

Developmental Psychology, in press (January 2019)

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A Boon and a Bane:

Comparing the Effects of Prior Knowledge on Memory Across the Lifespan

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Abstract

We tested 6–7-year-olds, 18–22-year-olds, and 67–74-year-olds on an associative memory task that consisted of knowledge-congruent and knowledge-incongruent object–scene pairs that were highly familiar to all age groups. We compared the three age groups on their memory congruency effect (i.e., better memory for knowledge-congruent associations) and on a schema bias score, which measures the participants' tendency to commit knowledge-congruent memory errors. We found that prior knowledge similarly benefited memory for items encoded in a congruent context in all age groups. However, for associative memory, older adults and, to a lesser extent, children overrelied on their prior knowledge, as indicated by both an enhanced congruency effect and schema bias. Functional Magnetic Resonance Imaging (fMRI) performed during memory encoding revealed an age-independent memory x congruency interaction in the ventromedial prefrontal cortex (vmPFC). Furthermore, the magnitude of vmPFC recruitment correlated positively with the schema bias. These findings suggest that older adults are most prone to rely on their prior knowledge for episodic memory decisions, but that children can also rely heavily on prior knowledge that they are well acquainted with. Furthermore, the fMRI results suggest that the vmPFC plays a key role in the assimilation of new information into existing knowledge structures across the entire lifespan. vmPFC recruitment leads to better memory for knowledge-congruent information but also to a heightened susceptibility to commit knowledge-congruent memory errors, in particular in children and older adults.

Key words: False memories, development, schema, aging, ventro-medial prefrontal cortex (vmPFC)

Word count: 8404 words

As we grow older, we accumulate abstracted knowledge structures (also called schemata), which help to guide our behavior in new situations. Decades of memory research have shown that these acquired knowledge structures also influence how new experiences are encoded, consolidated, and retrieved from memory (Alba & Hasher, 1983; Bartlett, 1932; Bransford & Johnson, 1972). While most of this research has been performed with young adults, age-comparative studies have shown that this also generally applies to children and older adults, respectively (e.g., Castel, 2005; Maril et al., 2011; Robertson & Köhler, 2007).

The impact of prior knowledge on memory – be it for items or associations between items – is usually quantified by computing the difference in memory performance for knowledge-congruent and knowledge-incongruent information. This difference score is typically positive in recognition memory paradigms in which congruent and incongruent information is presented equally often (for a meta-analysis in the domain of social expectations, see Stangor & McMillan, 1992). The superior memory performance for knowledge-congruent information, also called the memory congruency effect, is supposed to reflect more elaborative (i.e., semantic) encoding and facilitated memory search processes during retrieval due to existing semantic structures that guide memory search (Craik & Tulving, 1975; Moscovitch & Craik, 1976; Poppenk, Köhler, & Moscovitch, 2010). However, since the congruency effect is calculated as a difference score, its size may vary between tasks and groups due to differences in memory performance in the congruent or incongruent condition or both. This feature can make the congruency effect difficult to interpret when age comparisons are involved.

The magnitude of the memory congruency effect correlates with individuals' level of knowledge (i.e., schema strength) and increases across childhood (see Brod, Werkle-

Bergner, & Shing, 2013) . But it is unclear to what extent this increase is only due to the correlated gain in knowledge with age. By experimentally inducing prior knowledge to a comparable degree in children and young adults, Brod, Lindenberger, & Shing (2017) recently reported that children aged 8–11 showed a memory congruency effect that was as strong as younger adults'. Studies that have looked at developmental differences in knowledge-based false memory, which typically used a variant of the so-called Deese-Roediger-McDermott (DRM) paradigm in which participants are prone to commit schema-consistent memory errors, reported mixed findings. DRM studies that used word lists typically found an age-related increase in the number of schema-consistent memory errors (e.g., Brainerd, Reyna, & Forrest, 2002; Metzger et al., 2008), whereas studies that used age-appropriate pictures did not (Ghetti, Qin, & Goodman, 2002; Howe, 2006). To conclude, it seems highly likely that the age-related increase in knowledge contributes to the observed increase in both the memory congruency effect and in the tendency to commit schema-consistent memory errors. It is currently unclear, however, whether there are additional age-related increases in the extent to which prior knowledge is leveraged for memory.

From an ageing perspective, studies that have directly looked at changes in the memory congruency effect later in life are sparse. However, findings from a study on memory for grocery prices (Castel, 2005) found that the congruency effect was even more pronounced in older than in younger adults (but see Badham, Hay, Foxon, Kaur, & Maylor, 2016). A greater congruency effect in the elderly may have various, non-mutually exclusive reasons. First, it may reflect enhanced support of existing knowledge structures in the knowledge-congruent condition that disproportionately benefit older adults (Bäckman & Herlitz, 1990; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005; Umanath & Marsh, 2014). Second, it may reflect older adults' processing deficits at

encoding that particularly impair memory for knowledge-incongruent events (Carr, Castel, & Knowlton, 2015; Naveh-Benjamin, 2000). A third possibility is that it reflects older adults' enhanced susceptibility to commit knowledge-consistent memory errors at retrieval, similar to what has been shown for the DRM paradigm (e.g., Dennis et al., 2008). In line with these conjectures, research using the DRM paradigm revealed strikingly increased error rates in older adults (e.g., Dennis, Kim, & Cabeza, 2008; Watson, McDermott, & Balota, 2004; for reviews, see Jacoby & Rhodes, 2006; Schacter, Koutstaal, & Norman, 1997). In sum, findings in older adults point to a double-edged role of prior knowledge in memory for knowledge-congruent events: more true memories, but also more false ones. This suggests that, in order to get the full picture of how the effects of prior knowledge vary across the lifespan, it is paramount to not only look at the memory congruency effect, but to take into account false memories as well. Prior knowledge, thus, seems to introduce a bias that can be both advantageous and disadvantageous, depending on the memory task at hand (Brod, Werkle-Bergner, & Shing, 2013). This bias may be enhanced in older adults (Castel, 2005; Naveh-Benjamin, 2000). In this study, we introduced a schema bias score to quantify participants' tendency to endorse associations that are congruent to knowledge but not based on memory of actual experience.

Recent evidence from neuropsychology and cognitive neuroscience has shed light on the neural mechanisms underlying the memory congruency effect (for reviews, see Gilboa & Marlatte, 2017; Schlichting & Preston, 2015). By comparing brain activation between knowledge-congruent and knowledge-incongruent events, functional magnetic resonance imaging (fMRI) studies have shown an enhanced contribution of the ventromedial prefrontal cortex (vmPFC) to the successful encoding and retrieval of knowledge-congruent events (Bein, Reggev, & Maril, 2014; Brod, Lindenberger, Werkle-

Bergner, & Shing, 2015; Brod & Shing, 2018; van Kesteren, Rijpkema, Ruiters, & Fernandez, 2010; van Kesteren et al., 2013). Neuropsychological studies have shown that patients with lesions to the vmPFC do not show a memory congruency effect (Spalding, Jones, Duff, Tranel, & Warren, 2015). They do not commit as many schema-consistent memory errors as age-matched controls either (Warren, Jones, Duff, & Tranel, 2014). On the other hand, patients with vmPFC lesions also tend to confabulate, which is characterized by a failure in monitoring knowledge-congruent memories despite otherwise normal memory abilities (Moscovitch & Melo, 1997). These lesion data are in line with recent fMRI evidence suggesting that the vmPFC is not involved in knowledge-related memory per se, but that its contributions are specifically modulated by the perceived congruency between new information and existing schemata (Brod & Shing, 2018). The vmPFC, thus, biases memory processing towards congruency with prior knowledge.

