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

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RESEARCH HIGHLIGHTS

- Children showed less robust memory consolidation across short and long delay compared to young adults.
- Neural activity for remote memory increases from short to long delay in neocortical (parietal, prefrontal and occipital) and cerebellar brain regions in young adults, but not in children.
- Children showed reduced scene-specific reinstatement of neural patterns compared to young adults.
- Children relied more on gist-like, category-based neural reinstatement in medial-temporal, neocortical prefrontal and parietal, and cerebellar 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 (dis)similarity analysis (RSA). Our results showed that memory consolidation in children was less robust (i.e., more forgetting) compared to young adults. For correctly retained remote memories, young adults showed increased neural activation from short to long delay in neocortical (parietal, prefrontal and occipital) and cerebellar brain regions, while children showed increased neural activation in prefrontal and decrease in neural activity in parietal brain regions over time. In addition, there was an overall attenuated scene-specific memory reinstatement of neural patterns in children compared to young adults. At the same time, we observed category-based reinstatement in medial-temporal, neocortical (prefrontal and parietal), and cerebellar brain regions only 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, category-based neural reinstatement.

Keywords: object-scene associations, memory consolidation, representational (dis)similarity analysis, neural reinstatement

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).

To summarize, studies have shown that with passing time, memories of well-learned information increasingly engage cortical regions including the prefrontal, parietal, occipital, and anterior temporal brain areas that support retrieval of general and schematic memories, as well as complex associative information, while the recruitment of HC tends to decrease. However, most research focused on only a selected delay window and only on young adults.

Mnemonic reinstatement across consolidation

In addition to changes in neural activation during mnemonic retrieval over time, it is important to characterize the transformations 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 (Reyna & Brainerd, 1995; Sekeres et al., 2016). 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 memory reorganisation in HC and mPFC. Specifically, during a one-week delayed retrieval

compared to immediate retrieval the overlap in neural patterns reflected the overlap in stimulus features. 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 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 of mnemonic reinstatement between children and adults. For instance, univariate selectivity was reduced in children, while fine-grained representational similarity along the ventral visual stream for mnemonic reinstatement was similar in 5-11 years old children and adults (Cohen et al., 2019; Golarai et al., 2015). These findings indicate that mnemonic reinstatement may develop prior to univariate selectivity. Fandakova et al. (2019) also showed that neural specificity during encoding was similar in 8-to-15-year-old children and adults in the RSC, LOC and PHG. Neural specificity was also associated with subsequent memory in a similar way between children and adults. However, 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 6 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) 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, 2012a; Keresztes et al., 2022; Lebel et al., 2012; Shing et al., 2008, 2010a); (ii) a stable involvement of HC over time in adults and children due to relative maturity of the HC in middle childhood (Keresztes et al., 2017; Sekeres et al., 2018; Shing et al., 2008; Sluzenski et al., 2006); (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 category-based memory pattern reinstatement in children in comparison to more detailed item-specific neural pattern reinstatement in young adults over time (Reyna & Brainerd, 1995)).

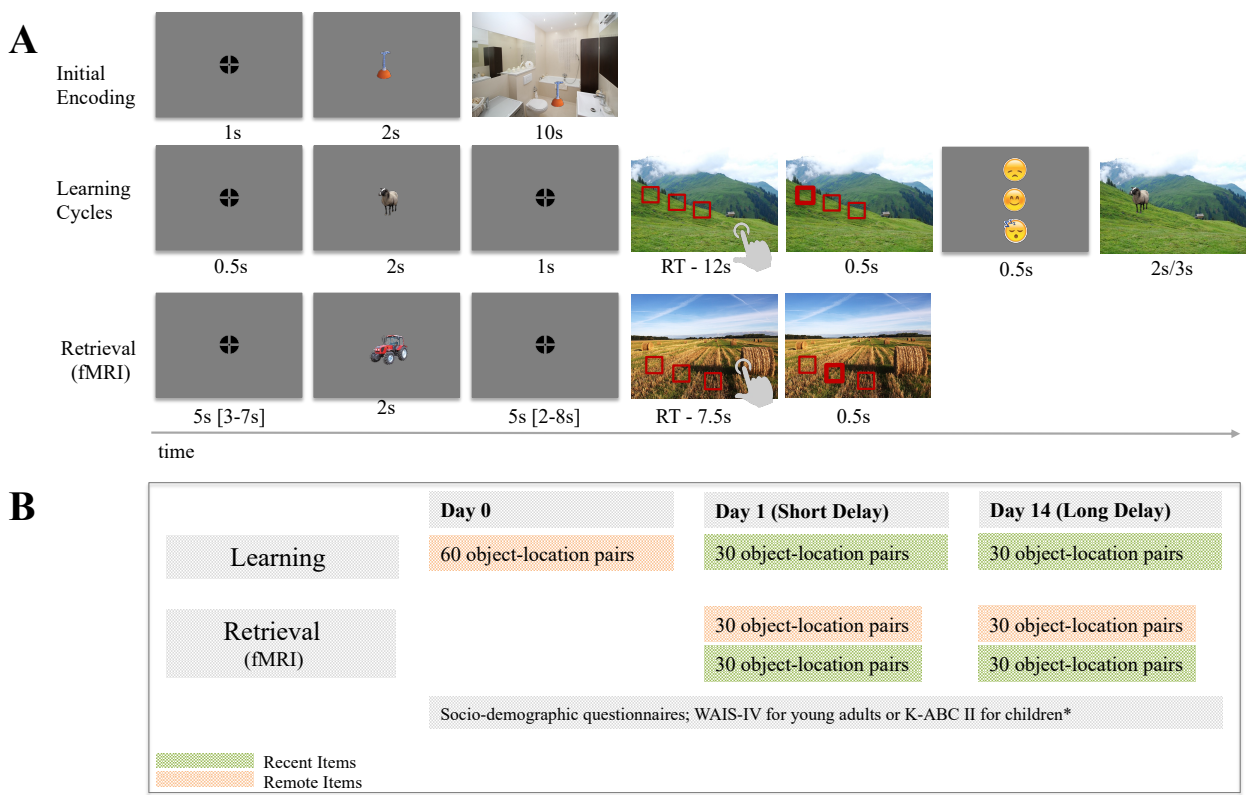
RESULTS

Behavioural results

Final Learning Performance

For final learning accuracy, operationalized as percentage of correctly identified locations relative to the total number of locations (see Fig. 1A for the task overview and Fig. 1B for experimental procedure overview), 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. 2A). 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



Memory Task and Experimental Procedure

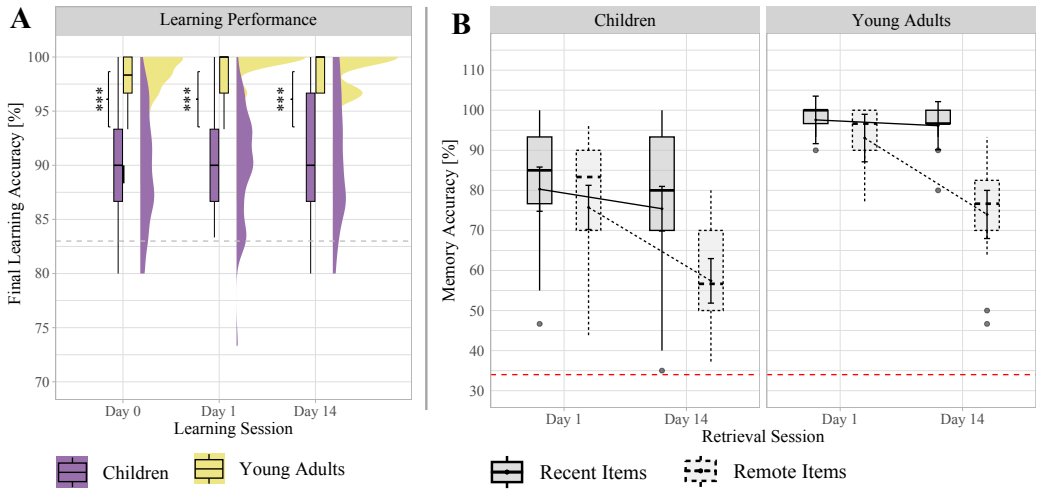
(A) Trial Structures in the Experimental Task. (i) In the *Initial Encoding* phase, participants were instructed to remember object-location pairs by creating a story or making a "mental photo" of the scene, memorizing the exact location of each object within the scene. (ii) In the *Learning Phase*, participants chose one location out of three choices and received feedback for their response. 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.

