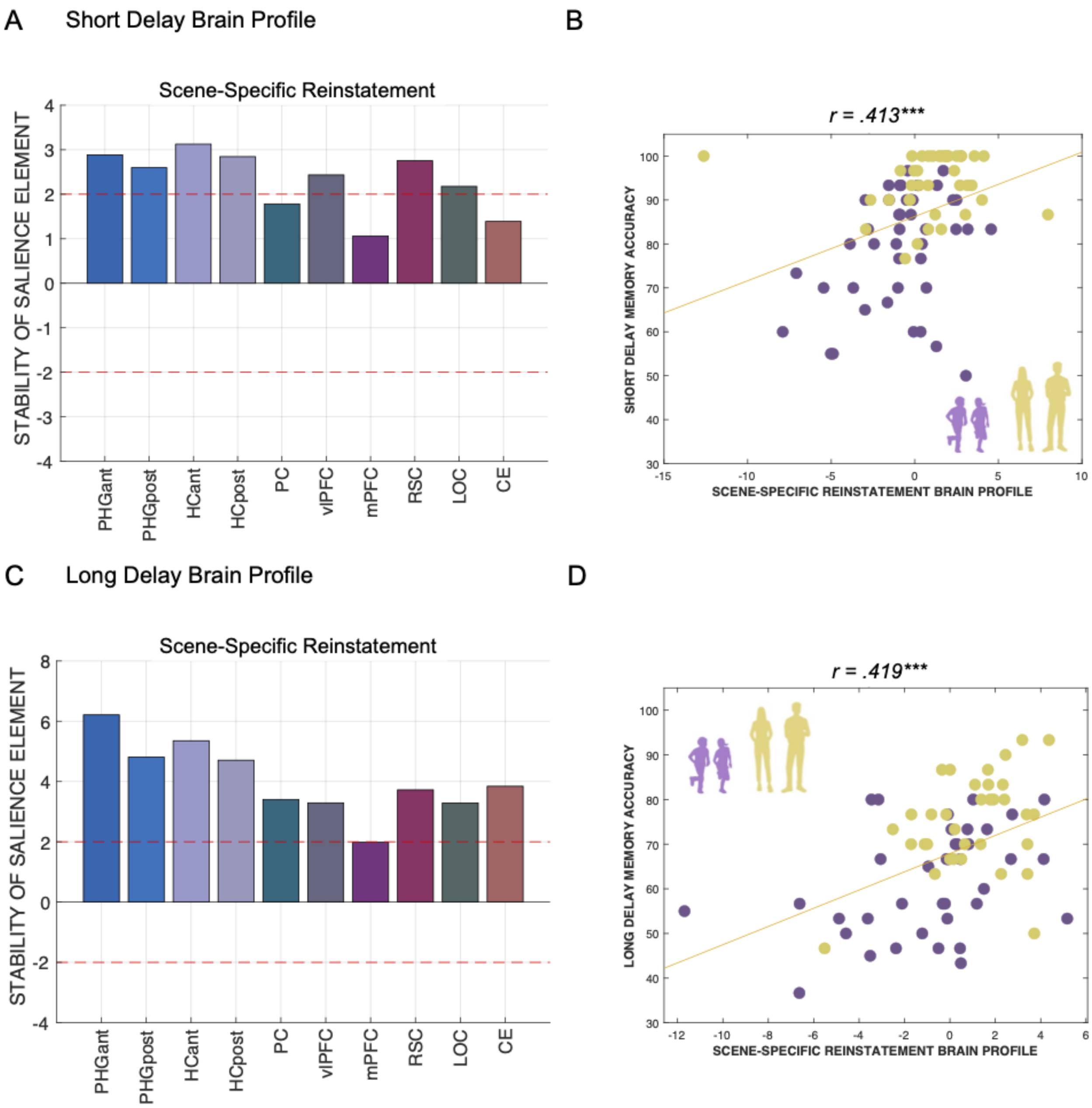
Neural-behavioural correlations (scene-specific reinstatement)

First, for short delay, the permutation test of significance resulted in a single latent variable that robustly represents the association of scene-specific reinstatement brain profile (Fig. 9A) and memory accuracy across both age groups (Fig. 9B, $r = .339$, $p = .0017$). With further bootstrapping we identified Z-scores estimates of robustness (larger/smaller than ± _1.96 ($a < 0.05$)) of the components within the multivariate brain profile. Thus, for short delay, we observed that higher memory accuracy was robustly associated with greater scene-specific reinstatement in the anterior PHG (Z-score = 2.885, $r = .371$), posterior PHG (Z-score = 2.597, $r = .342$), anterior HC (Z-score = 3.126, $r = .399$), posterior HC (Z-score = 2.844, $r = .375$), vlPFC (Z-score = 2.434, $r = .317$), mPFC (Z-score = 2.753, $r = .333$), and LOC (Z-score = 2.176, $r = .298$) across age groups.

Second, for long delay, the permutation test of significance resulted in a single latent variable that robustly represents the association of scene-specific reinstatement brain profile (Fig. 9C) and memory accuracy across both age groups (Fig. 9D, $r = .455$, $p = <.001$). Further, for long delay, we observed that higher memory accuracy was robustly associated with greater scene-specific reinstatement in the anterior PHG (Z-score = 6.213, r = .414), posterior PHG (Z-score = 4.810, r = .334), anterior HC (Z-score = 5.353, r = .389), posterior HC (Z-score = 4.707, r = .354), precuneous (Z-score = 3.404, r = .281), vlPFC (Z-score = 3.291, r = .266), RSC (Z-score = 3.72, r = .293), LOC (Z-score = 3.288, r = .282), and cerebellum (Z-score = 3.842, r = .308) across age groups.

Further, the linear regression analysis revealed similar relationship between identified brain profiles and memory accuracy between children and adult as indicated by non-significant *Scene-Specific Reinstatement Brain Score x Group* interactions for both short delay, F = 2.61 p = .110, w^2 = .02, and for long delay, F = .43 p = .836, w^2 = .00. Based on this, we ran Spearman's rank-order correlation analyses across both age groups to identify the strength of the relationship. For short delay, we observed that the stronger expression of scene-specific reinstatement brain score was moderately associated with higher short-delay memory retention rate (Fig. 8B), r = .413, $p < .001_{\text{FDR-adjusted}}$. Furthermore, for long delay, the results showed that stronger expression of scene-specific reinstatement brain score was also moderately associated with higher long-delay memory retention rates (Fig. 8D), r = .419, $p < .001_{\text{FDR-adjusted}}$. These significant correlations underscore the importance of scene-specific reinstatement in positively contributing to memory performance for detailed associative information both in children and adult. The lack of a significant difference between children and adults suggests that the fundamental relationship between scene-specific reinstatement and memory might also remain consistent across age groups.

Figure 9



Multivariate short- and long-delay brain profiles of scene-specific reinstatement are associated with variations in memory accuracy. A) *Short Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite short-delay scene-specific reinstatement brain profile. Stability of salience elements is defined by Z-scores (depicted as red line: a value larger/smaller than ± _1.96 is treated as reliably robust at (a <0.05). B) *Association between Short Delay Retention Rate and Short Delay Scene-Specific Reinstatement Brain Score*. Within-participant short delay scene-specific reinstatement brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against short delay memory retention rates defined as percentage of correctly recalled items on Day 1 relative to Day 0. C) *Long Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite long-delay scene-specific reinstatement brain profile. Stability of salience elements is defined by Z-scores (depicted as red line: a value larger/smaller than ± _1.96 is treated as reliably robust at (a <0.05). B) *Association between Long Delay Retention Rate and Long Delay Scene-Specific Reinstatement Brain Score*. Within-participant long delay scene-specific reinstatement brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against long delay memory retention rates defined as percentage of correctly recalled items on Day 14 relative to Day 0. *Note:* PHGa – anterior parahippocampal gyrus; PHGp – posterior parahippocampal gyrus; HCa – anterior hippocampus ; HCp – posterior hippocampus; PC– precuneous; vlPFC – ventrolateral prefrontal cortex; mPFC – medial prefrontal cortex; RSC – retrosplenial cortex; LOC – lateral occipital cortex; CE – cerebellum; r – Spearman's rank order correlation index.