Research on age differences in the neural correlates of the effects of prior knowledge on memory is still in its infancy (for an overview, see Brod, Werkle-Bergner, & Shing, 2013). Looking at the neural correlates of the memory congruency effect during encoding, Maril et al. (2011) found that children aged 8–11 relied more on posterior brain areas associated with perceptual processing, whereas adults recruited more anterior brain regions associated with semantic processing. Looking more closely at the vmPFC, Brod et al. (2017) found that its contributions to knowledge-congruent memory retrieval correlated positively with children's age. To the best of our knowledge, no fMRI study has examined the neural correlates of the memory congruency effect in older adults so far. A study that looked at the neural correlates of committing knowledge-consistent memory errors in the DRM paradigm revealed enhanced activation in left temporal regions in older adults, suggesting an increased reliance on semantic

knowledge (Dennis et al., 2008). The contribution of the vmPFC to the increased reliance on prior knowledge in older adults is as yet unknown. Compared to most neocortical areas and in contrast to the prolonged development of the lateral PFC, the vmPFC matures early (Shaw et al., 2008) and is scarcely affected by ageing (Salat et al., 2004). This rare structural stability from middle childhood up to old age provides an interesting testing case for examining whether the functional role of the vmPFC for mediating the effects of prior knowledge on memory is also similar in children and older adults.

Overview of the Present Study

In the current study, we attempted to perform a fair comparison of the behavioral and neural effects of prior knowledge on memory across the lifespan. We employed an extreme-group design, comparing children who were as young as possible for task-based fMRI studies (aged 6–7), recent high school graduates (aged 18–22), and retirees (aged 67–74). Of particular interest was the comparison between children and older adults. Based on our literature review above, an extrapolation of age pattern can be made, such that children underrely on their prior knowledge, while older adults overrely on it. However, in most of the studies (at least those involving children), it is questionable whether differences in familiarity with the stimulus material or differences in strategy use (or both) could have contributed to this observation.

All participants performed an identical, incidental object–scene congruency judgment task. They were later tested for their memory for the objects as well for their associative memory for the associated scene and for the location of the object. Pilot studies in children ensured that object and scene stimuli as well as their semantic relation were highly familiar to the children in order to avoid the common confound between age and prior knowledge. During retrieval of the associated scene (henceforth

called “semantic associative memory”), participants were prompted to use their prior knowledge because the object is always semantically related to one of the scenes. This feature helps them identify the correct scene for congruent object–scene pairs, but leads them astray for incongruent ones. After the semantic associative memory decision, participants were asked to recall the location of the object during encoding (henceforth called “spatial associative memory”). The object was either presented to the left or to the right of the scene. Location of the object was random, which means that participants cannot use prior knowledge here. This task was included as a source memory-like measure of the context that was present during encoding and that is as unbiased by semantic knowledge as possible.

In addition to computing congruency effects, the semantic associative memory test allowed us to derive a bias score that quantified participants’ tendency to erroneously endorse congruent associations. With this new score, which we henceforth call schema bias score, we aimed to measure the influence of prior knowledge on committing knowledge-consistent memory errors (presumably mediated by the vmPFC) more directly than with the common congruency effect, which does not explicitly take into account memory bias. In short, the score reflects the relative amount of knowledge-consistent memory errors. The schema bias score and the congruency effect together provide us with empirical indicators of the extent to which people of different age rely on their prior knowledge for making episodic memory decisions. We use the term “rely on” here to express that prior knowledge can lead both to veridical and false memory decisions.

We hypothesized that children and older adults would display similar overall memory performance, which should be lower than in younger adults. In terms of prior knowledge effects, we expected older adults to display a stronger knowledge effect on

memory than younger adults, that is, a stronger congruency effect and a higher schema bias score. This pattern would be in line with earlier age-comparative studies on knowledge-related true and false memories (e.g., Castel, 2005; Dennis, Kim, & Cabeza, 2008). The mixed findings from age-comparative studies in children made it difficult to derive a clear hypothesis regarding their performance. Based on earlier findings (Brod, et al., 2017), we predicted that the effects of prior knowledge would be at least as strong in the children than in the younger adults, and probably weaker than in the older adults. Likewise, we hypothesized that the recruitment of the vmPFC for the memory congruency effect would be enhanced in older adults, and that the magnitude of its recruitment should correlate positively with the schema bias across age groups.

Materials and Methods

Participants

The sample consisted of 36 children aged 6–7 (78–90 months, mean age 82.7 months, 18 females), 30 young adults (aged 18–22, mean age 18.6 years, 17 females), and 30 older adults (aged 67–74, mean age 71.1 years, 15 females). All participants were healthy, right-handed, native German speakers, and had normal or corrected-to-normal vision. All children were first-graders participating in a large-scale longitudinal study (see Brod, Bunge, & Shing, 2017). Two children had to be excluded because they did not follow the instructions, and a further two because their memory performance was below chance. This resulted in a final behavioral sample of 32 children (78–90 months, mean age 82.84 months, 16 females). Five children had to be excluded from the fMRI analyses due to excessive movement in the scanner (> 1.5 mm mean displacement and rating based on visual inspection) and one child was excluded due to too high performance, leaving too few (< 5) forgotten trials in at least one of the two conditions

(congruent/incongruent) for the subsequent memory analyses. This resulted in a final fMRI sample of 26 children. The young adults were recent high school graduates and were recruited through advertisements. Four young adults did not provide complete data because of technical failures in the experimental programs. This resulted in a final behavioral sample of 26 young adults (aged 18–22, mean age 18.6 years, 13 females). Four young adults had to be excluded from the fMRI analyses because of too high memory performance, resulting in a final fMRI sample of 22 young adults. The older adults were recruited from the participant database of healthy older adults of the Max Planck Institute for Human Development. They were additionally screened for cognitive impairment with the Mini-Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975). The data of three older adults were discarded because of a MMSE score below 27. This resulted in a final behavioral sample of 27 older adults (aged 68–74, mean age 71.0 years, 12 females). Two older adults had to be excluded from the fMRI analyses because of too high memory performance, resulting in a final fMRI sample of 25 older adults. Given these sample sizes, a sensitivity analysis performed in G*Power revealed that the minimum effect sizes needed to reliably detect a significant age x congruency interaction were $\eta^2_p = .04$ ($f = .20$) for the behavioral analyses and $\eta^2_p = .05$ ($f = .22$) for the fMRI analyses (with $\alpha = .05$ and $\beta = .90$).

Younger and older adults were paid 15 Euros for their participation, the children received small gifts instead. Ethics approval was obtained from the Ethics Committee of the German Psychological Society (DGPs, name of the project: Age differences in knowledge-based memory encoding and retrieval (HippoKnow)). Adult participants and the children's parents/legal guardians gave written, informed consent.

Stimuli

During encoding, participants saw a total of 22 scenes and 88 objects. Two parallel stimulus lists were created pseudo-randomly to counterbalance across participants: each contained all 22 scenes, with 2 congruent objects per scene (44 in total), and 2 incongruent objects per scene. The incongruent condition was created by pairing each scene with two objects that are congruent to different scenes based on face validity. In the two parallel stimulus lists, those objects that were congruent (i.e., presented together with their congruent scene) in one stimulus list were incongruent in the other, and vice versa. Thus, while each scene was presented four times, together with a different object each time, all objects were only shown once. All picture frames were identical in size, and the objects were presented against the same white background. During retrieval, in addition to the 88 “old” objects, participants saw 44 “new” objects.

The pictures of objects and scenes that were used in the object–scene memory task were determined in two pilot studies. The aim of the pilot studies was to ensure that all objects and scenes were familiar to children aged 6 by selecting scenes and object that were taught in the first school year, which all children underwent right before being tested. This should attenuate age differences in general knowledge of the stimulus material in our lifespan sample, which is a common confound in age-comparative memory research (cf. Stangor & McMillan, 1992). In the first pilot study, 10 elementary school teachers were given 38 scenes that were related to the first year curriculum (e.g., farm, forest, field) and had to indicate which scenes first graders know and which of these scenes they learn more about during first grade. In addition, they were asked to name objects associated with these scenes that first-graders should know. Based on these responses, we chose those 22 scenes with the highest familiarity and school-relevance ratings along with 6 congruent objects for each scene. In the second

pilot study, 11 first-graders rated the object–scene associations regarding their congruency as well as rating the familiarity of the objects. Based on these responses, we chose the four objects for each scene that had the highest congruency and familiarity ratings, and presented those during encoding. The two remaining objects per scene were used as new items during the retrieval task.