Memory Retention Across Time

In the following, we examined the change in memory performance for correctly learned items across time (Fig. 2B, Table S1-S2 for full overview). We observed significant main effects of *Session,* $F_{(1,241)} = 150.31$, $p < .001$, $w^2 = .38$, indicating higher overall memory retention on Day 1 compared to Day 14, $b = 10.9$, $t_{(250)} = 12.09$, $p < .001$; of *Item Type,* $F_{(1,229)} = 203.25$, $p < .001$, $w^2 = .47$, indicating higher overall memory retention for recent compared to remote items, $b = 12.3$, $t_{(238)} = 14.08$, $p < .001$; of *Group*, $F_{(1,84)} = 70.13$, $p < .001$, $w^2 = .45$, indicating lower overall memory retention in children compared to young adults, $b = -18$, $t_{(93)} = -8.08$, $p < .001$; and *Session* x *Item type* interaction, $F_{(1,229)} = 80.96$, $p < .001$, $w^2 = .26$. Model-based Sidak post hoc comparisons revealed that memory retention across both age groups was higher for recent than remote items on Day 1, $b = 4.5$, $t_{(238)} = 3.78$, $p < .001$, and on Day 14, $b = 20.08$, $t_{(238)} = 15.78$, $p < .001$. Moreover, this difference between recent and remote items was more pronounced on Day 14 compared to Day 1, $b = -15.5$, $t_{(238)} = -8.88$, $p < .001$. In sum, the results showed that children had overall worse memory retention rates compared young adults, indicating less robust memory consolidation in children. Memory retention immediately after learning were higher compared to overnight and 2-week-old memory retention. This pattern was similarly more pronounced on Day 1 compared to Day 14 for both age groups.

Figure 2



Overview if Mnemonic Performance

(A) ***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. 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. Grey dashed line indicates the criteria of 83% correctly learned items. **(B)** ***Memory retrieval.*** Memory accuracy is operationalized as the percentage of correct responses in the retrieval task conducted during the MRI scanning sessions. Memory accuracy for recently consolidated items did not differ between sessions in young adults, while for children, 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.

In the following section, the results of the univariate analysis of the selected ROIs are summarized, with a full statistical report on LME-model in Table 2 and model-based post hoc Sidak-corrected comparisons in Table S6. Results for the whole-brain analyses are available in Tables S3-5.

Our results showed that for the **anterior and posterior HC** (Fig. 3A) as well as for the **anterior PHG** (Fig. 3B)**,** difference in neural activation for the contrast of remote > recent remained similar across age groups and across sessions (all p > .450). However, we found a significant increase in remote > recent activation from Day 1 to Day 14 in the **posterior PHG** (Fig. 3B) in young adults (p = .006), but not in children (p = .66). This increase was significantly higher in adults than in children (p = .009). In contrast, we found that the activation difference in remote > recent in the ***mPFC*** (Fig. 3C) was higher in children than in young adults (p = .026), and it remained stable across time (p = .450), indicating a stable involvement of the mPFC in the retrieval of remote memories. Regarding the ***vlPFC*** (Fig. 3D), the results showed a significant increase in remote > recent activation from Day 1 to Day 14 (p = .005), while overall activation was higher in young adults in comparison to children (p <.001). In the ***cerebellum*** (Fig. 3E), the results revealed an increase from Day 1 to Day 14 in young adults (p = .005), as well as an overall higher remote > recent difference in young adults than in children (p = .024). Moreover, we found a significant decrease in the recruitment of the ***RSC*** (Fig. 3F) for remote > recent difference in children from Day 1 to Day 14 (p = .007). This decrease was also more pronounced in children than in adults (p = .012), indicating that over time children recruited the ***RSC*** less for remote memories, while the recruitment in young adults remained stable. We also found a significant decrease in the

recruitment of the ***precuneus*** (Fig. 3G) for remote > recent difference from Day 1 to Day 14 (p = .011). Overall, activation difference remote > recent was lower in children than in young adults (p = .012). Finally, remote > recent activation in the ***LOC*** (Fig. 3H) increased from Day 1 to Day 14 in young adults (p <.001), but not in children (p = .42). This effect was significantly higher in young adults than in children (p = .035), indicating that over time, LOC activation increases for successful retrieval of old detail-rich memories in young adults.

In summary, our results showed increased upregulation of neural activity from Day 1 to Day 14 for remembering remote > recent items in the posterior PHG, LOC and cerebellum in young adults only. Children showed time-invariant remote > recent activation in the mPFC, coupled with a decrease in contrast difference in the precuneus and the RSC from Day 1 to Day 14. Both young adults and children showed increased upregulation of neural activity for remote > recent difference in vlPFC over time. No changes were observed in the anterior and posterior HC and the anterior PHG for either group.

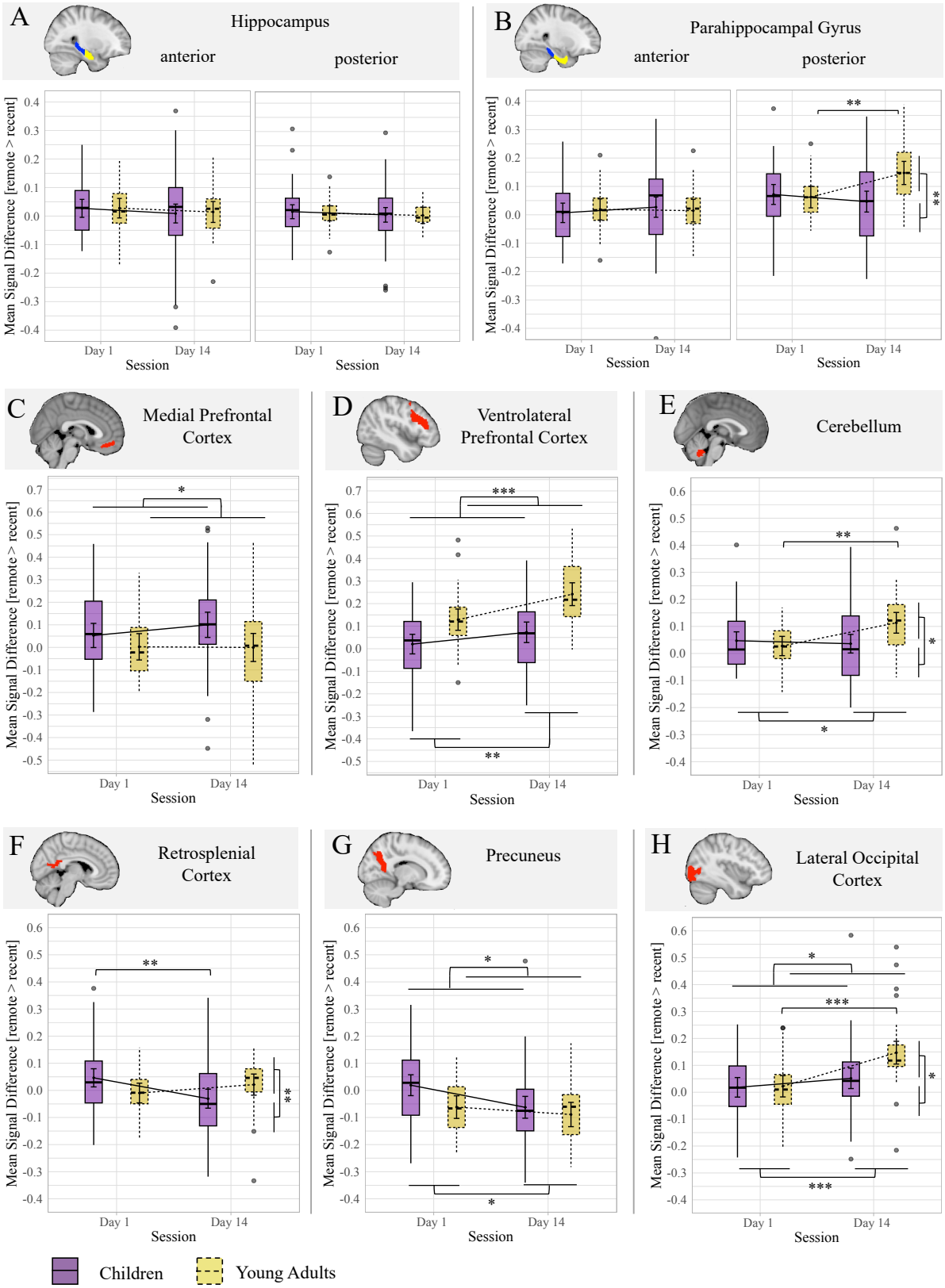
Table 2

Overview of the main and interaction effects of the linear mixed effects model for remote > recent neural activation