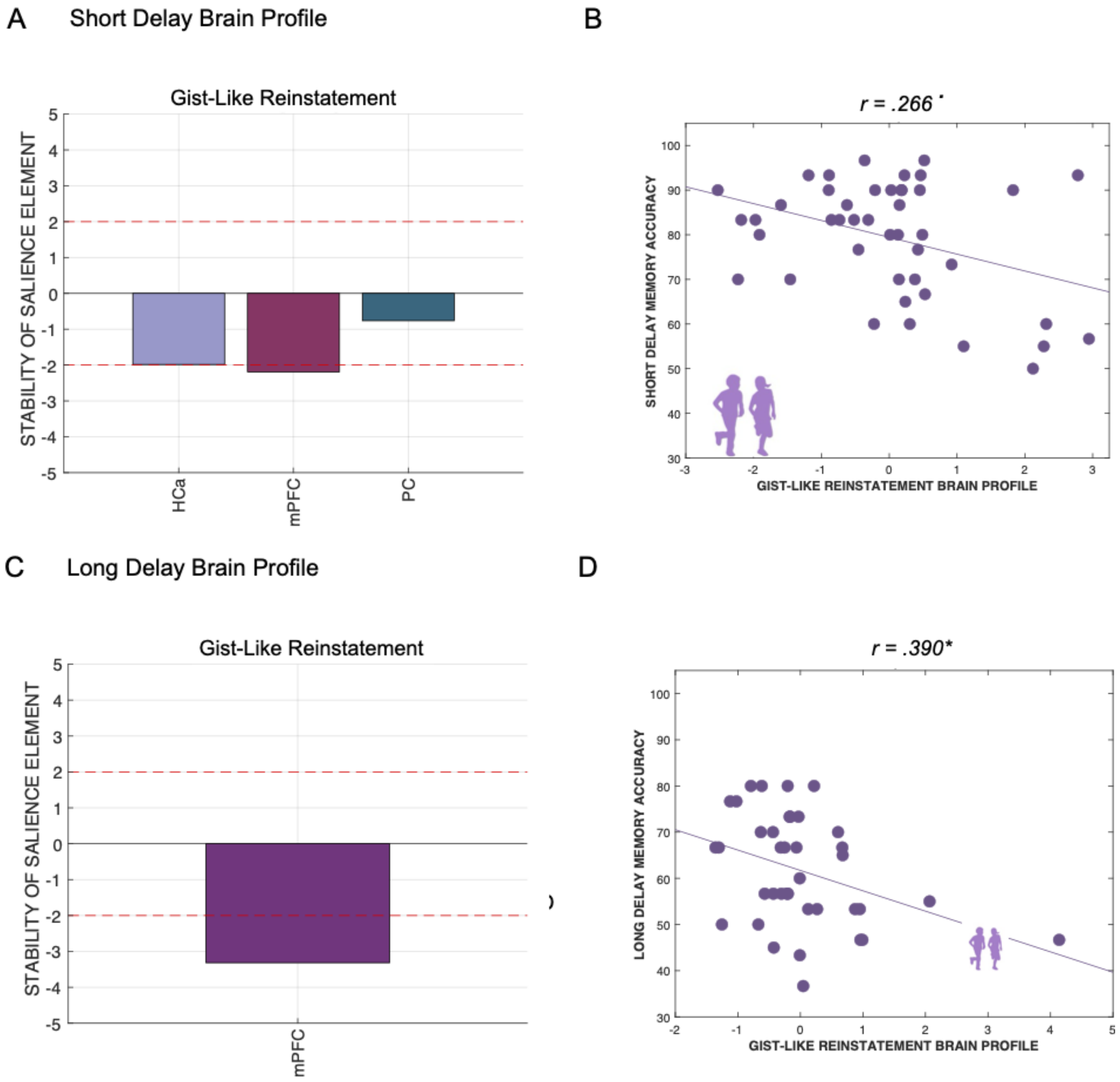
Neural-behavioural correlations (gist-like reinstatement)

First, for short delay, the permutation test of significance resulted in a single latent variable that robustly represents the association gist-like reinstatement brain profile (Fig. 10A) and memory accuracy in children (Fig. 10A, r = .379, p = .024). For short delay, we observed that higher memory accuracy was robustly negatively associated with greater gist-like reinstatement in the anterior HC (Z-score = -1.985, r = -.681), and mPFC (Z-score = -2.189, r = -.681) in children.

Second, for long delay, the permutation test of significance resulted in a single latent variable that robustly represents the association of scene-specific reinstatement brain profile (Fig. 10C) and memory accuracy across both age groups (Fig. 10D, r = .372, p = .015). Further, for long delay, we observed that higher memory accuracy was robustly associated with lower gist-like reinstatement in the mPFC (Z-score = -3.354, r = .371) in children.

Based on this, we ran Spearman's rank-order correlation analyses to identify the strength of these relationships in child group. For short delay, we observed a trend-level negative association between stronger expression of gist-like reinstatement brain score and memory performance (Fig. 8B), $r = .266$, $p = .08_{\text{FDR-adjusted}}$. Furthermore, for long delay, the results showed that stronger expression of gist-like reinstatement brain score was moderately associated with higher long-delay memory retention rates (Fig. 8D), $r = .390$, $p = .02_{\text{FDR-adjusted}}$. The significant correlation observed in children underscores the importance of gist-like reinstatement in being detrimental to memory performance for detailed associative information in children in long delay.

Figure 10



Multivariate short- and long-delay brain profiles of gist-like reinstatement are associated with variations in memory accuracy. A) *Short Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite short-delay gist-like reinstatement brain profile. Stability of salience elements is defined by Z-scores (depicted as red line: a value larger/smaller than ± _1.96 is treated as reliably robust at (a <0.05). B) *Association between Short Delay Retention Rate and Short Delay Gist-Like Reinstatement Brain Score*. Within-participant short delay gist-like reinstatement brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against short delay memory retention rates defined as percentage of correctly recalled items on Day 1 relative to Day 0. C) *Long Delay Brain Profile*. Latent variables weights or saliences for each ROI build up one latent variable that expresses a composite long-delay gist-like reinstatement brain profile. Stability of salience elements is defined by Z-scores (depicted as red line: a value larger/smaller than ± _1.96 is treated as reliably robust at (a <0.05). B) *Association between Long Delay Retention Rate and Long Delay Gist-Like Reinstatement Brain Score*. Within-participant long delay gist-like reinstatement brain scores that represents a within-participant robust expression of the defined latent variable's profile is plotted against long delay memory retention rates defined as percentage of correctly recalled items on Day 14 relative to

Day 0. *Note:* HCa – anterior hippocampus; PC– precuneous; mPFC – medial prefrontal cortex; r – Spearman's rank order correlation index.

Taken together, more differentiated detail-rich neural reinstatement was related to better memory retrieval in both children and young adults. On the other hand, uniquely in children, more gist-like neural reinstatement was related to worse memory retrieval.

DISCUSSION

In the present study, we investigated system-level memory consolidation of object-location associations after learning with immediate delay, one night of sleep as short delay and after two weeks as long delay. We tracked changes in neural activation and multivariate reinstatement patterns over time, comparing 5-to-7-year-old children and young adults. Our main findings are as follows: (i) Children showed greater decline in memory retention both in short and long delay compared to young adults. (ii) In terms of neural upregulation, reflected as the mean difference between remote > recent neural activation, age groups showed distinct changes over time. Young adults exhibited increase in neural upregulation in the posterior PHG, cerebellum and LOC over time, as well as overall higher neural upregulation in the vlPFC compared to children . In contrast, only children showed decrease in neural upregulation in the RSC over time, and they showed overall higher neural upregulation in the mPFC than adults. Distinct neural upregulation profiles with a specific set of brain regions were related to short and long delay memory accuracy. (iii) Using RSA, we found that differentiated scene-specific reinstatement was more prominent in adults than children and decreased over time in both age group. We observed that more generic gist-like reinstatement was present only in children in anterior hippocampal and medial prefrontal brain regions. Importantly, higher scene-specific reinstatement was related to better retention rates in both children and young adults, while higher gist-like reinstatement was related to lower retention rates only in children.