Task and Procedures

The task was identical for all three age groups (see Figure 1 for an illustration, the task can be found at <https://osf.io/tdw6k/>). Procedures were also highly similar for all groups, with only slight modifications in the children’s group due to their young age. Prior to entering the scanner, participants were instructed that they would have to make a binary decision whether the presented objects and scenes fit to each other or not. They were not told that there would be a memory test afterwards. Instead, they were told that the goal of the study was to investigate the neural basis of congruency judgments. The incidental nature of the memory test was confirmed via a questionnaire at the end of the session, which asked whether the participant had suspected that there might be some kind of memory test later. Indeed, no-one reported having expected a memory test. Whereas younger and older adults were alone in the scanner room during the fMRI session, the children were accompanied by an experimenter who stood next to them throughout the scan.

After entering the MR scanner, participants were instructed about which buttons to press to indicate a “fit together” or “do not fit together” using their left/right index finger. Left/right response mappings were counterbalanced across participants. The fMRI session started with a brief practice phase, during which participants practiced the task using scenes and objects that were not presented during the real study phase.

Following the practice phase, the real study phase started, which took about 10 min. Presentation of the scenes and objects was identical for the practice and the real task: the object and scene pairs were presented simultaneously next to each other on a black background for 3 s, followed by a white fixation cross. Two parallel stimulus lists were used (see Stimuli) and counterbalanced across participants. To optimize statistical efficiency of our rapid event-related design, jittered fixation periods were used (250 ms – 11.5 s), which were optimized with Optseq 2 (Dale, 1999). Object and scene frames were identical in size and presented on two screen locations (to the left or right of its center). The location (left/right) of the object and scene was randomized across trials. After the study phase, a structural (T1) sequence was performed, which took about 8 min. During this time, participants watched a child-friendly animated cartoon.

After having watched the cartoon, participants were taken out of the scanner and allowed to have a short rest (max. 5 min) during which they could drink or eat something. About 15 min after the end of the study phase, they were taken to a testing room, where the computerized retrieval task took place. Due to the children's young age, they provided their answers verbally, and the experimenter pressed the corresponding keys. Younger and older adults carried out the retrieval task themselves after receiving brief instructions. There was no fixed time limit for answering, but participants were asked to answer as accurately and as quickly as possible. On the computer screen, they were shown 132 object pictures; the 88 object pictures they saw in the scanner and 44 new objects, which served as lures. The lures were generated from the remaining two congruent objects per scene (2 x 22) that were not used during the study phase (see Stimuli). Participants were asked to decide whether they had seen these objects while in the scanner (i.e., item memory). For objects judged as old, in a second step, participants had to decide with which scene the object had been presented during the study phase

(i.e., semantic associative memory). They were shown three scenes (presented below the object) to choose from. All three scenes were equally familiar as they had all been presented four times during the study phase. One of the three scenes was always congruent to the object, independent of congruency conditions (i.e., even when the target scene was incongruent). Afterwards, in a third step, they were presented with the object again, which was presented twice on the screen: once in the upper left quadrant, and once in the lower right quadrant. They were asked to recall whether the object was presented to the right or the left of the screen during the study phase (i.e., spatial associative memory). For objects judged as new, the second and third steps of the retrieval task testing for associative memory were skipped.

fMRI Data Acquisition

T2*-weighted echo-planar images were acquired using a 3T Siemens TIM Trio MRI scanner (direction = transverse, interleaved ascending; FOV = 216 mm; TR = 2000 ms; TE = 30 ms; number of slices = 36; slice thickness = 3 mm; matrix = 72 x 72; voxel size = 3 x 3 x 3 mm; distance factor = 10%; 281 volumes each). To ensure that a steady-state condition was reached, the first four scans of each run were discarded. Structural data were acquired using a T1-weighted 3D magnetization-prepared rapid gradient echo sequence (TR = 2500 ms; TE = 2500 ms; sagittal orientation; spatial resolution 1 x 1 x 1 mm).

Statistical Analysis: Behavioral Data

Memory performance was analyzed using R (R Core Team, 2014, scripts can be found at <https://osf.io/tdw6k/>). For the study phase, we calculated mean classification accuracy per person as the percentage correct of congruent / incongruent judgments that were in accordance with the experimenters' classification. The experimenters' classification was validated in a pilot study. A one-way ANOVA was calculated along with

post-hoc pairwise group comparisons to determine age differences in congruency classification. Most importantly, to account for potential individual and age-related differences in perceived congruency of the object–scene pairs, participants’ individual classification during the study phase was used to sort the pairs into congruent and incongruent events for the following behavioral and fMRI memory analyses.

For the retrieval phase, memory performance was calculated separately for each of the three memory types and for the congruent and incongruent conditions as determined during the study phase. For the first step (old/new item memory), hits (“old” response to target items) and false alarms (“old” response to new items) were computed. To correct for guessing, a corrected recognition score was calculated (Pr-values: hits minus false alarms; Snodgrass & Corwin, 1988) and subjected to a mixed ANOVA to determine whether memory performance significantly differed between the two conditions (congruent, incongruent) and age groups (children, younger adults, older adults), and whether there was a significant interaction between the two. To follow up on a significant group effect, post-hoc pairwise group comparisons were performed.

We also looked at false alarm rates individually. From a total of 44 new items presented during retrieval, children on average made a false alarm for 4 (9.1 ± 7.9 [Mean % \pm SD]), younger adults for 3 (5.9 ± 2.8), and older adults for 4 (9.7 ± 5.2) items. Given these very low trial numbers in the majority of our participants, we did not perform any further analyses on false alarm trials.

For the latter two steps of the retrieval task (semantic and spatial associative memory), memory performance was calculated relative to the number of trials with correct item memory (i.e., with the number of correct “old” responses per condition in the denominator). For the semantic associative memory test, parallel analyses were performed for memory performance and schema bias. Memory performance was

evaluated by the percentage of correctly remembered associated scenes. To evaluate statistical significance, a two-way mixed ANOVA (age group by trial congruency) was conducted along with post-hoc pairwise group comparisons. In addition, the difference in memory performance between the congruent and incongruent condition (i.e., the congruency effect) was calculated per person and subjected to pairwise group comparisons.

The schema bias score was calculated as the percentage of erroneously chosen congruent scenes in the incongruent condition (i.e., for incongruent objects): $P(\text{choice of congruent scene} \mid \text{correctly identified incongruent object with wrong scene memory})$. The logic behind the schema bias score goes as follows: In the semantic associative memory test, three scenes were presented as options to choose from, always one congruent and two incongruent to the object. Thus, if participants were unbiased and did not remember the associated incongruent scene, they should be equally likely to choose the other incongruent scene or the congruent scene (i.e., 50% of the wrong choices were congruent scenes). However, if they were biased, they would choose the congruent scene more often. The schema bias score thus reflects a participants' tendency to erroneously endorse knowledge-congruent associations. Group differences in the schema bias were evaluated by a one-way ANOVA and subsequent post-hoc pairwise group comparisons. To further examine the relationship between schema bias and congruency effect, a correlation analysis was performed.

For the spatial associative memory test ("Where did the object appear on the screen?"), the percentage of correctly remembered spatial locations was calculated. To evaluate statistical significance, mixed ANOVAs were conducted along with post-hoc pairwise group comparisons. α was set at 0.05 throughout the behavioral analyses. All pairwise group comparisons reported were Bonferroni-Holm-corrected.