	Main Effect of Group		**Main Effect of Session**		**Group x Session Interaction**		
Regions of Interest	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	*R2*
Hippocampus Anterior	$.03_{(1,161)}$	.993	$.86_{(1,161)}$	.450	$.02_{(1,161)}$	.889	.006
Hippocampus Posterior	$.09_{(1,161)}$	.993	$.48_{(1,161)}$	.542	$.02_{(1,161)}$	.889	.004
Parahippocampal Gyrus Anterior	$.00_{(1,161)}$	.993	$.19_{(1,161)}$	.668	$.44_{(1,161)}$	.634	.004
Parahippocampal Gyrus Posterior	$5.32_{(1,86)}$	**.048**	$2.82_{(1,84)}$	.194	$9.62_{(1,84)}$	**.015**	.204
Medial Prefrontal Cortex	$5.27_{(1,88)}$	**.048**	$.85_{(1,83)}$	.450	$1.09_{(1,83)}$	.427	.360
Ventrolateral Prefrontal Cortex	$32.72_{(1,83)}$	**<.001**	$13.63_{(1,81)}$	**<.001**	$1.83_{(1,81)}$	.320	.297
Cerebellum	$2.68_{(1,161)}$	.173	$4.48_{(1,161)}$	.090	$7.53_{(1,161)}$	**.023**	.076
Retrosplenial Cortex	$.014_{(1,161)}$	.993	$1.62_{(1,161)}$	.342	$8.98_{(1,161)}$	**.015**	.067
Precuneus	$6.73_{(1,161)}$	**.048**	$6.93_{(1,161)}$	**.03**	$1.72_{(1,161)}$	.320	.093
Lateral Occipital Cortex	$5.41_{(1,161)}$	**.048**	$20.35_{(1,161)}$	**<.001**	$6.80_{(1,161)}$	**.027**	.321

Notes. Subject was included as random effect. Group (children, young adults), Session (Day 1 remote > recent, Day 14 remote > recent), and their interaction were included as fixed effect. The following reference levels where used: for Session – Day 1; for Group – Children; F – F-value; DF – degrees of freedom; p – p-value; FDR_adj – False Discovery Rate adjusted; R2 – amount of variance explained by the model. Type III Analysis of Variance Table with Satterthwaite's method. *p < .05; ** <.01, ***<.001 (significant difference). All main and interactions p-values were FDR-adjusted for multiple comparisons. All main and interactions p-values were FDR-adjusted for multiple comparisons.

Figure 3


A
Hippocampus
anterior
posterior
B
Parahippocampal Gyrus
anterior
posterior
C
Medial Prefrontal Cortex
D
Ventrolateral Prefrontal Cortex
E
Cerebellum
F
Retrosplenial Cortex
G
Precuneus
H
Lateral Occipital Cortex
Mean Signal Difference [remote > recent]
Day 1
Day 14
Session
Children
Young Adults

Model-based results for ROIs.

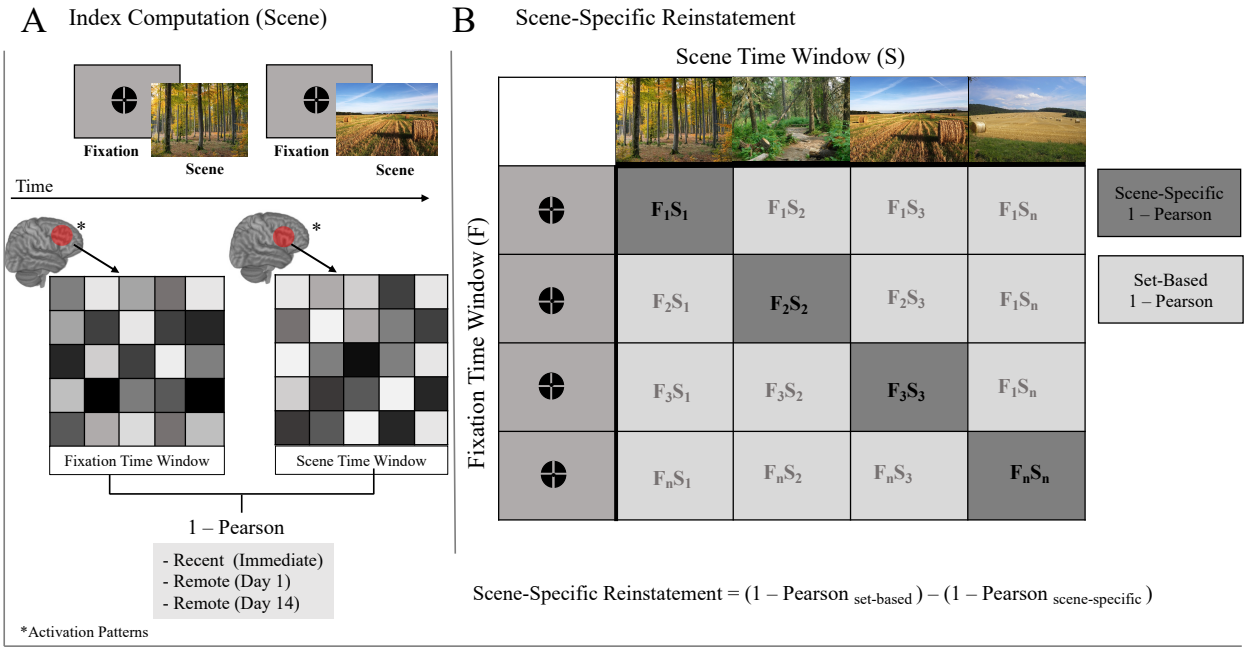
Mean signal difference for remote > recent memories on Day 1 and Day 14 in **(A)** anterior and posterior hippocampus; **(B)** anterior and posterior parahippocampal gyrus; **(C)** medial prefrontal cortex; **(D)** ventrolateral prefrontal cortex; **E)** cerebellum; **(F)** retrosplenial cortex; **(G)** precuneus; **(H)** lateral occipital cortex. *Note:* Error bars indicate standard error based on the underlying LME-model. **p* < .05; ***p* < .01; ****p* < .001(significant difference); non-significant differences were not specifically highlighted.