Our study extends previous adult-based findings and, for the first time, demonstrates that the retrieval of consolidated memories in children is accompanied by differential patterns of neural activation of some of the core retrieval brain regions, attenuated neural reinstatement of detailed specific memories, and stronger generic gist-like reinstatement. Our results suggest that adults can utilize their mature neural memory systems and extensive existing knowledge structure to encode and consolidate new complex information with detailed accuracy. In contrast, children utilize their neural resources, which are still undergoing maturation, to build up their sparse knowledge structures. Their memory system may tend to favour encoding and consolidating gist as a more solid building block for their still sketchy knowledge base, sacrificing detailedness. At this developmental stage, focusing on details may not be a priority (Keresztes et al., 2018). We discuss each finding in detail in the following sections.

Less robust short and long delay memory retention in children compared to young adults.

Our findings indicate that preschool 5-to-7-year-old children can encode and retain complex associative and highly contextualized information successfully over extended periods after adaptive learning. However, they had overall lower learning and retrieval performance compared to young adults. In addition, these children exhibited more pronounced declines in retention rates over both short and long delays decrease for correctly learned information, suggesting less robust memory consolidation compared to young adults.

Concerning learning, overall children needed more cycles to memorize object-scene associations and showed lower learning performance after initial strategic encoding compared to young adults. Although we did not expect children to show similar learning rates to adults due to the complex and associative nature of the task (Pressley et al., 1981), we aimed to maximize children’s learning capacities through adaptive learning. Therefore, attention allocation and motivation during encoding and learning were controlled for by the constant presence of the experimenter and feedback questionnaires. Moreover, all participants underwent training to create elaborative memories that help to support retrieval.

Overall, our findings on learning suggests that children were less adept at utilizing strategic control over encoding by creating and maintaining stories to aid their retrieval as successfully as adults. This is consistent with previous literature, showing continuous improvement in children’s ability to use elaborative strategies between ages 4 and 8 (Bjorkund et al., 2009; Crowley & Siegler, 1999; Pressley, 1982). Additionally, children at this age may experience difficulties in controlling (Ruggeri et al., 2019) and effectively using their learning strategies over time (Brod, 2021; Shing et al., 2010). Observed lower learning rates may also be attributed to less efficient binding processes in children compared to young adults (Shing et al., 2010; Sluzenski et al., 2006). Although we included only stimuli from the primary school curriculum to reduce age differences in knowledge availability, ongoing maturation of the memory brain network in 5-to-7-year-old children may have attenuated their benefit from pre-existing knowledge and memory aid through strategic elaboration (Ghetti & Bunge, 2012; Lenroot & Giedd, 2006; Nishimura et al., 2015; Ofen, 2012; Shing et al., 2008). Despite these challenges, 5-to-7-year-old children were capable of learning complex associative information to a considerable extent, which aligns with their ability to gradually accumulate world knowledge (Bauer, 2021; Brod & Shing, 2022; Wagner, 2010).

Concerning memory consolidation, our results are in line with previous studies that reported worse memory retention for associative information in school age children compared to adults (Østby et al., 2012; Schommartz et al., 2023, 2024). On the other hand, our results are not in line with sleep-related beneficial effects on mnemonic performance of 7-to-12-year-old children after one night delay (Peiffer et al., 2020; Wang et al., 2018) that were shown for novel stimuli not related to any prior knowledge (in the sense of arbitrary stimuli). As we opted for well-learned information that should allow for rapid creation of new schemas or integration of new associations into already existing schemas, our findings indicate that the beneficial role of sleep on memory consolidation in children compared to adults may not apply for repeatedly and strategically learned information. Deliberate learning is potentially more advantageous for subsequent memory retention in young adults, as this information may be integrated into pre-existing knowledge structures faster (van Kesteren et al., 2013), with higher strategic control of memories upon retrieval and therefore greater accessibility of consolidated memories (Fandakova et al., 2017; Gaudreau et al., 2001). Taken together, our findings indicate that compared to young adults, 5-to-7-year-old children exhibit less robust memory consolidation for well-learned information, suggesting an overall reduced ability to retain detailed memories in children.

Our findings indicate suggest that lower memory performance in children potentially indicate lower memory strength. Therefore, we conducted exploratory analysis with drift diffusion modelling (Lerche & Voss, 2019; Palada et al., 2016; Ratcliff et al., 2011, 2012; Ratcliff & McKoon, 2008; Zhou et al., 2021), deriving memory strength using as drift rate parameter (see Figure S1 and section S2.1 in Supplementary Materials). Our results demonstrate that children have significantly lower drift rate compared to young adults, indicating slower evidence accumulation and noisier recall. As drift rate closely correlates with memory accuracy

(Ratcliff et al., 2011), our findings on the memory strength align with those on memory accuracy during retrieval in both age groups. Our neural findings suggest that differences in functional engagement of the retrieval network and the characteristics of memory representations being created and retained may underlie the observed behavioural differences.

Differential upregulation of remote > recent neural activation over time in children in comparison to young adults.

Analyses of neural upregulation (i.e., remote > recent difference in neural activation) over time allowed us to control for the effects of rapid consolidation during repeated learning, while examining changes in short- or long-delay neural activation (Brodt et al., 2016b, 2018; Yu et al., 2022). First, we observed increased upregulation in the vlPFC over time in both age groups, with vlPFC upregulation being higher in young adults. Furthermore, we observed stable upregulation in the mPFC over time in both age groups, with the overall mPFC upregulation being higher in children. On the one hand, this may indicate a stronger strategic control over retrieval processes over time in young adult, due to vlPFC's role in strategic remembering and retrieval of stored memories (Badre & D'Esposito, 2009; Kuhl et al., 2012). Over time, cognitive control during memory retrieval may increase as it requires greater effort to recollect elaborative stories to remember the associated spatial context. Strategic control over memories may be present but less pronounced in children due to the more protracted developmental trajectories of prefrontal cortex maturation (Ghetti & Bunge, 2012c; Gogtay et al., 2004; Ofen, 2012; Shing et al., 2010b). On the other hand, our results indicate a more pronounced schema-related retrieval that may be mediated by mPFC to a greater extent in children than in young adults. This extends previous findings on the involvement of mPFC in structured and schema-related retrieval of long-term memories (Takashima et al., 2006; Yamashita et al., 2009) to a child developmental cohort. Interestingly, higher mPFC upregulation in long delay was negatively related to long delay memory accuracy, suggesting that schema-reliance is detrimental to the retention of detailed associative memories. In addition, it may suggest consolidation-related transformation of memory traces into less differentiated, more generic and gist-like memories(Gilboa & Marlatte, 2017; Gilboa & Moscovitch, 2021).

Second, in other constituents of the recollection network (Ranganath & Ritchey, 2012), we observed increased in upregulation from short to long delay in the posterior PHG and overall lower upregulation in precuneous (i.e., remote > recent) in young adults, while children showed a corresponding decrease in the RSC. As young adults showed higher memory retention rates for more detail-rich information, this superior memory may be mediated by higher upregulation in the posterior PHG involved in contextual associations and scene memory (Aminoff et al., 2013). In children, PHG goes through prolonged maturation (Golarai et al., 2007), and its increased functional maturation is related to long-term scene recollection (Chai, 2010). In addition, higher mnemonic distinctiveness of more recent memories (i.e., higher retention rates for detailed information) may also be mediated by RSC and precuneous activation profiles, as these regions are involved in mnemonic vividness, spatial, and associative memory as indicated by other findings from immediate delays (Brodt et al., 2016b; Hebscher et al., 2019; Mitchell et al., 2018; Richter et al., 2016; Tambini & D'Esposito, 2020; Vann et al., 2009). Moreover, lower short delay precuneus upregulation and higher long delay RSC upregulation was related to better memory performance. Time-related decrease in the posterior brain regions in children is also in line with previous findings (DeMaster & Ghetti, 2013), which showed that the involvement of parietal regions in the recollection of correct memories increased with age in 8-to-11-year-old children. Therefore, the continuing maturation of parietal regions in 5-to-7-year-old children (Sowell et al., 2002) presumably underlies the age-related differences in consolidation-related upregulation in these regions.