Statistical Analysis: fMRI Data

Data were preprocessed and analyzed using FEAT in FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>; Smith, Jenkinson, & Woolrich, 2004). Functional data were corrected for motion (using MCFLIRT from FSL), slice acquisition times, then high-pass filtered (80 Hz), and spatially smoothed using a 5-mm full-width half-maximum Gaussian filter. Data were first co-registered with the structural image and then spatially normalized into MNI space. Given the young age of the children, we also created sample-specific brain templates for the children group, used those for spatial normalization, and subsequently transferred the activation maps into MNI space for age-comparative analyses (as described in Brod et al., 2017). Results of this two-step approach did not differ significantly from the direct normalization into MNI space, which is why we only report the latter here.

After preprocessing, first-level analyses were conducted using general linear modelling (GLM). Individual time series were modelled with a Gamma hemodynamic response function (a 3-second boxcar function linked to the onset of encoding events) with different regressors for each of the four events (subsequently remembered/forgotten congruent events, subsequently remembered/forgotten incongruent events). An additional reaction time (RT) regressor was included as a regressor of no interest to control for potential condition differences in RT. It contained all events and their associated encoding RTs, and was orthogonalized to the other regressors (following the recommendations in Mumford, Poline, & Poldrack, 2015). In addition, six motion parameters were included as regressors of no interest.

Across-subject analyses were carried out using a mixed-effects model in the FLAME framework in FSL. Z-statistic images were thresholded at a voxel-wise threshold of $z > 2.3$, with a FWE-corrected cluster threshold of $p < 0.05$, using FLAME1 in FSL.

Based on our a-priori hypothesis about differences in the vmPFC, we created an anatomical mask of the vmPFC based on FSL's Harvard-Oxford Cortical Structural Atlas, which consisted of the bilateral frontal medial cortex. First, we searched for regions within the vmPFC that exhibited a congruency (congruent, incongruent) by memory (remembered, forgotten) interaction, independent of groups. Exploratory whole-brain analysis was also performed to find out whether additional brain regions showed a congruency by memory interaction (voxel-wise threshold $z > 2.3$, FWE-corrected cluster threshold of $p < 0.05$). Second, to specifically test for an age-group effect and its interaction with congruency and memory, we extracted percent signal change from the vmPFC cluster identified in the first analysis, separately for congruent and incongruent trials. These trials were further split up by remembered and forgotten events, which enabled us to determine subsequent memory effects (SMEs). These values were subjected to a mixed ANOVA with the within-subject factor congruency and the between-subject factor group (children, younger adults, older adults). Third, we correlated individuals' extracted percent signal change scores from step two with their schema bias score.

Results

Congruency Judgments

Children classified 87.30% (SD = 7.25%), younger adults 95.04% (SD = 5.60%), and older adults 91.30% (SD = 3.46%) of all object–scene pairs in accordance with our congruency classification. A one-way ANOVA yielded a significant effect of age ($F(2,82) = 13.09$, $p < .001$, $\eta^2_G = .24$). Post-hoc pairwise group comparisons yielded significant differences between children and younger adults ($p < .001$), children and older adults ($p = .019$), as well as between younger and older adults ($p = .020$). In sum, participants'

subjective congruency judgments were relatively consistent with our intended condition sorting in all age groups. Nevertheless, given the statistically significant group differences in perceived congruency, participants' individual classification during the study phase was used to sort each of the object–scene pairs into congruent and incongruent conditions for the following behavioral and fMRI memory analyses.

Memory Performance

Item Memory. Descriptive statistics are shown in Figure 2. Testing for differences between groups and conditions in item memory (using the corrected recognition score Pr), an F-test revealed a main effect of age ($F(2,82) = 6.20, p = .003, \eta^2_G = .11$), a main effect of congruency ($F(1,82) = 76.87, p < .001, \eta^2_G = .14$), indicating better memory performance for congruent than for incongruent events, and no interaction ($F(2,82) = .81, p = .447, \eta^2_G = .003$). Post-hoc pairwise group comparisons yielded significant differences between children and younger adults ($p < .001$) as well as between younger and older adults ($p = .011$), but none between children and older adults ($p = .219$). Together, the item memory results indicate better performance in the younger adults as compared to children and older adults, and an age-independent memory benefit for items encoded in a congruent than in an incongruent context.

Semantic Associative Memory and Schema Bias. The semantic associative memory data and the schema bias scores are presented in Figure 3. Looking at performance differences in semantic associative memory, a mixed ANOVA revealed a main effect of age ($F(2,82) = 27.18, p < .001, \eta^2_G = .28$); a main effect of condition ($F(2,82) = 449.64, p < .001, \eta^2_G = .69$) indicating better performance for congruent than for incongruent events; and a significant interaction ($F(2,82) = 34.86, p < .001, \eta^2_G = .26$). Post-hoc pairwise group comparisons yielded significant differences in overall

memory performance between children and older adults ($p = .021$) as well as between younger and older adults ($p < .001$), and a trend towards a significant difference between children and younger adults ($p = .059$). To follow up on the significant group by condition interaction (i.e., group differences in the memory congruency effect), we calculated the difference in memory performance between the congruent and incongruent conditions per person and performed post-hoc pairwise group comparisons on these difference scores. These comparisons revealed a significant difference between children and younger adults ($p = .017$), as well as significant differences between children and older adults ($p < .001$) and between younger and older adults ($p < .001$). Taken together, the semantic associative memory data indicate that older adults show the largest congruency effect, followed by children and younger adults.

However, the close-to-ceiling performance of all three groups in the congruent condition limits the conclusions that can be drawn from these results with regard to the congruency effect, since the effect was largely driven by older adults' poor memory performance in the incongruent condition. The schema bias score circumvents this problem because it focuses on wrong associative memory decisions in the incongruent condition, for which performance was clearly below ceiling in all three age groups. Nevertheless, the schema bias score and the congruency effect were substantially correlated ($r = .42$, $t(83)=4.22$, $p < .001$; controlling for age: $r = .40$, $t(82)=3.92$, $p < .001$), which suggests that they may measure overlapping cognitive processes (for a summary of intercorrelations between the main measures used in the study, see Supplementary Table 1). Comparing the bias score of the three age groups, a one-way ANOVA yielded a significant effect of age ($F(2,82) = 5.97$, $p = .004$, $\eta^2_G = .13$). Post-hoc pairwise group comparisons revealed significant differences between younger and older adults ($p = .003$), but neither between younger adults and children ($p = .108$) nor between children

and older adults ($p = .108$). These results suggest that older adults show the largest and younger adults the smallest schema bias. The children's group was not significantly different from the other two groups, with their schema bias score falling between the two.

In sum, older adults show both the largest congruency effect and the strongest schema bias, followed by children and young adults, who are the least biased.

Spatial Associative Memory. Memory performance was clearly above chance (all $p < .01$) for both congruent and incongruent events in children (Con: 63.4 ± 13.9 [Mean % \pm SD]; Incon: 62.2 ± 16.9), younger adults (Con: 69.0 ± 15.7 ; Incon: 69.3 ± 15.1), and older adults (Con: 61.4 ± 12.0 ; Incon: 57.6 ± 23.2). A mixed ANOVA revealed a main effect of age ($F(2,82) = 3.30, p = .042, \eta^2_G = .05$); no effect of condition ($F(2,82) = 0.665, p = .417, \eta^2_G = .002$), and no interaction ($F(2,82) = 0.388, p = .680, \eta^2_G = .003$). Post-hoc pairwise group comparisons yielded significant differences in memory performance between younger and older adults ($p < .001$) as well as between children and younger adults ($p = .012$) and between children and older adults ($p = .019$). The lack of a congruency effect suggests that, as hypothesized, prior knowledge does not affect memory for spatial positions. The group differences in overall memory performance suggest that younger adults display the best spatial associative memory performance, followed by children and older adults.

fMRI Results

The goal of our fMRI analyses was to determine age-related differences in the neural correlates of the semantic congruency effect, and to test whether these were related to our proposed measure of schema bias. Based on strong evidence from neuroimaging and lesion studies indicating that the vmPFC is the key brain region mediating the congruency effect (Brod et al., 2016; Spalding et al., 2015; van Kesteren et

al., 2013), we focused our analyses on this anatomical region (for unthresholded whole-brain statistical masks, see <http://neurovault.org/collections/EORVZWLP/>).