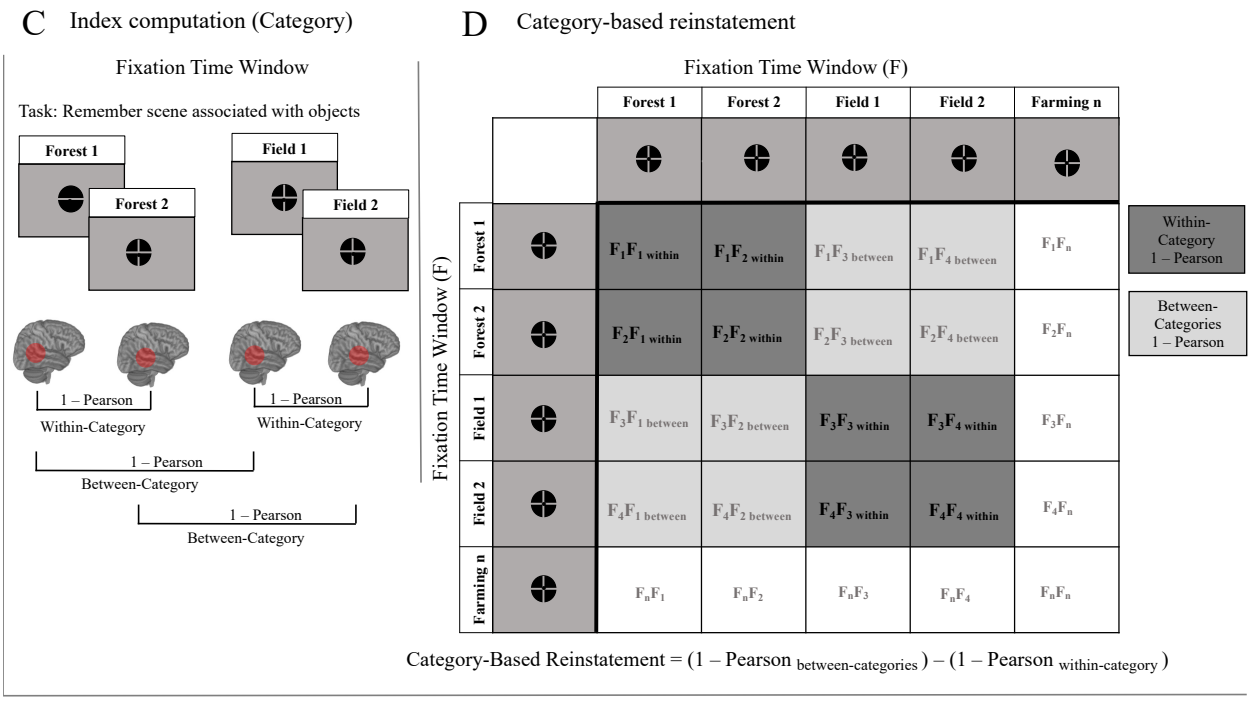
Representational (dis)similarity results.

3.2.2.1 Corrected scene-specific reinstatement.

The following section presents the results of scene-specific neural reinstatement in the selected ROIs (see Fig. 4A for index calculation overview), with a full statistical report on the LME-model in Table 3 and model-based post-hoc Sidak-corrected comparisons in Table S9. 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 > .68) and adults (p > .14). All scene-specific reinstatement indices for remote and recent items were significantly different from zero (all $p < .05_{\text{FDR-adjusted}}$; Table S7). The only exceptions were for remote items on Day 14 in the PHG, the mPFC, the RSC, and the precuneus for children.

Figure 4





Representational (Dis)similarity Analysis.
(A) Index Computation (Scene). A representational dissimilarity index was computed by assessing the average dissimilarity between fixation and scene time window separately for recent, remote (Day 1), and remote (Day 14) scenes. **(B) Scene-specific index computation**. A corrected scene-specific reinstatement index was computed by assessing the average dissimilarity in fixation and scene time window within each trial and subtracting it from the average set dissimilarity between the fixation and scene time window across trials. **(C) Index Computation (Category).** A representational dissimilarity index was computed by assessing the average dissimilarity for fixation time window for within-category and between-category scenes separately for recent, remote (Day 1), and remote (Day 14) scenes. **(D) Category-based index computation**. A category-based reinstatement index was computed by assessing the average dissimilarity in fixation time window for same-category pairs and subtracting it from the any-other-category pairs. S – scene time window; F – fixation time window; r – Pearson's correlation index.

We observed significant group main effects for all ROIs (all $p < .003$) except for the vlPFC ($p = .892$). Namely, our results showed higher overall scene-specific reinstatement in young adults compared to children in the HC ($p <.001$; Fig. 5A), PHG ($p = .003$; Fig. 5B), cerebellum ($p < .001$; Fig. 5C), LOC ($p <. 001$; Fig. 5D), mPFC ($p < .001$; Fig. 5E), RSC ($p <. 001$; Fig. 5G), and precuneus ($p < .001$; Fig. 5H), but not in vlPFC ($p = .89$; Fig. 5F). These results indicate that scene-specific reinstatement was generally more attenuated in children than in young adults. Concerning significant session effect for all ROIs (all $p < .001$), the results showed a significant decrease from recent to short delay in all ROIs (all $p <.001$), while a further significant decrease from short to long delay was observed only in the vlPFC ($p = .039$) and the RSC ($p = .012$). We did not observe any group x session interactions (all $p > .077$). These results indicate that the main decrease in

scene-specific neural reinstatement for successfully consolidated memories occurs after a short overnight delay.

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 in all ROIs and remained further stable after a 2-week-period for all ROIs, except for the vlPFC and the RSC.

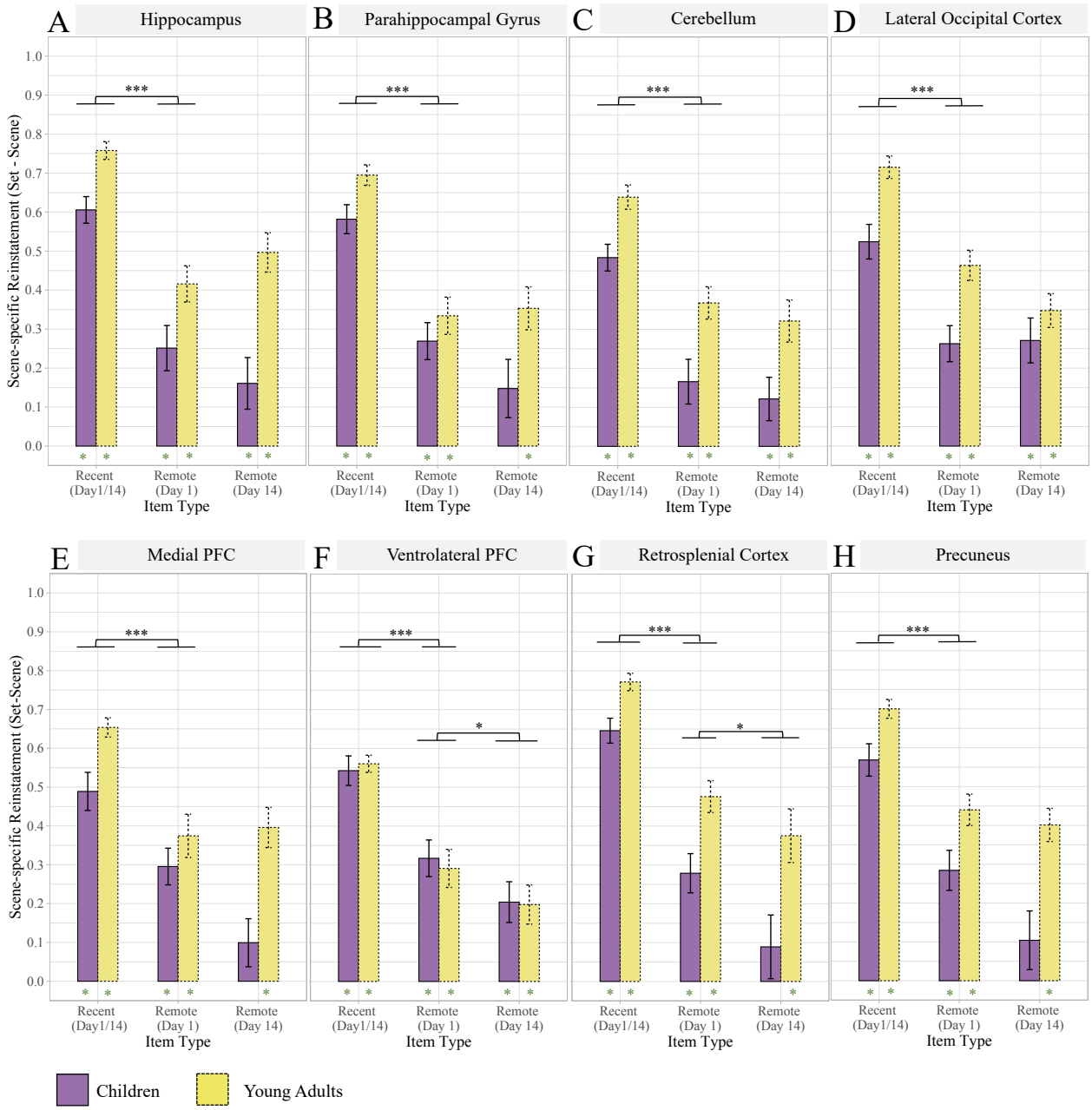
Table 3

Statistical overview of the main and interaction effects of the linear mixed effects model for scene-specific reinstatement.