Third, the observed increase in neural upregulation from short to long delay in the LOC and the cerebellum in young adults is also in line with the previous findings showing that the cerebellum supports rapid cortical storage of memory traces after repeated exposure even after 24 hours (Stroukov et al., 2022), and showed upregulation of neural activation for long-term episodic memory (Andreasen et al., 1999). Concerning the LOC, previous studies also showed that HC-LOC activation was related to scene-related associative memory consolidation (Tambini et al., 2010), and human object recognition (Grill-Spector et al., 2001). Moreover, the network of angular gyrus and LOC has been shown to enhance the overnight retention of schema-related memories in young adults (van der Linden et al., 2017). In line with this, we also observed that higher long delay LOC upregulation was related to better memory performance. The more pronounced upregulation from short to long delay in these regions in adults suggests that the cerebellum and LOC support long-delay memory retention and their functional role is underdeveloped in middle childhood.

Finally, our findings on age-group and delay-invariant activation in the anterior HC and PHG, and posterior HC during the retrieval of detail-rich memories (i.e., the exact location of an object within a scene) are in line with Nadel & Moscovitch (1997),who postulated that the hippocampal formation and related structures remain involved in detail-rich memories upon their retrieval, irrespective of memory age. For example, Du et al. (2019) reported stable hippocampal involvement during retrieval of associative memory across delays of one day, one week and one month in young adults. Tanrıverdi et al. (2022) also demonstrated that post-encoding coactivation of hippocampal and cortical brain regions may lead to experience-dependent change in memories, highlighting the importance of hippocampal involvement during consolidation. Furthermore, the absence of age-related differences in HC and anterior PHG involvement are also in line with developmental studies that have reported the relative maturity of the HC in middle childhood (Keresztes et al., 2017; Lee et al., 2014; Shing et al., 2010b), which is concomitant with an improvement in the ability to bind event features together into a coherent representation around the age of six years (Sluzenski et al., 2006). Specifically, our finding on hippocampal engagement being robust in children and adults extends the Multiple Trace Theory to a child developmental cohort (Moscovitch & Gilboa, 2022; Nadel et al., 2000). Taken together, the similar engagement of medial-temporal cortex over time in children and adults indicated that the retrieval of well-learned detail-rich memories is mediated by these brain structures already in middle childhood.

To summarize, we provide novel evidence about changes in neural upregulation for successfully consolidated memories over short and long delay, relative to immediately learned memories. While children exhibited adult-like stable neural activation for recent and remote memories in medial-temporal brain regions, young adults relied more on prefrontal, occipital, cerebellar, and parietal brain regions over time, compared to more pronounced reliance on medial prefrontal regions in children. Adults show more mature neocortical consolidation-related engagement, resulting in stronger and more durable detailed memories over time while in children immature neocortical engagement may lead to consequent reduction in memory retention of detailed memories.

Reduced scene-specific reinstatement over time in children and young adults.

We found that scene-specific reinstatement decreased over time both in children and young adults, aligning with delay-related decrease in memory retention. Additionally, it was overall more attenuated in children compared to young adults. Higher scene-specific neural reinstatement was related to better memory performance in short and long delay in both age groups.

Our findings contribute to the memory consolidation literature by demonstrating that scene-specific neural reinstatement observed in neocortical, medial temporal and cerebellar brain regions supports reinstatement of detailed specific contextual memories. This observation is consistent with the Contextual Binding Theory (Yonelinas et al., 2019), which posits that stronger reinstatement of contextual details can enhance memory retention. The similar decay of these processes over time in both children and adults suggests that the basic mechanisms of contextual binding are present early in development. Additionally, in line with the Trace Transformation Theory (Moscovitch & Gilboa, 2022), our findings suggest that reinstatement patterns continuously transform over time. This transformation, observed across all considered memory-related regions, indicates a consistent and systematic consolidation-related reshaping of the unique scene-specific memory representations over time (Chen et al., 2017).

Our findings on scene-specific reinstatement align with and add to the previous literature that show reliable reinstatement of unique events. For example, our findings align with the effects observed by Masís-Obando et al. (2022) for the immediate recall of story details in key memory regions. Consistent with Oedekoven et al. (2017), our results show that memory representations for unique events can be reliably detected through scene-specific reinstatement even after extended delays. Furthermore, we build on Guo & Yang (2022) by demonstrating how specific ROI-related profiles of neural reinstatement during retrieval correlate with long-term memory retention. Unlike Oedekoven et al. (2017), who reported no time-related differences in reinstatement effects and used the same video clips for immediate and delayed recall – which could have inadvertently reinforced memory through reactivation – our study employed unique stimulus sets for each retrieval sessions, preventing any reconsolidation of mnemonic representations. This approach revealed a significant attenuation of reinstatement patterns after an overnight delay, which further diminished after two weeks, highlighting the importance of intentional reactivation for maintaining the specificity of neural reinstatement.

Our findings indicate similar patterns of scene-specific neural reinstatement between children and young adults. Building on Fandakova et al. (2019), who found similar distinctiveness of neural representations during encoding in 8-to-15-year-old children and adults, our results suggest that this similarity extends to younger ages, showing comparable distinctiveness of neural representations for unique memories from middle to late childhood and early adolescence. Additionally, our research supports the presence of scene-specific reinstatement in 5-to-7-year-old children, albeit at a lower level compared to adults, aligning with previous studies (Benear et al., 2022; Cohen et al., 2019; Golarai et al., 2015), which demonstrated reliable mnemonic reinstatement for visual input (i.e., faces, movie clips) in 5-to-11-year-old children. Furthermore, we extend these findings, by showing that successful of long-term memory retrieval is associated with more differentiated neural reinstatement in both children and young adults, indicating similar mechanisms of detail-rich memory consolidation present as early as 5-to-7 year.

Our results indicate that higher scene-specific neural reinstatement over time correlated with better memory retention in both children and adults. This is in line with the neural fidelity hypothesis (Xue, 2018), suggesting that more similar neural reinstatement reflect less noisy representations of mnemonic information. Convergent evidence showed that higher fidelity of neural representation across study episodes leads to successful memory (Xue et al., 2010, 2013). Similarly, Masís-Obando et al. (2022) reported that more specific neural representations predicted subsequent memory performance in young adults.

Of note, our study design, which resulted in temporal autocorrelation in the BOLD signal between memory retrieval (i.e., fixation time window) and scene observation and response (i.e., scene time window), was consistent across all three delay windows. Since the retrieval procedure remained unchanged over time and was similarly influenced by temporal autocorrelations, we attribute our RSA findings to differences in reinstatement between recent and remote trials. Given that the scene time window for the 3AFC task was constant, the brain signals should exhibit similar perception-based but variably memory-based patterns across all delays.

Furthermore, all items, regardless of retrieval delay, underwent extensive learning and showed successful consolidation, as evidenced by correct recall. This suggests that both the fixation and scene time windows engaged memory-related neural processes. According to Brodt et al., (2016, 2018), rapid consolidation-related neural reorganization can occur immediately after learning, indicating that even during recent retrieval, scenes are processed in a memory-oriented manner. Additionally, during the scene time window, participants engaged in retrieval by selecting the correct object location within the scene. Thus, while the scene time window involved perceptual processing, its impact is consistent across all items due to uniform exposure to repeated learning, making them equally familiar to participants. Although our paradigm per se cannot arbitrate between perception-based and memory-based nature of retrieval during scene presentation, our exploratory univariate analysis during the scene presenations time window (see Figure S3, Table S9 in Supplementary Materials) revealed higher neural engagement in the key memory regions with passing time, supporting memory-related processing during the scene time window.

Taken together, our findings provide novel evidence that although children exhibit more attenuated scene-specific reinstatement compared to young adults, the consolidation-related decrease in differentiated reinstatement follows similar patterns as in adults. This highlights that despite less robust memory consolidation and lower memory strength, children's neural transformations of distinct memories over time may share the same mechanisms as adults, with scene-specific reinstatement proving beneficial for memory retention in both groups.

Unique Gist-like Reinstatement in Children.