First, we searched for clusters within the vmPFC that exhibited a stronger SME for congruent as compared to incongruent trials (i.e., congruency by memory interaction) across all participants, regardless of age group. This analysis revealed a cluster in central vmPFC (peak: -8, 52, -10; 165 voxels; $Z_{\max} = 3.3$, see Figure 4a). The opposite contrast revealed no significant clusters. Whole-brain analysis was performed as a follow-up and found no significant clusters outside of the vmPFC. Second, we explored potential group differences in this cluster by extracting percent signal change for each subject's congruent and incongruent SMEs (see Figure 4b). A two-way mixed ANOVA revealed a main effect of condition ($F(1,70) = 6.70$, $p = .011$, $\eta^2_G = .05$), indicating stronger SMEs for congruent compared to incongruent trials, which is to be expected given the way the cluster was identified. Most importantly, there was no main effect of group ($F(1,70) = .68$, $p = .509$, $\eta^2_G = .01$), and no congruency by group interaction ($F(1,70) = .68$, $p = .511$, $\eta^2_G = .01$). These results suggest that the vmPFC is involved in mediating the memory congruency effect in a similar way across all age groups.

Third, based on the well-established role of the vmPFC in schema-based false memories (Berkers et al., 2016; Warren et al., 2014), we sought to test whether the amount of vmPFC recruitment during successful memory encoding was predictive of the tendency to commit schema-based memory errors during retrieval. We correlated the subjects' percent signal change scores for congruent and incongruent SMEs with our schema bias score. As expected, these analyses revealed a positive correlation between subjects' congruent SME and schema bias score ($r = .25$, $t(70)=2.17$, $p = .017$, see Figure 4c; controlling for age: $r = .25$, $t(70)=2.18$, $p = .016$), and no correlation between

subjects' incongruent SME and schema bias score ($r = -.021$, $p = .863$), with the difference between the two correlation scores being marginally significant ($z = 1.59$, $p = .056$). These findings indicate that those participants who recruited the vmPFC more strongly when encoding congruent trials showed an enhanced tendency to falsely endorse the congruent association during retrieval of incongruent trials.

To conclude, the vmPFC exhibited a congruency by memory interaction across the three age groups. The magnitude of the vmPFC recruitment during encoding of congruent associations predicted participants' tendency to commit schema-based memory errors, which was enhanced in children and older adults.

Discussion

The present study investigated age differences in the effects of prior knowledge on episodic memory and their neural correlates. Participants of three different age groups (aged 6–7, 18–22, and 67–74) were tested on an episodic memory task that distinguished memory for items, semantic associations, and spatial associations. We minimized (1) age-related differences in familiarity with the stimulus material by using scenes and objects that were piloted to be highly familiar to the children and (2) age-related differences in strategy use by ensuring that the participants were not aware during encoding that there would be a memory test later on. The effects of prior knowledge on episodic memory were quantified via the well-established semantic congruency effect and via a new schema bias score, which we proposed as a measure to assess participants' tendency to commit schema-based memory errors.

Summary of Main Findings

Overall memory performance for the three retrieval types (item, semantic associative, spatial associative) followed a common pattern: younger adults > first

graders > older adults –though the latter difference did not reach statistical significance for item memory. In terms of prior knowledge effects, for item memory, we observed a strong, age-independent memory benefit for items encoded in a congruent context compared to items encoded in an incongruent context. For semantic associative memory, all three age groups displayed significant memory congruency effects and schema bias scores, but these were highest in older adults, which suggests that their associative memory was most affected by prior knowledge. Most interestingly, the magnitudes of children’s semantic congruency effect and schema bias score were also in between the ones of younger and older adults, suggesting that their associative memory was strongly affected by prior knowledge as well. As hypothesized, no congruency effect was observed for spatial associative memory, which tested memory for the location of the object during encoding that is inherently unrelated to the semantics of the task.

Concerning the neural correlates of the semantic congruency effect, all three age groups showed a similarly strong congruency by memory interaction in the vmPFC. Furthermore, the magnitude of vmPFC recruitment during encoding of congruent associations was positively correlated with the schema bias score. Together, these results suggest that while older adults are most prone to rely on their prior knowledge for episodic memory decisions, children can also rely heavily on their prior knowledge to remember information with which they are well-acquainted. This was reflected both in their high rate of schema-based memory errors and in their strong recruitment of the vmPFC. Our findings further indicate that the vmPFC plays a key role in mediating the effects of prior knowledge on memory across the entire lifespan.

Contributions to the Literature

The present study is the first lifespan age-comparative study of the effects of prior knowledge on memory. It makes several novel contributions to the literature, which will be considered in turn.

First, this study demonstrates that children rely more strongly on their prior knowledge than younger adults for associative memory decisions if they have high levels of knowledge of the stimuli/situation. This result stands in contrast to many earlier findings that the congruency effect and the tendency to commit schema-based memory errors increases across childhood (e.g., Brainerd, Reyna, & Forrest, 2002; Metzger et al., 2008; for an overview see Stangor & McMillan, 1992). However, in most of these studies, age-related increases in knowledge of the stimulus material were not controlled for, which leaves open the possibility that differences in knowledge level drive the observed increases in the influence of prior knowledge on memory (but see Metzger et al., 2008). Support for this conjecture comes from three studies using pictorial stimulus material that was highly familiar to the children. These studies revealed comparable schema-consistent recognition memory errors (Ghetti et al., 2002) as well as comparable semantic congruency effects (Brod et al., 2017; Maril et al., 2011) in children and younger adults. Adding to these studies, our results show that children can display an even stronger associative congruency effect than younger adults when knowledge is comparable. To the best of our knowledge, stronger congruency effects have thus far been shown only for older adults. This stronger associative congruency effect exists in parallel to children's comparable item congruency effect and their lower overall semantic and spatial associative memory performance. These findings may reflect children's deficient retrieval monitoring and inhibition of schematic influences, resulting from immature frontostriatal control circuits (Brod et al., 2017). This could make them more vulnerable to schema biases at retrieval (see Loftus & Davies, 1984, for

a similar conjecture). A non-exclusive alternative hypothesis could be that seeing an object that is knowledge-congruent—in this case, to a specific scene—is less common for a child than for an adult and therefore more salient, and that this draws a child to falsely endorse the congruent object. To conclude, our findings suggest that children's memory can be heavily biased by their prior knowledge, provided that they possess high levels of knowledge of the stimuli/context.