	Main Effect of Group		**Main Effect of Session**		**Group x Session Interaction**		
Regions of Interest	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	*R2*
Hippocampus	$31.38_{(1,238)}$	**<.001**	$37.61_{(2,238)}$	**<.001**	$2.20_{(2,238)}$	.384	.315
Parahippocampal Gyrus	$9.51_{(1,85)}$	**.003**	$41.23_{(2,162)}$	**<.001**	$1.11_{(2,162)}$	.444	.318
Medial Prefrontal Cortex	$15.62_{(1,77)}$	**<.001**	$27.46_{(2,152)}$	**<.001**	$2.61_{(2,152)}$	.384	.348
Ventrolateral Prefrontal Cortex	$.02_{(1,83)}$	.892	$37.46_{(2,158)}$	**<.001**	$.13_{(2,158)}$	.880	.291
Cerebellum	$24.46_{(1,240)}$	**<.001**	$33.31_{(2,240)}$	**<.001**	$.17_{(2,240)}$	.880	.274
Retrosplenial Cortex	$24.17_{(1,240)}$	**<.001**	$47.09_{(2,240)}$	**<.001**	$1.23_{(2,240)}$	.444	.333
Precuneus	$24.86_{(1,77)}$	**<.001**	$34.44_{(2,156)}$	**<.001**	$1.72_{(1,161)}$	.384	.291
Lateral Occipital Cortex	$15.43_{(1,83)}$	**<.001**	$34.31_{(2,158)}$	**<.001**	$1.67_{(2,156)}$	.384	.357

Notes. Subject was included as a random effect. Group (children, young adults), Delay (recent, remote (Day 1), remote (Day 14)), and their interaction were included as fixed effect. The following reference levels where used: for Delay, recent; for Group, Children; F – F-value; DF – degrees of freedom; p – p-value; FDR_adj – False Discovery Rate adjusted; R2 – amount of variance explained by the model (Stoffel et al., 2021). Type III Analysis of Variance Table with Satterthwaite's method. *p < .05; ** <.01, ***<.001 (significant difference). All main and interactions p-values were FDR-adjusted for multiple comparisons. All main and interactions p-values were FDR-adjusted for multiple comparisons.

Figure 5



Corrected scene-specific neural reinstatement.
All FDR-adjusted scene-specific reinstatement indices that were significantly different from zero were marked with green asterisk (Table S6). (**A**) Hippocampus; (**B**) Parahippocampal Gyrus; (**C**) Cerebellum; (**D**) Lateral Occipital Cortex; (**E**) Medial Prefrontal Cortex; (**F**) Ventrolateral Prefrontal Cortex; (**G**) Retrosplenial Cortex; (**H**) Precuneus. *$p < .05$; **$p < .01$; ***$p < .001$(significant difference). Error bars indicate standard error.

Category-based neural reinstatement.

In the following section, the results of the category-based neural reinstatement analyses with the selected ROIs are summarized (see Fig. 4B for index calculation overview),, with a complete

statistical report on the LME-model in Table 4 and model-based post-hoc Sidak-corrected comparisons in Table S10. First, we combined the category-based reinstatement indices for recent fixations across sessions, as there were no significant differences between sessions in ROIs in children (all $p > .64$) and adults ($p > .87$). We tested whether category-based reinstatement significantly differed from zero in all ROIs for recent (immediate after learning) and remote items (Day 1, Day14) for both age groups (for full overview see Table S8). FDR-corrected values revealed that young adults did not show any category-based reinstatement (all $p > .51$), while this was true for children only in the LOC (all $p > .15$).

We observed higher overall category-based reinstatement in children compared to young adults in the HC ($p < .001$; Fig. 6A), PHG ($p < .001$; Fig. 6B), cerebellum ($p < .001$; Fig. 6C), mPFC ($p < .001$; Fig. 6E), vlPFC ($p < .001$; Fig. 6F), RSC ($p < .001$; Fig. 6G), and precuneus ($p < .001$; Fig. 6H), but not in LOC ($p = .052$; Fig. 5D). These results indicate that overall category-based reinstatement was generally higher in children compared to young adults. We did not observe any session effects (all $p > .136$). Moreover, category-based reinstatement for remote items from Day1 to Day 14 was significantly higher in children, compared to young adults, in the HC ($p = .002$) and in the PHG ($p = .014$).

Taken together, only the child group showed category-based reinstatement in the medial-temporal, the cerebellar, the prefrontal, and the parietal brain regions. We observed a significant increase in category-based reinstatement in medial-temporal brain regions over time in children, indicating a higher level of gist-like representations in long delay memories after a 2-week-period.

Table 4

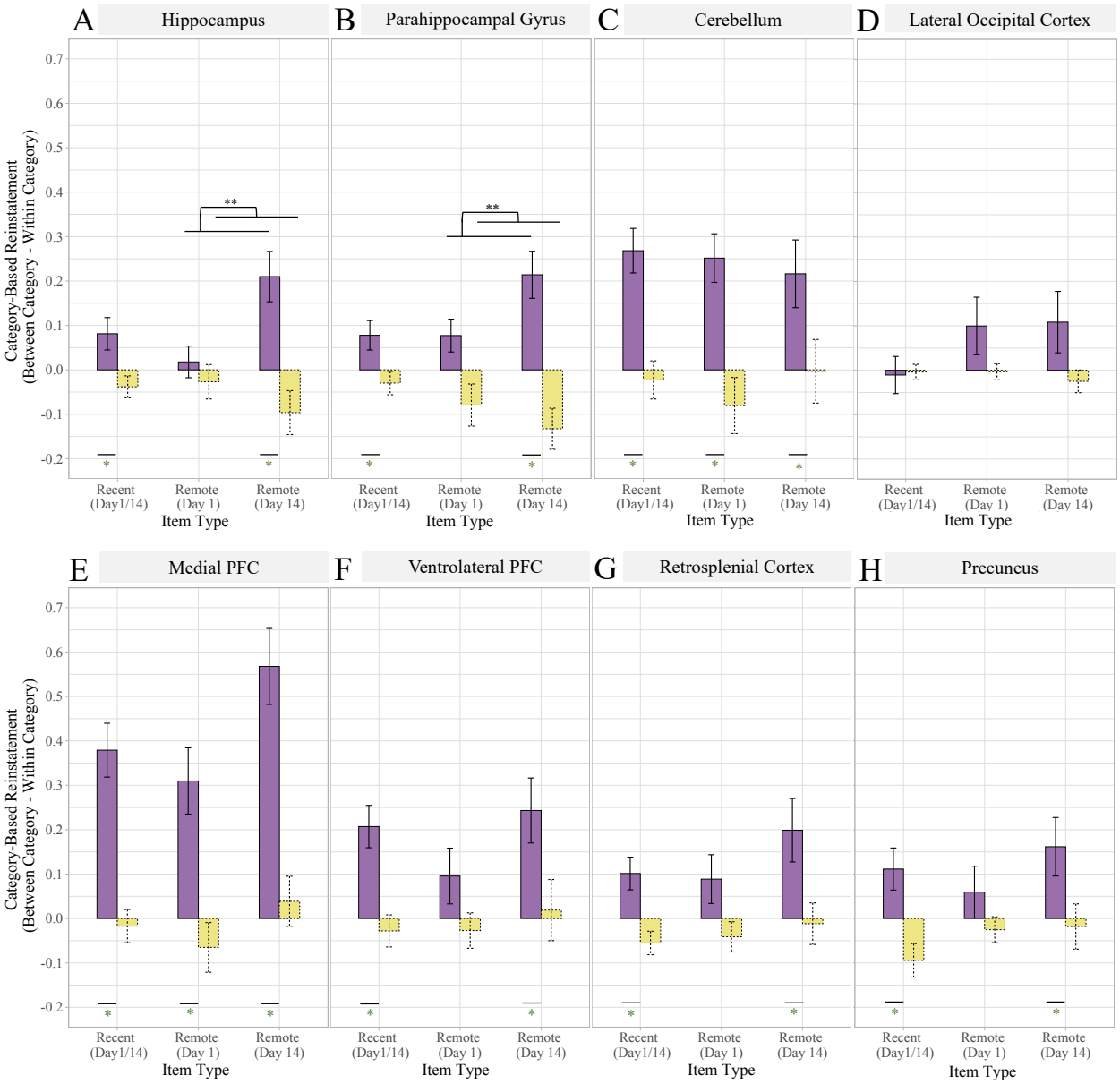
Statistical overview of the main and interaction effects of the linear mixed effects model for category-based reinstatement.