In terms of more generic gist-like reinstatement, our results showed that only children demonstrated such reinstatement in anterior hippocampal, prefrontal, and parietal brain regions during successful retrieval. Furthermore, higher short-delay gist-like reinstatement in the anterior hippocampus and mPFC was associated with poorer short-delay memory accuracy in children. Similarly, higher long-delay gist-like reinstatement was associated with poorer long-delay memory accuracy in children. With these findings, we provide the first neural empirical evidence to support the Fuzzy Trace Theory (Brainerd & Reyna, 2002; Reyna & Brainerd, 1995), showing neural reorganization of memory representations in children.

The Fuzzy Trace Theory aims to characterized the shifts in ongoing balance between precise, detailed “verbatim” memory and more generalize, simplified “gist” memory (Brainerd & Reyna, 2002) from a developmental perspective. Our associative object-location task allowed the investigation of these “dichotomy” as it was aimed to cultivate detailed, precise memories for retrieval. Simultaneously, it enabled generalization by creating of more generic representations due to the presence of related category-based information. Adults were able to build upon solid pre-existing knowledge by embellishing them with details and integrating them into these structures. Children, in contrast, with their sparser knowledge, may have focused more on solidifying the structure with overlapping information. Aligning with the Fuzzy Trace Theory, our results suggest that reliance on gist-like memory representations is less effective for long-term retention of complex associative information compared to detailed verbatim memory, which seems to be characteristic of adults.

The association between short-delay, gist-like reinstatement in the anterior hippocampus and mPFC in children align with the findings that, in middle childhood, the anterior hippocampus is generally functionally connected with frontal brain regions and associated with semantic memory (Plachti et al., 2023). Earlier maturation of anterior hippocampus in middle childhood (Canada et al., 2021), along with its more pronounced role in associative memory (Lee et al., 2020), contribute to our understanding of its role in consolidation-related neural reorganization in children. On the other hand, studies with adult subjects show that gist-like reinstatement in posterior hippocampal is linked to more generic semantic gist of the original memory in adults (Dandolo & Schwabe, 2018; Krenz et al., 2023). In line with this, more schema-based representations in posterior hippocampus were related to pooper subsequent performance in adults (Masís-Obando et al., 2022). A more prolonged maturation of the posterior hippocampus, along with the functional shift within the anterior-posterior hippocampal axis with respect to episodic memory, suggest that neural transformations of mnemonic representations in children may be governed by inherently different neural mechanisms. The mechanisms may result in weaker memories for detailed, complex information over long time in children (Canada et al., 2021; Ghetti & Lee, 2013; Plachti et al., 2023). Particularly, pronounced functional connectivity between the anterior hippocampus and frontal regions in children, coupled with less differentiated functional specification and broad cognitive covariance network within these regions (Plachti et al., 2023), may underlie more sparse retention patterns and less differentiated memory reorganization in children.

The gist-like neural reinstatement in the mPFC in children may reflect consolidation-related integration of memory representations into more abstract, generic forms. This aligns with the mPFC’s known role in integrating across memories (Schlichting et al., 2015), the increase in semantically transformed representations for related information over time in adults (Krenz et al., 2023),and the integration new information into schema (Gilboa & Marlatte, 2017; Preston & Eichenbaum, 2013). While gist-like neural representations may support the generalization of information to bolster the sparse knowledge structures in children, this occurs at the costs of memory precision (Reyna et al., 2016). Consequently, there is a negative association between gist-like memory reinstatement in the mPFC and memory accuracy both in short and long delay. In contrast to our findings, Masís-Obando et al. (2022) demonstrated that more schema-based representations in the mPFC were associated with better subsequent memory performance in adults. However, the study utilized stimuli with clearly differentiable schema and details components. Future studies may use this approach to further explore these differences and the specific conditions under which schema-based representations enhance memory performance, and the age differences therein.

Overall, our results are in line with Brainerd et al. (2002), showing that in middle childhood, precise mnemonic representations (i.e., scene-specific reinstatement) and gist mnemonic representations (i.e., gist-like reinstatement) co-exist also on the neural level. We performed exploratory analysis that revealed a negative relationship between detailed scene-specific reinstatement and generic gist-like reinstatement in children (see section S3.1, Figure S5 in Supplementary Materials). Therefore, children with lower item-specific menminic representations tend to show more generic gist-like representations. Extending on the postulations from Keresztes et al. (2018) and Ngo et al. (2021) that 5-to-7-year-old children tend to rely more on generalization, our findings suggest that retaining memories with less specific details may allow for faster integration of overlapping features into emerging knowledge structures (Bauer, 2021; Gilboa & Marlatte, 2017).

On the other hand, adults could form strong, highly detailed memories aided by effective strategic retrieval methods, without the need to form gist-like representations. Moreover, they may have employed different retrieval neural mechanisms than children, as indicated by our exploratory findings that higher neural engagement over time was associated with the decrease in scene-specific neural reinstatement in adults (see section S3.1, Figure S5 in Supplementary Materials); suggesting a higher recruitment of neural resources to compensate for decaying memory reinstatement.

Taken together, our findings provide novel evidence that an enhanced reliance on gist information characterizes children’s memory retrieval across time. With this we provide the first empirical evidence to support the Fuzzy trace theory on the level of gist-like neural representations evolvement in children.

LIMITATIONS

Several limitations of the current study should be noted. First, our test for memory was based on a 3-alternative forced choice procedure, which was intended to reduce the need for strategic search (e.g., in free recall). As reorganization and stabilization in consolidation depend on the psychological nature of mnemonic representations (Moscovitch & Gilboa, 2022), future studies may employ more demanding recall-based memories to characterize memory consolidation more comprehensively. Particularly, future studies may differentiate mnemonic accessibility vs. precision (Murray et al., 2015; Richter et al., 2016), as they may show differential temporal dynamics in the developing brain and involve differential neural mechanisms. Second, as we included only stimuli congruent with prior knowledge, future studies may introduce knowledge-incongruent information to investigate the beneficial effect of prior knowledge on memory consolidation more directly. Prior knowledge may impact learning and consolidation of information over time differentially by development (McKenzie & Eichenbaum, 2011; van Kesteren et al., 2013; Wang& Morris, 2010). Third, we concentrated on a limited age range in middle childhood. To characterize how neural mechanisms of memory consolidation evolve over time, future studies should include other developmental cohorts. Fourth, we acknowledge that our study design leads to temporal autocorrelation in the BOLD signal when calculating RSA between fixation and scene time windows. Although we argue that our results, given the identical procedure over time, are more attributed to the delay-related changes in the neural reinstatement, future studies should tailor the design of the retrieval procedure to warrant cross-run comparisons. This could be achieved by introducing the same items repeatedly across different runs. Fifth, our task may not have been demanding enough for young adults to fully challenge their memory retention and encourage the formation of more gist-like representations. Future studies could explore this further by using more challenging conditions to enhance the formation of more generic memories in adults, avoid bias related to prior knowledge. Sixth, although we focused on ROIs associated with the recollection network and implicated in retrieval of visual information, we did not investigate the connectivity between these brain regions and how it changes as memories age. Future studies should investigate consolidation-related neural connectivity patterns and their temporal dynamics in the developing brain. Finally, children in our sample were positively biased in socio-demographical score and IQ compared to young adults, which may restrict the generalizability of our results.

CONCLUSIONS

In this study, we present novel empirical evidence on the neural mechanisms underlying the less robust memory retention of intentionally learned object-location associations in 5-to-7-year-old children compared to young adults. Our findings reveal that over time, children show attenuated consolidation-related upregulation in neocortical and cerebellar brain regions during successful retrieval. Furthermore, children may form different neural memory representations than young adults, as evidenced by the coexistence of both detailed scene-specific and generic gist-like reinstatement. Our results suggest that, unlike the mature consolidation systems in young adults, the developing brains of early school-age children show attenuated yet adult-like item-specific representations and reduced neural upregulation in core retrieval networks. Additionally, gist-based representations play a significant role in children’s retrieval processes, possibly aiding the building up of schema knowledge.

Data availability statement

The datasets generated and analysed during the current study are available from the corresponding authors upon reasonable request.

Conflict of interest disclosure

We have no known conflict of interest to disclose.