Second, our data revealed that older adults' semantic associative memory is most strongly influenced by prior knowledge. In the semantic associative memory test, prior knowledge could be leveraged for a memory decision at retrieval (in contrast to the spatial associative memory, which had no congruency effect). Older adults exhibited both the strongest congruency effect in semantic associative memory and the strongest schema bias among the three age groups. This stands in contrast to the lack of age differences in congruency effect in the item memory. Together, this may suggest that older adults have particular difficulties at retrieval to go against choosing options that are congruent to prior knowledge. These data resonate well with findings from ageing research demonstrating better memory for knowledge-congruent events (e.g., Bäckman & Herlitz, 1990; Castel, 2005; Umanath & Marsch, 2014) and an enhanced tendency to commit knowledge-congruent memory errors (e.g., Dennis, Kim, & Cabeza, 2008; Watson, McDermott, & Balota, 2004). Following the behavioral differences, an unexpected aspect of the fMRI results is that we did not find age differences in vmPFC activation. At the same time, the relationship between vmPFC activation at encoding and schema-based memory errors is age-independent. Additional mechanisms must therefore be responsible for the stronger schema bias of older adults. Akin to the children, deficient monitoring and schema inhibition at retrieval due to impaired frontostriatal circuits are prime candidates (e.g. Fandakova, Lindenberger, & Shing,

2014). In addition, older adults exhibit deficits in associative binding at encoding (Old & Naveh-Benjamin, 2008), which is linked to senescent changes in medio-temporal lobe structures (e.g., Shing et al., 2010). Future studies need to examine its role by performing functional scanning both at encoding and retrieval. To conclude, our results indicate that prior knowledge introduces a bias into memory processing that can play out both as an advantage and as a disadvantage depending on the memory task at hand, and that this bias is enhanced in older adults.

Third, this study demonstrates that the vmPFC contributes to the congruency effect and, more broadly, to the effects of prior knowledge on memory encoding across the entire lifespan. We found that all three age groups showed a strong congruency by memory interaction in vmPFC activation, and that there was a positive correlation between vmPFC recruitment during encoding of knowledge-congruent events and the schema bias score across age groups. This correlation indicates that the more participants recruit the vmPFC during encoding, the more likely they are to later commit knowledge-congruent errors. These results are in line with prevalent theories of the vmPFC's role in memory, which argue that it weights the influence of prior knowledge on memory – with more activation reflecting a stronger influence (Brod et al., 2015; Gilboa & Marlatte, 2017; Warren et al., 2014). On a cognitive level, the positive correlation might, thus, reflect that participants with a more schematic-based processing during encoding tend to commit more knowledge-consistent errors during recognition. A challenge for these interpretations, which is true for the field of cognitive neuroscience of memory more generally, is that the effects of vmPFC recruitment during encoding on memory performance can only be inferred indirectly based on retrieval performance, which necessarily reflects a mix of encoding and retrieval effects. The interpretation is further complicated by the fact that the vmPFC is implicated in

knowledge-congruent memory retrieval as well (Brod et al., 2015; van Kesteren et al., 2010). Thus, an alternative interpretation of the observed correlation could be that participants who display a stronger vmPFC recruitment during encoding also display a stronger vmPFC recruitment during retrieval, which is actually driving the correlation. Both interpretations, however, speak for an important role of the vmPFC in mediating the effects of prior knowledge on memory.

The observed stability of brain activation in the vmPFC across the lifespan matches its structural stability. While most parts of the vmPFC mature early (Shaw et al., 2008), there is also little structural change during ageing (Salat et al., 2004). Stable vmPFC contributions to memory processing across the adult lifespan have been demonstrated in research on processing of self-relevant information (Gutchess, Kensinger, Yoon, & Schacter, 2007; Gutchess, Kensinger, & Schacter, 2007) as well as on false recollection (Dennis, Bowman, & Peterson, 2014). In sum, the current findings are in line with earlier research in younger adults on the vmPFC's key role in mediating the effects of prior knowledge on memory. They extend these earlier findings by showing that it serves this role across the entire lifespan and relates to individual differences in the susceptibility to commit knowledge-consistent memory errors.

Finally, this study demonstrates the utility of the introduced schema bias score to quantify a person's tendency to rely on his or her prior knowledge and to commit schema-based memory errors. By measuring the ratio of congruent and incongruent associative memory errors in incongruent trials, it gives an estimate of schema reliance that is unbiased by the ceiling performance in the congruent condition. The high performance in the congruent condition posed a challenge for the semantic congruency effect, which is a difference score comparing memory for congruent and incongruent events and thus highly dependent on the validity of both scores. Nevertheless, the

schema bias score and the semantic congruency effect were substantially correlated ($r = .45$). While the schema bias score captures participants' erroneous reliance on prior knowledge more directly than the semantic congruency effect, the latter gives a more general estimate of the effect of prior knowledge on memory, capturing both the advantages (higher memory performance) and disadvantages (more knowledge-consistent false memories) of prior knowledge. Of note, the schema bias score correlates positively with the strength of vmPFC recruitment during memory encoding, which indexes an increase in schematic memory processing that in turn results in knowledge-consistent memory errors (Berkers et al., 2016; Spalding et al., 2015; Warren et al., 2014). Thus, we believe that the introduced schema bias score qualifies as a complementary tool to quantify the effects of prior knowledge on memory because it captures participants' erroneous reliance on prior knowledge more directly than the semantic congruency effect.

Limitations and Future Directions

A potential concern for our lifespan comparison is that we tailored the memory task particularly to the children. We used common scenes and congruent objects that they had just learned about in school. Although these scenes and objects are highly familiar to adults as well, this setting might have put an additional burden on children to reject the congruent lure scenes. While one might argue that this experimental setting is an untypical scenario, we believe that it is not devoid of meaning for memory in the real world. In fact, a child having such high knowledge of a particular context resembles a real-world scenario in which children are questioned about events that happened in their close environment. Under these circumstances, it has been shown that children are

indeed highly prone to memory distortions, especially when accurate source memory is required (Johnson & Foley, 1984; Loftus & Davies, 1984; Reyna & Lloyd, 1997).

Another limitation of our study is its extreme-group design in terms of age. While this is an efficient way to test broad age-related trends, it does not allow us to draw definite conclusions concerning potential non-linear dynamics that could take place in the age ranges outside our age groups, for example during puberty. On a related note, cross-sectional studies like ours are inherently limited when the goal is to describe age-related changes within individuals. Future studies are needed both to fill in the age gaps left by this study and to investigate potential intra-individual changes due to increased age and/or knowledge. Finally, our study is limited in that it investigated age differences in the effects of prior knowledge on memory encoding only. Whether the observed pattern holds for memory retrieval is yet to be determined.

Conclusion

Prior knowledge exerts a strong influence on item and associative memory across the entire lifespan. Items encoded in a congruent context were better remembered as compared to items encoded in an incongruent context, independent of the age of the learner. Associative memory decisions about which scene was presented with a particular object were likewise biased by knowledge of the probability of the two occurring together (i.e., schema). This bias was enhanced in both children and older adults (particularly in the latter group), presumably reflecting common deficiencies in monitoring and schema inhibition at retrieval due to immature/atrophic frontostriatal control circuits. The vmPFC underlay the memory congruency effect across age groups, and its recruitment correlated positively with the schema bias. Both the behavioral and the brain data of our study thus exemplify the double-edged role that prior knowledge

plays for memory across the entire lifespan: more true memories, but also more false ones.

Open Practices

Behavioral data and analysis scripts along with the stimulus material are available via the Open Science Framework and can be accessed at <https://osf.io/tdw6k/>

fMRI: Unthresholded statistical maps as well as more detailed information regarding analysis parameters are available via NeuroVault and can be accessed at <http://neurovault.org/collections/EORVZWLP/>

Acknowledgments

The study was conducted within the ‘Cognitive and Neural Dynamics of Memory across the Lifespan’ (ConMem) project at the Center for Lifespan Psychology, Max Planck Institute for Human Development. This work was funded by the Max Planck Society with a Minerva Research Group awarded to YLS. YLS has been funded by the European Union (ERC-2018-StG-PIVOTAL-758898) and a Fellowship from the Jacobs Foundation (JRF 2018–2020). We thank the student assistants for their help in collecting the data, Julia Delius for editorial assistance, and Ulman Lindenberger for valuable discussions.