	Main Effect of Group		**Main Effect of Session**		**Group x Session Interaction**		
Regions of Interest	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	$F_{(DF)}$	$p_{(FDR_adj)}$	*R2*
Hippocampus	$17.60_{(1,85)}$	**<.001**	$1.47_{(2,162)}$	.387	**$6.37_{(2,162)}$**	**.008**	.278
Parahippocampal Gyrus	$27.03_{(1,86)}$	**<.001**	$.83_{(2,162)}$	.502	**$6.76_{(2,162)}$**	**.008**	.387
Medial Prefrontal Cortex	$64.43_{(1,83)}$	**<.001**	$4.16_{(2,162)}$	.136	$.87_{(2,162)}$	.561	.273
Ventrolateral Prefrontal Cortex	$13.87_{(1,86)}$	**<.001**	$1.93_{(2,162)}$	.387	$.88_{(2,162)}$	.561	.283
Cerebellum	$29.25_{(1,80)}$	**<.001**	$.24_{(2,158)}$	.786	$.36_{(2,158)}$	.700	.224
Retrosplenial Cortex	$16.26_{(1,76)}$	**<.001**	$1.78_{(2,154)}$	.387	$.49_{(2,154)}$	.698	.173
Precuneus	$11.91_{(1,78)}$	**<.001**	$1.43_{(2,155)}$	.387	$1.06_{(2,155)}$	.561	.239

Lateral Occipital Cortex	$3.89_{(1,76)}$	.052	$1.03_{(2,155)}$	.480	$1.48_{(2,155)}$	.561	.100

Notes. Subject was included as random effect. Group (children, young adults), Delay (recent, remote (Day 1), remote (Day 14)), and their interaction were included as fixed effect. The following reference levels where used: for Delay, recent; for Group, Children; F – F-value; DF – degrees of freedom; p – p-value; FDR_adj – False Discovery Rate adjusted; R2 – amount of variance explained by the model (Stoffel et al., 2021). Type III Analysis of Variance Table with Satterthwaite's method. *p < .05; ** <.01, ***<.001 (significant difference). All main and interactions p-values were FDR-adjusted for multiple comparisons.

Figure 6



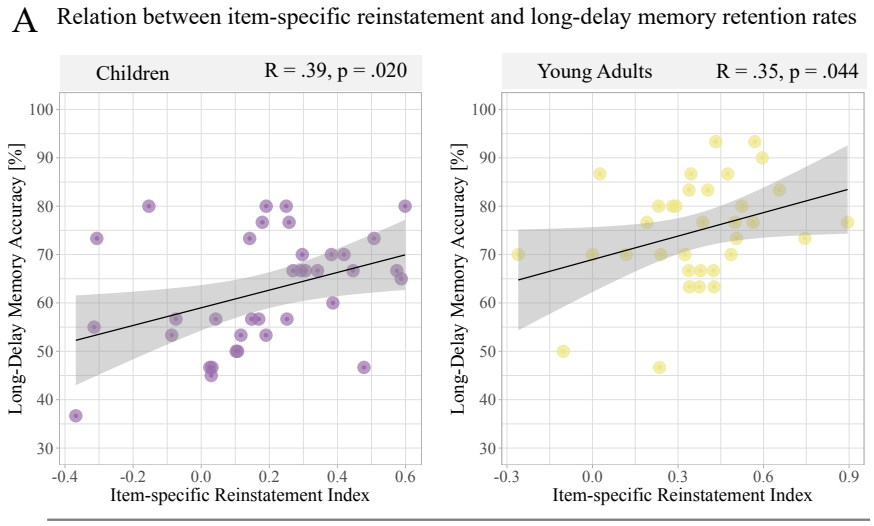
Category-based reinstatement.
Category-based reinstatement depicts the difference between pattern dissimilarity for within-category items and between-category items during fixation period before the actual scenes were shown. Higher values mean higher category-based reinstatement. The index was tested for significance against zero and all results were FDR corrected for multiple comparisons. Significant reinstatement of category-based information is depicted by a green asterisk (*)

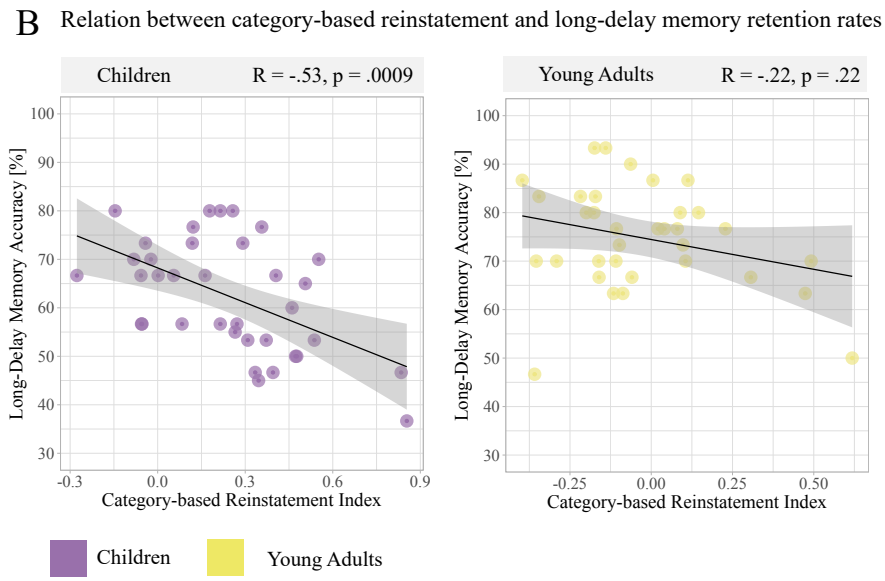
(**A**) Hippocampus; (**B**) Parahippocampal Gyrus; (**C**) Cerebellum; (**D**) Lateral Occipital Cortex; (**E**) Medial Prefrontal Cortex; (**F**) Ventrolateral Prefrontal Cortex; (**G**) Retrosplenial Cortex; (**H**) Precuneus; **p* < .05; ***p* < .01; ****p* < .001(significant difference); non-significant difference was not specifically highlighted. Error bars indicate standard error.

Neural-behavioural Correlations

Finally, we examined whether item-specific and category-based neural reinstatement is beneficial to memory performance for both children and young adults, correlating reinstatement indices with memory retention rate for Day 14. First, we combined the indices across ROIS, as there were no significant differences between ROIs in relation to reinstatement index x retention rate correlation (all p > .44). The results revealed that a higher item-specific reinstatement index (Fig.7A) was positively related to memory retention rates in children, r = .39, t = 2.44, p = .02, ($p = .044_{\text{FDR adjusted}}$), and in young adults, r = .35, t = 2.10, p = .044, ($p = .044_{\text{FDR adjusted}}$). Furthermore, higher category-based reactivation index (Fig. 7B) was negatively related to memory retention rates in children, r = -.53, t = -3.63, p = .0009, ($p = .0018_{\text{FDR adjusted}}$), but not in young adults, p = .22. Taken together, more differentiated detail-rich neural reinstatement was related to better recollection of consolidated memories in both children and young adults. On the other hand, more gist-like neural reinstatement was related to worse recollection of consolidated memories in children but not young adults.