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Author contributions

Y.L.S, C.B., A.K secured funding. I.S and Y.L.S, C.B., A.K contributed to conception and design of the study. I.S. and P.L. performed data collection and data curation. I.S., P.L., and J.O.-T. performed the statistical analysis. I.S. wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

MATERIALS AND METHODS

Participants

Sixty-three typically developing children and 46 young adults were recruited to participate in the study through advertisement in newspapers, on the university campus, word-of-mouth, and city registry. All participants had normal vision with or without correction, no history of psychological or neurological disorders or head trauma, average IQ > 85, and were term-born (i.e., born after 37 weeks of pregnancy). Fourteen children were excluded due to : (i) incomplete task execution and missing data (n = 2); (ii) poor quality of the data (n = 7); (iii) technical issues during data acquisition (n = 5). Seven young adult participants were excluded due to incomplete task execution and missing data (n=5) or being identified as extreme outlier (n=2) based on interquartile range (IQR; above $Q3_{\text{upper quartile(75th percentile)}}$ + 3xIQR or below $Q1_{\text{lower quartile(25th}}$

percentile) – 3xIQR (Hawkins, 1980)) for memory behavioural measures. The excluded participants were comparable in terms of age, sex, and socio-economic status to the final sample. The final total sample consisted of 49 children (22 female, mean age: 6.34 years, age range: 5.3 – 7.1 years), and 39 young adults (19 female, mean age: 25.60 years, age range: 21.3 – 30.8 years; see Table 1 for more details).

All participants or their legal guardians gave written informed consent prior to participation. The study was approved by the ethics committee of the Goethe University Frankfurt am Main (approval E 145/18). The participants received 100 Euro as compensation for taking part in the study.

Table 1

Sample characteristics by age group

	Children (CH; N = 49)		Young adults (YA; N = 39)		Group effect (CH vs YA)	
Demographic measures	*M*	*SD*	*M*	*SD*	*p-value*	ω^2
Age	6.34	.43	25.60	2.79	***	.96
Sex (M/F)	27/22	-	20/19	-	-	-
IQ Score	117.90	12.92	107.64	12.49	***	.13
Socioeconomical Status						
ISCED – Father	6.22	1.43	4.39	1.75	***	.29
ISCED - Mother	6.17	1.34	4.08	1.85	***	.24

Notes. Income is based on a 1-7 Scale (1 = less than 15.000 €, 7 = more than 100.000 €); ISCED = International Standard Classification of Education 2011 (*International Standard Classification of Education*, 2011); IQ = Intelligence Quotient based on K-ABC (Kaufman & Kaufman, 2015) for children and WAIS-IV (Wechsler, 2015) for young adults; M = mean; SD = standard deviation; ω^2 = omega squared; *p < .05; ** < .01, *** < .001 (significant difference).

Materials and Procedure

Object-location associations task

Stimuli for the object-location association task were chosen based on the social studies and science curriculum for German primary school first and second graders (see similar procedure in Brod & Shing, 2019). The themes were chosen based on ratings provided by four primary school teachers on the familiarity of first graders with the topics. 60 different themes (e.g., classroom, farm, etc.) were chosen, each belonging to one of seven categories (i.e., field, water, housing, forest, infrastructure, indoor, farming). Four scene stimuli and four thematically congruent object pictures were selected for each theme (see Fig. 1 for an example), resulting in 240 individual scenes and 240 individual objects. The 240 object-scene pairs were assigned to versions A and B, each containing 120 object-scene pairs. Each participant was randomly assigned either version A or version B. There were six possible object locations across all scenes. Around each location, there were three possible object placements. The distribution of locations across scenes was controlled to ensure realistic placement of the objects within the scenes (for more detailed information see Supplementary Methods section). The object-location association task consisted of three phases (see Fig. 1):

(i) *Initial encoding phase* (Day 0, Day 1, Day 14). A total of 120 object-location pairs were used to create the trials in this phase, with 60 pairs presented on Day 0, 30 pairs on Day 1, and 30 pairs on Day 14. During each trial, participants viewed an object in isolation for 2 seconds, followed by the same object superimposed on a scene at a particular location for 10 seconds. After this, a blank screen with a fixation cross was presented for 1 second. Participants were instructed to memorize the object-location pairs and to remember the exact location of the object within the scene using elaborative encoding strategies, such as creating a story or making a “mental photo” of the scene. Such elaborative encoding strategies have been shown to improve memory performance in both children and adults (Craik & Tulving, 1975; Pressley, 1982; Pressley et al., 1981; Shing et al., 2008);

(ii) *Learning phase* (Day 0, Day 1, Day 14). Following the initial encoding phase, participants underwent further learning of the correct location of the object within the scene by undergoing adaptively repeated retrieval-encoding cycles. These cycles ranged from a minimum of two to a maximum of four. During each trial, participants were first presented with an isolated object for 2 seconds, followed by a one-second blank screen with a fixation cross. They were then shown a scene containing three red-framed rectangles, indicating possible location choices. Participants had to select the correct location by choosing one of the rectangles within 12 seconds, and the chosen rectangle was highlighted for 0.5 seconds. After this, feedback in the form of a smiley face was given, with the happy face for a correct answer, a sad face for an incorrect answer, and a sleeping face for a missed answer. Following the feedback, correct object-location associations were displayed for two seconds if the choice was correct and for three seconds if the choice was incorrect or missed. The cycles ended when participants provided correct responses to 83% of the trials or after the fourth cycle was reached.

(iii)*Retrieval phase* (Day 1 and Day 14). The retrieval phase was conducted inside the MRI scanner. Participants were instructed to recollect and visualize ("put in front of their mental eyes") as vividly as possible the location of the object within the scene. In this way we prompted the recall of the scene and the location of the object within this scene. Each trial began with a fixation cross jittered between 3 to 7 seconds (mean of 5 seconds). Participants were then presented with an isolated object for 2 seconds, followed by the presentation of another fixation cross jittered between 2 to 8 seconds (mean of 5 seconds). Following the fixation cross, participants were prompted with the associated scene and were required to recall the location of the object by selecting one of the three red rectangles on the scene within 7.5 seconds. If participants failed to respond within the deadline, the trial was terminated. No time-outs were recorded for young adults, while 5,4 % of time-out trials were recorded for children and these trials were excluded for analysis. After a choice was made or the response deadline was reached, the scene remained on the screen for an additional 0.5 second. The jitters and the order of presentation of recent and remote items were determined using OptimizeXGUI (Spunt, 2016)which followed an exponential distribution (Dale, 1999). Ten unique recently learned items (from the same testing day) and ten unique remotely learned items (from Day 0) were distributed withing each run (in total three runs) in the order as suggested by the software as the most optimal. There were three runs with unique sets of stimuli, each resulting in thirty unique recent and thirty unique remote stimuli overall.

Assessment of demographic and cognitive covariates

IQ scores were assessed using the German version of the "Kaufman Assessment Battery for Children – Second Edition" (K-ABC II; Kaufman & Kaufman, 2015) in children and the "Wechsler Adult Intelligence Scale – Fourth Edition" (WAIS -IV; Wechsler, 2015) in young adults. General socio-demographic questionnaires to assess socio-demographic characteristics of the participants were administered as well.

Experimental Procedure

The testing was conducted over three days (see Fig. 1B). On Day 0, the experiment began with a short training session aimed at familiarizing participants with the object-location associations task and elaborative encoding strategy, using five object-location pairs. The experimental task started with the initial encoding of unique sets of object-location associations. Participants had to learn two unique sets comprised of 30 object-location associations each. After encoding each set, participants engaged in a brief distraction task where they listened to and had to recall a string of numbers. Next, they underwent a learning phase with retrieval-encoding cycles until they reached a criterion of 83% (or a maximum of four cycles). This was done to minimize variances attributed to encoding, allowing for more accurate comparison of subsequent memory consolidation. Afterwards, the children visited a mock-scanner to become familiar with the MRI scanning environment. This procedure involved teaching the children the sounds of MRI scanning and training them to stay still during scanning.