References

- Alba, J. W., & Hasher, L. (1983). Is memory schematic? *Psychological Bulletin*, 93(2), 203–231.
- Backman, L., & Herlitz, A. (1990). The Relationship Between Prior Knowledge and Face Recognition Memory in Normal Aging and Alzheimer’s Disease. *Journal of*

- Gerontology*, 45(3), P94–P100. <http://doi.org/10.1093/geronj/45.3.P94>
- Badham, S. P., Hay, M., Foxon, N., Kaur, K., & Maylor, E. a. (2016). When does prior knowledge disproportionately benefit older adults' memory? *Neuropsychology, Development, and Cognition. Section B, Aging, Neuropsychology and Cognition*, 23(3), 338–65. <http://doi.org/10.1080/13825585.2015.1099607>
- Bartlett, F. C. (1932). *Remembering: An experimental and social study*. Cambridge, UK: Cambridge University Press.
- Bein, O., Reggev, N., & Maril, A. (2014). Prior knowledge influences on hippocampus and medial prefrontal cortex interactions in subsequent memory. *Neuropsychologia*, 64, 320–330. <http://doi.org/10.1016/j.neuropsychologia.2014.09.046>
- Berkers, R. M. W. J., van der Linden, M., de Almeida, R. F., Müller, N. C. J., Bovy, L., Dresler, M., ... Fernández, G. (2016). Transient medial prefrontal perturbation reduces false memory formation. *Cortex*. <http://doi.org/10.1016/j.cortex.2016.12.015>
- Brainerd, C. J., Reyna, V. F., & Forrest, T. J. (2002). Are Young Children Susceptible to the False-Memory Illusion? *Child Development*, 73(5), 1363–1377. <http://doi.org/10.1111/1467-8624.00477>
- Bransford, J. D., & Johnson, M. K. (1972). Contextual prerequisites for understanding: Some investigations of comprehension and recall. *Journal of Verbal Learning and Verbal Behavior*, 11(6), 717–726. [http://doi.org/10.1016/S0022-5371\(72\)80006-9](http://doi.org/10.1016/S0022-5371(72)80006-9)
- Brod, G., Bunge, S. A., & Shing, Y. L. (2017). Does One Year of Schooling Improve Children's Cognitive Control and Alter Associated Brain Activation? *Psychological Science*, 95679761769983. <http://doi.org/10.1177/0956797617699838>
- Brod, G., Lindenberger, U., & Shing, Y. L. (2017). Neural activation patterns during retrieval of schema-related memories: differences and commonalities between children and adults. *Developmental Science*, 20(6), e12475.

<http://doi.org/10.1111/desc.12475>

Brod, G., Lindenberger, U., Werkle-Bergner, M., & Shing, Y. L. (2015). Differences in the neural signature of remembering schema-congruent and schema-incongruent events. *NeuroImage*, *117*, 358–366.

<http://doi.org/10.1016/j.neuroimage.2015.05.086>

Brod, G., & Shing, Y. L. (2018). Specifying the role of the ventromedial prefrontal cortex in memory formation. *Neuropsychologia*, *111*(March 2018), 8–15.

<http://doi.org/10.1016/j.neuropsychologia.2018.01.005>

Brod, G., Werkle-Bergner, M., & Shing, Y. L. (2013). The influence of prior knowledge on memory: a developmental cognitive neuroscience perspective. *Frontiers in Behavioral Neuroscience*, *7*, 139. <http://doi.org/10.3389/fnbeh.2013.00139>

Carr, V. A., Castel, A. D., & Knowlton, B. J. (2015). Age-related differences in memory after attending to distinctiveness or similarity during learning. *Aging, Neuropsychology, and Cognition*, *22*(2), 155–169. <http://doi.org/10.1080/13825585.2014.898735>

Castel, A. D. (2005). Memory for Grocery Prices in Younger and Older Adults: The Role of Schematic Support. *Psychology and Aging*, *20*(4), 718–721.

<http://doi.org/10.1037/0882-7974.20.4.718>

Craik, F. I., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, *104*(3), 268–294.

<http://doi.org/10.1037//0096-3445.104.3.268>

Dale, A. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*(2–3), 109–114. [http://doi.org/10.1002/\(SICI\)1097-](http://doi.org/10.1002/(SICI)1097-0193(1999)8:2/33.0.CO;2-W)

[0193\(1999\)8:2/33.0.CO;2-W](http://doi.org/10.1002/(SICI)1097-0193(1999)8:2/33.0.CO;2-W)

Dennis, N. A., Bowman, C. R., & Peterson, K. M. (2014). Age-related differences in the neural correlates mediating false recollection. *Neurobiology of Aging*, *35*(2), 395–

407. <http://doi.org/10.1016/j.neurobiolaging.2013.08.019>

Dennis, N. a, Kim, H., & Cabeza, R. (2008). Age-related differences in brain activity during true and false memory retrieval. *Journal of Cognitive Neuroscience*, *20*(8), 1390–402. <http://doi.org/10.1162/jocn.2008.20096>

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). “Mini-mental state”. A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, *12*(3), 189–198. [http://doi.org/10.1016/0022-3956\(75\)90026-6](http://doi.org/10.1016/0022-3956(75)90026-6)

Ghetti, S., Qin, J., & Goodman, G. S. (2002). False memories in children and adults: Age, distinctiveness, and subjective experience. *Developmental Psychology*, *38*(5), 705–718. <http://doi.org/10.1037//0012-1649.38.5.705>

Ghosh, V. E., Moscovitch, M., Melo Colella, B., & Gilboa, A. (2014). Schema Representation in Patients with Ventromedial PFC Lesions. *Journal of Neuroscience*, *34*(36), 12057–12070. <http://doi.org/10.1523/JNEUROSCI.0740-14.2014>

Gilboa, A., & Marlatte, H. (2017). Neurobiology of Schemas and Schema-Mediated Memory. *Trends in Cognitive Sciences*, *21*(8), 618–631. <http://doi.org/10.1016/j.tics.2017.04.013>

Gutchess, A. H., Kensinger, E. A., Yoon, C., & Schacter, D. L. (2007). Ageing and the self-reference effect in memory. *Memory (Hove, England)*, *15*(8), 822–837. <http://doi.org/10.1080/09658210701701394>

Gutchess, A. H., Kensinger, E. a, & Schacter, D. L. (2007). Aging, self-referencing, and medial prefrontal cortex. *Social Neuroscience*, *2*(2), 117–133. <http://doi.org/10.1080/17470910701399029>

Howe, M. L. (2006). Developmentally Invariant Dissociations in Children ’ s True and False Memories : Not All Relatedness Is Created Equal. *Child Development*, *77*(4),

1112–1123. <http://doi.org/10.1111/j.1467-8624.2006.00922.x>

Jacoby, L. L., & Rhodes, M. G. (2006). False remembering in the aged. *Current Directions in Psychological Science*, *15*(2), 49–53. <http://doi.org/10.1111/j.0963-7214.2006.00405.x>

Johnson, M. K., & Foley, M. A. (1984). Differentiating Fact from Fantasy: The Reliability of Children's Memory. *Journal of Social Issues*, *40*(2), 33–50. <http://doi.org/10.1111/j.1540-4560.1984.tb01092.x>

Loftus, E. F., & Davies, G. M. (1984). Distortions in the Memory of Children. *Journal of Social Issues*, *40*(2), 51–67. <http://doi.org/10.1111/j.1540-4560.1984.tb01093.x>

Maril, A., Avital, R., Reggev, N., Zuckerman, M., Sadeh, T., Ben Sira, L., & Livneh, N. (2011). Event congruency and episodic encoding: a developmental fMRI study. *Neuropsychologia*, *49*(11), 3036–45. <http://doi.org/10.1016/j.neuropsychologia.2011.07.004>

Metzger, R. L., Warren, A. R., Shelton, J. T., Price, J., Reed, A. W., & Williams, D. (2008). Do children “DRM” like adults? False memory production in children. *Developmental Psychology*, *44*(1), 169–81. <http://doi.org/10.1037/0012-1649.44.1.169>