Figure 7





Neural-behavioural Correlations.
Reinstatement indices were averaged across ROIs with significant reinstatement index. **(A)** Item-specific reinstatement indices were significantly positively related to long-delay memory retention rates in children (in purple) and young adults (in yellow). **(B)** Category-based reinstatement indices were significantly negatively related to long-delay memory retention rates in children (in purple), but not in young adults (in yellow). R = correlation coefficient, p = p-value. All p-values were FDR-adjusted for multiple comparisons.

DISCUSSION

In the present study, we investigated system-level memory consolidation of object-location associations after learning with immediate delay, after one night of sleep as short delay and after two weeks as long delay. We tracked changes in neural activation level 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 overall greater decline in memory retention compared to young adults. (ii) In terms of activation level, both age groups showed similar activation in the HC and the anterior PHG, increase in the vlPFC, and decrease in the precuneus over time. Young adults exhibited higher increase in neural activation in the posterior PHG, the cerebellum, and the LOC over time, and time-invariant higher activation in the vlPFC compared to children. In contrast, children showed higher decrease in the RSC activation over time, and time-invariant higher activation in the mPFC compared to young adults. (iii) Using RSA, we found that children exhibited attenuated scene-specific neural reinstatement compared to young adults. The decline in scene-specific neural reinstatement occurred mainly overnight, while over longer delay it remained stable in all ROIs and declined further only in the vlPFC and the RSC. We observed that category-

based or less differentiated gist-like reinstatement was present only in children in medial-temporal, cerebellar, parietal, and prefrontal brain regions. This pattern significantly increased over time in the HC and PHG only in children. Importantly, higher item-specific reinstatement was related to better retention rates in children and young adults, while higher category-based 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 decreased neural activation of core retrieval brain regions, more attenuated reinstatement of memory details, and more category-based, gist-like reinstatement. We discuss each finding in detail in the following sections.

Less robust overall memory retention in children compared to young adults.

Children showed overall less robust mnemonic performance for complex associative information compared to young adults. Specifically, we showed that already during learning, children needed more cycles to memorize object-scene associations and have a lower learning performance, which may be attributed to less efficient binding and strategy use as well as schema-integration processes in children compared to young adults (Shing et al., 2010). 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, 2012b; Ofen, 2012; Shing et al., 2008). Furthermore, 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., 2021). 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.

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

Analyses of remote > recent difference in neural activation over time allowed us to control for the effects of rapid consolidation during repeated learning, examining changes in short- or long-delay neural activation relative to immediate retrieval activation (Brodt et al., 2016a, 2018; Yu et al., 2022). First, we observed increased activation in the vlPFC over time in both age groups, while overall vlPFC activation was higher in young adults. Furthermore, we observed stable activation in the mPFC over time in both age groups, while overall mPFC activation was higher in children. This may indicate that both age groups engaged more strategic control over retrieval processes over time, and schema activation for retrieval irrespective of time delay. This is in line with previous studies that have shown the involvement of mPFC in structured and schema-related retrieval of long-term memories (Takashima et al., 2006; Yamashita et al., 2009), as well as the role of vlPFC in strategic remembering and retrieval of stored memories, executing a cognitive control role over mnemonic interferences during retrieval (Badre & D'Esposito, 2009; Kuhl et al., 2012). Here, we show not only involvement of medial and lateral PFC in remote memories, but that their role increases as consolidation progresses over time in both age groups, supporting the notion of (Milton et al., 2011) on growing prefrontal role during delayed recollection. Over time, cognitive control during memory retrieval may increase as it requires greater effort to recollect elaborative stories to remember the associated spatial context. On average, 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, 2012b; Gogtay et al., 2004; Ofen, 2012; Shing et al., 2010b). Children also showed overall higher activation in mPFC during retrieval of short and long delay memories, indicating possible schema-related retrieval that may be mediated by mPFC in children to a greater extent than in young adults, who may rely more on strategic retrieval.

Second, in other constituents of the recollection network (Ranganath & Ritchey, 2012), we observed increased activation from short to long delay in the posterior PHG and stable activity in the precuneus and the RSC in young adults, while children showed a decrease in posterior brain regions. As young adults showed higher memory retention rates for more detail-rich information, this superior memory may be mediated by higher activation 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 in young adults (i.e., higher retention rates for detailed information) may also be mediated by stable RSC and precuneus activation, as these regions are involved in mnemonic vividness, spatial, and associative memory (Brodt et al., 2016a; Hebscher et al., 2019; Mitchell et al., 2018; Richter et al., 2016; Tambini & D'Esposito, 2020; Vann et al., 2009). 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 underlied the age-related differences in activation patterns in these regions.

Third, the observed increase in neural activation 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). 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). Activation increases in the cerebellum and LOC in young adults compared to children indicate that these regions support long-delay memory retention in young adults and undergo development into later 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. 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). 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 activation for successfully consolidated memories over short and long delay, relative to immediately learned memories. While we showed adult-like activation in medial-temporal brain regions in children, young adults relied more on prefrontal, occipital, cerebellum, and parietal brain regions over time, compared to more pronounced reliance on medial prefrontal region in children.

Reduced scene-specific and enhanced category-based reinstatement in children compared to young adults.

Scene-specific reinstatement was more attenuated in children in comparison to young adults. Concerning the overall time-related decline, we observed that the drop in scene-specific reinstatement occurred mainly overnight with short-delay consolidation, indicating that neural patterns lost mnemonic specificity as memories aged. Moreover, more differentiated reinstatement of scene was related to higher retention rates both in children and young adults.

Our findings concerning scene-specific reinstatement are in line with the reinstatement effects for immediate recall of story details shown by Masís-Obando et al. (2022) in mPFC, posterior medial cortex, PHG, etc. We show that scene-specific reinstatement can be observed even after longer time delays. Moreover, we extend the findings of Guo & Yang (2022) on neural reinstatement in LOC during encoding and its relatedness to successful memory performance, showing neural reinstatement in LOC for successfully recollected memories over time. Additionally, our findings are in line with the reported reinstatement effects for visual clips shown

by Oedekoven et al. (2017) for encoding, immediate recall, and 1-week-delayed recall in precuneus, medial temporal gyrus, occipital gyrus, HC, and PHG. However, in contrast to Oedekoven et al. (2017), who did not observe any time-related differences in the neural reinstatement effect, we showed a major attenuation in reinstatement patterns in all ROIs after an overnight delay, followed by further reinstatement attenuation after a 2-week-period. These discrepancies in findings may be because Oedekoven et al. (2017) used the same set of video clips for immediate and delayed recall, possibly introducing additional retraining or mnemonic reactivation that may have boosted the fidelity of mnemonic reinstatement over time. Contrary to that, we used unique sets of stimuli for each retrieval, avoiding any reconsolidation of the mnemonic representations. Thus, these results show that without intentional reactivation and reconsolidation, the specificity of neural reinstatement fades over time. Additionally, in line with our findings, Xiao et al. (2017) showed item-specific neural reinstatement of scenes in frontoparietal cortex after learning.