On Day 1, participants first learned a new set of 30 object-location associations, using the same learning procedure as on Day 0. This was followed by retrieval in the MRI scanner, during which they were required to recall 30 object-location associations learnt on Day 0 (short-delay, remote) and another 30 learnt on Day 1 (recent). On Day 14, the same procedure was followed as on Day 1, with a new set of 30 object-location associations. They were again required to recall 30 object-location associations learnt on Day 0 (long-delay, remote) and another 30 learnt on Day 14 (recent). In total, participants completed 60 retrieval trials in the MR scanner on Day 1 and Day 14 each, which took approximately 15-20 minutes. Besides the primary task, participants also completed other psychometric tests across all testing sessions. Additionally, socio-demographic questionnaires were administered to young adults and legal guardians of children.

Data acquisition

Behavioural data acquisition

The task paradigm during all phases was presented using Psychtoolbox (Kleiner et al., 2007) software in MATLAB 9.5, R2018b (MATLAB, 2018). During the encoding and learning phases, stimuli were presented on a computer screen with the resolution of 1920x1080 pixels. During the retrieval phase, an MR-compatible screen with identical resolution was used, and participants used an MR-compatible button box with three buttons. To minimize head movements, foam cushions were placed inside the head coil, and MR-compatible headsets and ear plugs were used to reduce the scanner noise.

Magnetic resonance imaging data acquisition

MR images were acquired on a 3 Tesla SIEMENS PRISMA MRI scanner (Siemens Medical Solutions, Erlangen, Germany) using a 64-channel head coil at Berlin Center for Advanced Neuroimaging, Charité Universitätsmedizin Berlin. Each session started with the acquisition of a localizer and head scout sequences for field-of-view-alignment (FoV) based on anatomical landmarks. T1-weighted structural images were obtained with the magnetization prepared rapid gradient echo (MP-RAGE) pulse sequence (TR = 2500 ms, echo time = 2.9 ms, flip angle = 8°, FoV = 256 mm, voxel size = 1x1x1 mm^3, 176 slices). Functional images were acquired using echo-planar imaging sequences (TR = 800 ms, echo time = 37 ms, flip angle = 52°, FoV = 208 mm, 72 slices, voxel size = 2x2x2 mm^3, maximally 588 volumes). In addition, gradient echo images (field maps) were acquired before each functional run for correction of magnetic field inhomogeneities.

Behavioural data analysis

Learning and Consolidation

The behavioural analyses were performed with R packages (R Core Team, 2022) in RStudio 2022.07.0 (RStudio, Inc.). Throughout the analyses, statistical significance level was set at $< .05$.

All p-values were FDR-adjusted for multiple comparisons due to multiple ROIs. As a measure of baseline memory performance, final learning accuracy was defined as the percentage of correctly learned locations in relation to the total number of items at the end of the learning phase of each day. To examine memory consolidation, we quantified memory retention across delays, focusing on trials that were correctly learned on Day 0. From these trials, we calculated the percentage of correct responses, separately for Day 1 and Day 14. We conducted a linear mixed-effect model (LME model) for memory measures using the lmer function from the lme4 package in R (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017). All LME models were calculated with maximum-likelihood estimation and Subject as the random intercept to account for between-subject variability in retention accuracy.

First, to investigate baseline memory performance, we analysed whether final learning accuracy in all three sessions differed between groups. For that, we included the within-subject factor of *Session* (Day 0, Day 1, and Day 14) and the between-subject factor of *Group* (children and young adults) in the LME model. Second, for memory retention rates, we included *Session* (Day 1, Day 14), *Item Type* (recent, remote), and *Group* (children, young adults) as fixed factors in the LME model. In addition, we added *Subjects* as random factor, as well as *IQ*, *Sex*, and *Handedness* (Kang et al., 2017; Willems et al., 2014) as covariates. Degrees of freedom were adjusted using the Satterthwaite's method (Kuznetsova et al., 2017) if the assumptions of homogeneity of variances were violated. Significant effects were followed up with Sidak post-hoc multiple comparisons. For further group differences in socio-demographic measures, we performed one-way independent analysis of variance (ANOVA) or Games-Howell test (S. Lee & Lee, 2018). The effect size estimation was performed using omega squared (w^2) as a less biased estimate for reporting practical significance of observed effects (Okada, 2013). To determine the amount of variance explained by the model, we used partR2 package (Stoffel et al., 2021).

fMRI data pre-processing

Anatomical and functional MR data was pre-processed using fMRIPrep 22.0.0 (Esteban et al., 2019), based on Nipype 1.8.3 (Gorgolewski et al., 2011). Detailed description of the anatomical and functional data pre-processing can be found in Supplementary Methods section.

fMRI data analysis

FMRI data analysis was conducted with FEAT in FSL (Version 6.0.1, FMRIB's Software Library, Jenkinson et al., 2012; Smith et al., 2004; Woolrich et al., 2009). Prior to that, single runs were excluded if there was (i) root-mean-square realignment estimates(Jenkinson et al., 2002) exceeding 1mm; and (ii) framewise displacement (FD) > 1, and (iii) less than two correct trials in the entire run. Based on these criteria, 14 single runs and two complete sessions in children were excluded from further analysis.

General Linear Model for Mean Activation

For each participant's fMRI data, a first-level analysis was performed separately for each run using a general linear model (GLM) with eight experimental regressors. The regressors represented the onset and duration of the following events: (i) object recent$_{\text{correct}}$, (ii) object remote$_{\text{correct}}$, (iii) scene recent$_{\text{correct}}$, (iv) scene remote$_{\text{correct}}$, (v) object recent$_{\text{incorrect}}$, (vi) object remote$_{\text{incorrect}}$, (vii) scene recent$_{\text{incorrect}}$, (viii) scene remote$_{\text{incorrect}}$. The duration of object events was two seconds, while the duration of scene events was dependent on the reaction time (RT). The regressors were convolved with a hemodynamic response function, modelled with a double-gamma function with first and second derivatives. Confounding regressors were also included in the GLM and were calculated with fMRIPrep, namely global signal, six rigid body realignment parameters, framewise displacement, and standardised DVARS (D, temporal derivatives over time courses; VARS, variance over voxels). In addition, six anatomic component-based noise correction (CompCor) regressors and cosine drift terms were included, based on previous methodological studies (Ciric et al., 2017; Esteban et al., 2020; Jones et al., 2021; Satterthwaite et al., 2013). The functional images were spatially smoothed with SUSAN (Smallest Univalue Segment Assimilating Nucleus, Smith & Brady, (1997)), applying a Gaussian kernel with a full-width at half-maximum of 6 mm. A high-pass Gaussian filter with a cut-off period of 80 s was applied. Contrasts were defined for each run per subject, and within-subject fixed-effects averaging across runs within each session was conducted per subject. Group-level analysis was performed with FLAME1 (Woolrich et al., 2004) within each session, based on the statistical maps obtained from the first-level analysis. The main contrast of interest was *object remote* > *object recent*, as we were primarily interested in the reinstatement of object-scene association before the scene was shown. Univariate analysis was performed with statistical tests voxel-wise and corrected for multiple comparisons with cluster-based thresholding using a z threshold of $z > 3.1$ and a two-tailed probability of 0.001.

Several a priori regions of interest (ROI) were selected based on anatomical masks: bilateral anterior/posterior hippocampus (HC), bilateral anterior/posterior parahippocampal gyrus (PHG), and RSC. The masks for the medio-temporal lobe ROIs were taken from the Harvard-Oxford Cortical and Subcortical Atlases (threshold at 30% probability; (Desikan et al., 2006)), and the mask for RSC was taken from the Talairich Atlas (threshold at 30% probability; Lancaster et al., 2000; Talairich & Tournoux, 1988) . For further ROIs in large cortical regions (namely mPFC, precuneus, LOC, vlPFC, and cerebellum), anatomical masks derived from Harvard-Oxford Cortical and Subcortical Atlases or Juelich Atlas (Amunts et al., 2020) were combined with a functional task-related map, based on mean activation across recent and remote objects across all participants and sessions, at voxel-wise threshold of $z > 3.1$ and a two-tailed probability of 0.001. With these masks, the mean percent signal change (from the contrast of $\textit{object remote}_{correct} > \textit{object recent}_{correct}$) was extracted using FEAT in FSL for each session of each participant, which were then submitted to statistical analysis in R. A linear mixed-effect model (as described in section 2.5) was set up to model percent signal change. The linear mixed effect model was calculated with maximum-likelihood estimation and *Subject* as random intercept to account for between-subject variability. As fixed factors, we included *Session* (Day 1, Day 14) and *Group* (children, young adults). We also added *IQ and sex and handedness* and mean reaction time as covariates to the model.