Moscovitch, M., & Craik, F. I. M. (1976). Depth of processing, retrieval cues, and uniqueness of encoding as factors in recall. *Journal of Verbal Learning and Verbal Behavior*, *15*(4), 447–458. [http://doi.org/10.1016/S0022-5371\(76\)90040-2](http://doi.org/10.1016/S0022-5371(76)90040-2)

Moscovitch, M., & Melo, B. (1997). Strategic retrieval and the frontal lobes: Evidence from confabulation and amnesia. *Neuropsychologia*, *35*(7), 1017–1034. [http://doi.org/10.1016/S0028-3932\(97\)00028-6](http://doi.org/10.1016/S0028-3932(97)00028-6)

Mumford, J. A., Poline, J. B., & Poldrack, R. A. (2015). Orthogonalization of regressors in fMRI models. *PLoS ONE*, *10*(4), e0126255. <http://doi.org/10.1371/journal.pone.0126255>

- Naveh-Benjamin, M. (2000). Adult age differences in memory performance: tests of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(5), 1170–1187. <http://doi.org/10.1037//0278-7393.26.5.1170>
- Naveh-Benjamin, M., Craik, F. I. M., Guez, J., & Kreuger, S. (2005). Divided Attention in Younger and Older Adults: Effects of Strategy and Relatedness on Memory Performance and Secondary Task Costs. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(3), 520–537. <http://doi.org/10.1037/0278-7393.31.3.520>
- Old, S. R., & Naveh-Benjamin, M. (2008). Differential Effects of Age on Item and Associative Measures of Memory: A Meta-Analysis. *Psychology and Aging*, *23*(1), 104–118. <http://doi.org/10.1037/0882-7974.23.1.104>
- Poppenk, J., Köhler, S., & Moscovitch, M. (2010). Revisiting the novelty effect: when familiarity, not novelty, enhances memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*(5), 1321–30. <http://doi.org/10.1037/a0019900>
- R Core Team. (2014). R: A Language and Environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Reyna, V. F., & Lloyd, F. (1997). Theories of false memory in children and adults. *Learning and Individual Differences*, *9*(2), 95–123. [http://doi.org/10.1016/S1041-6080\(97\)90002-9](http://doi.org/10.1016/S1041-6080(97)90002-9)
- Robertson, E. K., & Köhler, S. (2007). Insights from child development on the relationship between episodic and semantic memory. *Neuropsychologia*, *45*(14), 3178–89. <http://doi.org/10.1016/j.neuropsychologia.2007.06.021>
- Salat, D. H., Buckner, R. L., Snyder, A. Z., Greve, D. N., Desikan, R. S. R., Busa, E., ... Fischl, B.

- (2004). Thinning of the cerebral cortex in aging. *Cerebral Cortex*, *14*(7), 721–730.
<http://doi.org/10.1093/cercor/bhh032>
- Schacter, D. L., Koutstaal, W., & Norman, K. a. (1997). False memories and aging. *Trends in Cognitive Sciences*, *1*(6), 229–236. [http://doi.org/10.1016/S1364-6613\(97\)01068-1](http://doi.org/10.1016/S1364-6613(97)01068-1)
- Schlichting, M. L., & Preston, A. R. (2015). Memory integration: neural mechanisms and implications for behavior. *Current Opinion in Behavioral Sciences*, *1*, 1–8.
<http://doi.org/10.1016/j.cobeha.2014.07.005>
- Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., ... Wise, S. P. (2008). Neurodevelopmental Trajectories of the Human Cerebral Cortex. *Journal of Neuroscience*, *28*(14), 3586–3594. <http://doi.org/10.1523/JNEUROSCI.5309-07.2008>
- Shing, Y. L., Werkle-Bergner, M., Brehmer, Y., Müller, V., Li, S.-C., & Lindenberger, U. (2010). Episodic memory across the lifespan: The contributions of associative and strategic components. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1080–1091.
<http://doi.org/10.1016/j.neubiorev.2009.11.002>
- Smith, S., Jenkinson, M., & Woolrich, M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage*, *23*, 208–219.
- Spalding, K. N., Jones, S. H., Duff, M. C., Tranel, D., & Warren, D. E. (2015). Investigating the Neural Correlates of Schemas: Ventromedial Prefrontal Cortex Is Necessary for Normal Schematic Influence on Memory. *Journal of Neuroscience*, *35*(47), 15746–15751. <http://doi.org/10.1523/JNEUROSCI.2767-15.2015>
- Stangor, C., & McMillan, D. (1992). Memory for expectancy-congruent and expectancy-incongruent information: A review of the social and social developmental literatures. *Psychological Bulletin*, *111*(1), 42–61. <http://doi.org/10.1037//0033->

2909.111.1.42

- Umanath, S., & Marsh, E. J. (2014). Understanding How Prior Knowledge Influences Memory in Older Adults. *Perspectives on Psychological Science*, *9*(4), 408–426. <http://doi.org/10.1177/1745691614535933>
- van Kesteren, M. T. R., Beul, S. F., Takashima, A., Henson, R. N., Ruiter, D. J., & Fernández, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. *Neuropsychologia*, *51*(12), 2352–2359. <http://doi.org/10.1016/j.neuropsychologia.2013.05.027>
- van Kesteren, M. T. R., Rijpkema, M., Ruiter, D. J., & Fernandez, G. (2010). Retrieval of Associative Information Congruent with Prior Knowledge Is Related to Increased Medial Prefrontal Activity and Connectivity. *Journal of Neuroscience*, *30*(47), 15888–15894. <http://doi.org/10.1523/JNEUROSCI.2674-10.2010>
- Warren, D. E., Jones, S. H., Duff, M. C., & Tranel, D. (2014). False Recall Is Reduced by Damage to the Ventromedial Prefrontal Cortex: Implications for Understanding the Neural Correlates of Schematic Memory. *Journal of Neuroscience*, *34*(22), 7677–7682. <http://doi.org/10.1523/JNEUROSCI.0119-14.2014>
- Watson, J. M., McDermott, K. B., & Balota, D. A. (2004). Attempting to avoid false memories in the Deese/Roediger-McDermott paradigm: assessing the combined influence of practice and warnings in young and old adults. *Memory & Cognition*, *32*(1), 135–141. <http://doi.org/10.3758/BF03195826>

Figure Captions

Figure 1. Illustration of the memory task. Top: During the incidental study phase, participants had to decide whether scene and object “fit together” (i.e., are congruent) or “do not fit together” (i.e., incongruent). Bottom: During the test phase, participants had

to decide whether they had seen this object while in the scanner (item memory). For objects judged as old, they then had to decide with which scene the object had been presented during the study phase (semantic associative memory) and whether the object was presented to the right or the left of the screen during the study phase (spatial associative memory).

Figure 2. Item Memory Performance. Younger adults displayed higher memory performance than children and older adults, whose performance did not differ from another. Performance was enhanced for items encoded in a congruent context. There was no congruency x age group interaction, suggesting that the beneficial of congruency on item memory (i.e., the memory congruency effect) was comparable across age groups.

Figure 3. Semantic Associative Memory Performance and Schema Bias. a) Younger adults displayed the best memory performance, followed by children and older adults, who performed worst. This order was inverted for the congruency effect (i.e., congruent – incongruent) as well as for b) the schema bias score (% knowledge-consistent memory errors): older adults displayed the strongest congruency effect and schema bias, followed by children and younger adults, who were the least biased.

Figure 4. Congruency by memory interaction in the ventromedial prefrontal cortex (vmPFC). (a) Cluster (165 voxels) within the vmPFC that exhibited a stronger subsequent memory effect (SME, remembered > forgotten) for congruent than for incongruent trials across all participants; (b) percent signal change in the vmPFC cluster, separately for congruent and incongruent events by age groups; (c) correlation between participants' congruent SME (rem = remembered, forg = forgotten) and their schema bias score.

Study (MRI scanner)



3 s

Test (computer, self-paced)