In terms of age differences, in contrast to our findings of more attenuated neural reinstatement in children compared to young adults, Fandakova et al. (2019) showed that neural specificity during encoding was similar in 8-to-15-year-old children and adults in RSC, LOC and PHG. However, Fandakova et al. (2019) tested neural specificity with a slightly older cohort of children, suggesting that in late childhood to early adolescence there is already adult-level specificity of neural patterns reinstatement (Ghetti & Bunge, 2012b; Gogtay et al., 2004). Furthermore, our findings on the presence of scene-specific reinstatement in 5-to-7-year-old children, albeit being at a lower level compared to adults, are also in line with previous studies (Benear et al., 2022; Cohen et al., 2019; Golarai et al., 2015) that showed reliable mnemonic reinstatement for visual input (i.e., faces, movie clips) in 5-to-11-year-old children. Moreover, we extend previous finding, showing that successful retrieval of long-term memories is related to more differentiated neural reinstatement both in children and young adults, indicating at similar mechanisms of detail-rich memory consolidation already 5-to-7-year-old children and young adults.

In terms of category-based reinstatement, our results showed that only children demonstrated category-based reinstatement of to-be-retrieved memories in medial-temporal, prefrontal, parietal, and cerebellar brain regions, while no category-based reinstatement was observed in occipital brain regions. Furthermore, category-based reinstatement increased from immediate or short delay to

long delay in the HC and PHG only in children. Parietal and medial temporal brain regions were reported to carry event-specific information for episodic memories (Jonker et al., 2018; Sekeres et al., 2016; Sestieri et al., 2017; Winocur et al., 2007). However, in children in long delay these regions show neural reinstatement for only gist-like memories, possibly reflecting a faster decay of information specificity that these regions otherwise carry in young adults. As for prefrontal brain regions, gist-like neural reinstatement in this region in children may reflect integration of memory representations into more abstract categorical representations, considering mPFC's role in integrating across memories (Schlichting et al., 2015), and integrating new information into schema (Gilboa & Marlatte, 2017; Preston & Eichenbaum, 2013).

Overall, these results are in line with Brainerd et al. (2002), showing that in middle childhood exact memories (i.e., scene-specific reinstatement) and gist-memories (i.e., category-based reinstatement) co-exist. In long delay, on the other hand, children's retrieval was based on less-specific gist-like mnemonic reinstatement in the frontal, cerebellar, medial temporal, and parietal brain regions, in the absence of detail-rich scene-specific memories in these brain regions. This is in line with Keresztes et al. (2018) and Ngo et al. (2021) and extend their postulations, showing that 5-to-7-year-old children tend to rely more on generalization not only during encoding but also during long-delay memory consolidation, which is reflected through category-based neural pattern reinstatement during memory retention over time.

Exploring reinstatement and behavioural performance relationships, our results showed that over time higher scene-specific reinstatement is related to better mnemonic recollection both in children and young 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). In addition, we found that higher long-delay gist-like reinstatement was related to worse memory retention rates only in children. In general, only children exhibited gist-like reinstatement of scenes, which further increased as memories aged. Convergent with the observed reverse effect of scene-specific and category-based reinstatement on memory recollection, Masís-Obando et al. (2022) reported similar effects in adults. Namely, the authors showed that more specific neural representations predicted subsequent memory performance in young adults. On the other hand, more schema-based representations in posterior HC were related to pooper subsequent performance, while more schema-based

representations in mPFC were related to better subsequent memory. However, Masís-Obando et al. (2022) used stimuli with clearly differentiable schema and details components, which may have rendered significant neural representations in young adults. Future studies may use this approach to examine the benefits of schema-based representations, and the age differences therein.

Taken together, our findings provided novel evidence that children showed more attenuated scene-specific reinstatement compared to young adults. Nevertheless, scene-specific reinstatement was beneficial for memory retention in both groups. At the same time, children showed more category-based reinstatement, which was negatively related to memory retention. Therefore, both reduced differentiated reinstatement and enhanced reliance on gist information are characteristic of children's memory retrieval across time.

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, 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 regarding the neural mechanisms underlying less robust memory retention of intentionally learned object-location associations in 5-to-7-year-old children compared to young adults. Our findings indicate that over time, children exhibited less activation in core recollection and cerebellar brain regions during successful retrieval of remote memories. Additionally, they showed less differentiated neural reinstatement over time, but enhanced category-based reinstatement of retrieved memories. Taken together, our results suggest that compared to younger adults' mature consolidation system, memories of the developing brain in early school years are characterized by attenuated specificity of mnemonic representations and lower activation during retrieval in core retrieval brain network regions. At the same time, gist-based, schema representations play an important role in children's retrieval. This knowledge could potentially be used to design interventions that focus on enhancing long-term memory retention in children. Specifically, memory training programs may be tailored towards young school children to promote strategies that encode and retrieve specific and detailed representations of memories by capitalizing and making explicit connections to relevant gist-based, 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.

Acknowledgements

We thank all the children and parents who participated in the study. This work conducted at the Berlin Center for Advanced Neuroimaging (BCAN) and was supported by the Deutsche Forschungsgemeinschaft (DFG; German Research Foundation, Project-ID 327654276, SFB 1315, "Mechanisms and Disturbances in Memory Consolidation: from Synapses to Systems"). The work

of YLS was also supported by the European Union (ERC-2018-StG-PIVOTAL-758898) and the Hessisches Ministerium für Wissenschaft und Kunst (HMWK; project 'The Adaptive Mind'). We also thank Henriette Schultz and Nina Wald de Chamorro for their assistance with study management and data collection.

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 $Q3_{\text{upper quartile(75th percentile)}} + 3\text{xIQR}$ or below $Q1_{\text{lower quartile(25th percentile)}} - 3\text{xIQR}$ (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);

(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. 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 were determined using OptimizeXGUI (Spunt, 2016), which followed an exponential distribution (Dale, 1999). Thirty recently learned pairs (from the same testing day) and thirty remotely learnt items (from Day 0) were pseudo-randomly distributed among three runs. In each run, 10 recent and 10 remote pairs were presented in a pseudo-randomized order (see Fig. 2).

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

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 $recent_{correct}$, (ii) object $remote_{correct}$, (iii)

scene recent$_{correct}$, (iv) scene remote$_{correct}$, (v) object recent$_{incorrect}$, (vi) object remote$_{incorrect}$, (vii) scene recent$_{incorrect}$, (viii) scene remote$_{incorrect}$. 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 *object remote* > *object*

recent) 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 did not add *IQ and sex and handedness* as covariates to the model, as these effect were not significant (all p >.16) in an overall model with *Group x ROI* interaction (see Table S5).

Representational (dis)similarity analysis for neural reinstatement.

For the multivariate analysis, single-event (i.e., for every event on each trial) β (beta) estimates 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 category-based, we used the single-event beta estimates of each trial to compute two types of Representational Dissimilarity Matrices (RDMs; Kriegeskorte, 2008). Each RDM was computed separately for each previously identified ROI. All subsequent analyses were performed with homebrew scripts available at https://github.com/iryna1schommartz/memokid_fmri.

Scene-specific reinstatement*:** To measure the extent of scene reinstatement following object presentation, we computed a *scene-specific reinstatement index* for each neural RDM, separately for recent and remote scenes of each session (see Figure 2A-B)***. For each specific scene, we computed the index as the average distance between the "*fixation*" and "*scene period*" (Fisher-transformed 1 – Pearson's r; Fig. 2B), 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 1 – 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. To test for significance, one-sample permutation t-test with Monte-Carlo permutation percentile confidence interval was used (Chung & Romano, 2013; Efron & Tibshirani, 1994; Janssen, 1997). 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.

Category-based reinstatement: Based on the seven overarching thematic categories identified during stimuli selection (i.e., field, water, housing, forest, infrastructure, indoor, farming), a category-based reinstatement index was computed by subtracting within-categories from between-categories distances ([between $\text{category}_{\text{recent}}$ – within $\text{category}_{\text{recent}}$] and [between $\text{category}_{\text{remote}}$ – within $\text{category}_{\text{remote}}$] for each session, Fig. 2C-D) . Non-zero values in this index reflect category-based *reinstatement,* as the distance would be higher for pairs of trials with different categories than for pairs with the same category. These indices were computed for each run and then averaged across all runs. We applied a one-sample permutation t-test to test for significance in each ROI. Similar to the procedure described above, category-based 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 to analyse any delay-related differences in category-based reinstatement index for successfully retrieved trials. Finally, we also explored whether over time, long-delay item-specific and category-based 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.

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