Representational similarity analysis for neural reinstatement.

For the multivariate analysis, single-event (i.e., for every event on each trial) β (beta) estimates [1] were first computed by modelling BOLD time course with a series of Generalized Linear Models (GLM) using the Least Square Separate method (LSS; Abdulrahman & Henson, 2016; Mumford et al., 2012). Each trial contained three events (i.e., object, fixation, and scene), hence a total of 30 GLMs (i.e., ten for objects, ten for fixations, and ten for scenes) were computed for each run, session, and participant. Each of the GLMs contained four experimental regressors: for instance, one for the single fixation of interest and three more for the rest of the events (i.e., for all other fixations except the fixation of interest, for all objects, and for all scenes). The same set up was followed for the object GLMs and the scene GLMs. The regressors were convolved with the hemodynamic response function, which was modelled with a double-gamma function with first and second derivatives. Additionally, the same confounding regressors as the ones for mean-activation analysis were included.

Next, to assess whether mnemonic reinstatement during the fixation period, during which participants were supposed to recollect the scenes associated with the objects, was more item-specific or gist-like, we used the single-event beta estimates of each trial to compute two types of Representational Similarity Matrices (RSMs; Kriegeskorte, 2008). Each RSM was computed separately for each previously identified ROI. All subsequent analyses were performed with homebrew scripts available at https://github.com/iryna1schommartz/memokid_fmri.

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[1] Beta estimates were obtained from a Least Square Separate (LSS) regression model. Each event was modeled with their respective onset and duration and, as such, one beta value was estimated per event (with the lags between events differing from trial to trial). The jitter was included to enable an estimation of the patterns evoked by the events and all subsequent RSA analyses were conducted normally on these estimates without further controls.

Scene-specific reinstatement*:** To measure the extent of scene reinstatement following object presentation, we computed a *scene-specific reinstatement index* for each neural RSM, separately for correctly remembered recent and correctly remembered remote scenes of each session (see Figure 5A-B)***. For each specific scene, we computed the index as the average distance between the "*fixation*" and "*scene period*" (Fisher-transformed Pearson's r; Fig. 5B), which was the correlation between neural patterns during fixation and neural patterns when viewing the scene. We averaged the index across all items, all runs within a session, and then within subjects, resulting in a single value per predefined ROIs and sessions. In addition to scene-specific reinstatement, we also calculated a *set-based reinstatement index* as a control analysis, which was calculated as an average distance between "*fixation*" and "*scene period*" for a scene and every other scene within the stimuli set (Deng et al., 2021; Ritchey et al., 2013; Wing et al., 2015). The set-based reinstatement index reflects the baseline level of non-specific neural activation patterns during reinstatement. We then calculated the *corrected scene-specific reinstatement index* as the difference between set-based and scene-specific Fisher-transformed Pearson's values (Deng et al., 2021; Ritchey et al., 2013; Wing et al., 2015). A higher value in this index denotes more distinct scene reinstatement patterns. Only correctly retrieved items were included for this analysis. We obtained the corrected scene-specific reinstatement indices for recent items on Day 1 and Day 14 and tested them for session-related differences. If no differences were observed, the set-corrected scene-specific reinstatement indices for recent scenes on Day 1 and 14 were averaged to obtain a single value per ROI and participant. We then conducted a final LME model, separately for each ROI, with *Subject* as the random factor and *Delay* (recent, remote Day 1, remote Day 14) and *Group* (children, young adults) as fixed factors. In addition, mean neural activation was added as a covariate into the model.

Gist-like reinstatement: Seven overarching thematic categories were identified during stimuli selection (i.e., field, water, housing, forest, infrastructure, indoor, farming). A within-category similarity indices were computed based on fixation time window of correctly remembered items belonging to the same category and excluding the similarity computation for the fixation time windows of correctly remembered items with itself. A between-category similarity indices were computed based on fixation time window of correctly remembered items belonging to different categories. These indices were computed for each run, Z-standardized and then averaged across all runs. A gist-like reinstatement index was computed by subtracting between-categories from within-categories Z-transformed distances ([within category$_{recent}$ – between category$_{recent}$] and [within category$_{remote}$ – between category$_{remote}$] for each session, Fig. 7A-B) . The non-zero values in this corrected index reflect gist-like *reinstatement*, as the similarity distance would be higher for pairs of trials with the same categories than for pairs with different categories. We applied a one-sample permutation t-test to test for significance in each ROI. Similar to the procedure described above, gist-like reinstatement indices for recent items on Day 1 and Day 14 were averaged when no difference was found, obtaining a single value per ROI and participant. We then conducted a final LME model, separately for each ROI, with *Subject* as the random factor and *Delay* (recent, remote Day 1, remote Day 14) and *Group* (children, young adults) as fixed factors and mean neural activation as a covariate, to analyse any delay-related differences in gist-like reinstatement index for successfully retrieved trials. Finally, we also explored whether over time, long-delay item-specific and gist-like reinstatement is beneficial or detrimental for memory performance by correlating the index with memory retention rates. We tested whether this correlation within each group differs based on ROI. If no differences were observed, we averaged reinstatement indices across ROIs that showed significant reinstatement in long delay.

Brain-behavioural relations

To examine the connections between brain function and behavior, we utilized brain metrics generated via the application of a multivariate method known as Partial Least Square Correlation (PLSC) (Abdi & Williams, 2013; McIntosh et al., 1996; Schommartz et al., 2023). This approach focuses on multivariate links between specified neural measures in Regions of Interest (ROIs) and fluctuations in memory performance over short and long delays across different age cohorts. We argue that this multivariate strategy offers a more comprehensive understanding of the relationships between brain metrics across various ROIs and memory performance, given their mutual dependence and connectivity (refer to Genon et al. (2022) for similar discussions).

Initially, we established a cross-subject correlation matrix that included (i) a matrix (n x 10) comprising short and long delay brain indices (encompassing both neural upregulation, scene-specific and gist-like indices) for all specified ROIs, and (ii) a vector (n-sized) that represents a continuous assessment of either short-delay or long-delay memory performance (RR): R = CORR (RR, ROIs). Prior to the correlation, all metrics were standardized. The decomposition of this correlation matrix, R = USV', was performed using singular value decomposition, yielding singular vectors U and V, or saliences. Here, the left singular vector symbolizes the weights for short- or long-delay memory accuracy (U), while the right singular vector represents ROI weights (V) indicating specific neural indices that optimally represent R, with S being a matrix of singular values.

Subsequently, PLSC identifies a singular estimable latent variable (LV), uncovering pairs of latent vectors with maximal covariance that best describe the association between memory retention rates and ROI neural indices. Therefore, LV delineates distinct patterns of neural indices across ROIs closely linked to either short- or long-delay retention rates. Moreover, we computed a singular value for each participant, termed an within-person “profile,” summarizing the robust expression of the defined LV’s pattern. This was achieved by multiplying the model-derived ROI weight vector (V) with the within-person estimates of ROI neural metrics.

To verify the generalizability and significance of the saliences or LV, we performed 5000 permutation tests to derive a p-value. We also determined the stability of the within-LV weights by bootstrapping with 5000 resamples, calculating a bootstrap ratio (BSRs) by dividing each ROI’s salience by its bootstrap standard error. BSRs, analogous to Z-scores, serve as normalized robustness estimates; hence, values exceeding 1.96 ($p < .05$) indicate statistically stable saliences. Utilizing PLSC for multivariate statistical analysis in one step eliminates the need for multiple comparisons correction across all ROIs (McIntosh et al., 1996).

To avoid multicollinearity and redundancy, which might diminish the power to uncover neural-behavioral links through conventional statistical approaches, we initially derived a single metric per participant—a participant’s expression of the latent brain pattern (i.e., brain score) for neural indices that share the most variance with either short-delay or long-delay memory accuracy variations. We further explored how these brain patterns correlate with memory performance.

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