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Neural correlates of successful memory encoding in kindergarten and early elementary school children: Longitudinal trends and effects of schooling

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From age five to seven, there are remarkable improvements in children's cognitive abilities ("5-7 shift"). In many countries, including Germany, formal schooling begins in this age range. It is, thus, unclear to what extent exposure to formal schooling contributes to the "5-7 shift". In this longitudinal study, we investigated if schooling acts as a catalyst of maturation. We tested 5-year-old children who were born close to the official cutoff date for school entry and who were still attending a play-oriented kindergarten. One year later, the children were tested again. Some of the children had experienced their first year of schooling whereas the others had remained in kindergarten. Using two fMRI tasks that assessed episodic memory formation (i.e., subsequent memory effect), we found that children relied strongly on the medial temporal lobe (MTL) at both time points but not on the prefrontal cortex (PFC). In contrast, older children and adults typically show subsequent memory effects in both MTL and PFC. Both children groups improved in their memory performance, but there were no longitudinal changes nor group differences in neural activation. We conclude that successful memory formation in this age group relies more heavily on the MTL than in older age groups.

Keywords: Memory, Schooling, fMRI, subsequent memory effect, hippocampus, prefrontal cortex

At around 5-7 years, children's cognitive abilities change remarkably fast. This observation has been called the "5-7 years shift" (e.g., Sameroff & Haith, 1996) and describes changes in attention, memory, and executive functions (Burrage et al., 2008). For example, a longitudinal study has shown that associative memory improves at a relatively fast rate between 5 and 7 years of age, and more gradually in later childhood and early adolescence (Riggins, 2014). This age range coincides often with the start of formal schooling. In many countries, including Germany, formal schooling is much more structured than kindergarten, which is play-oriented. In school, children usually go through a standardized curriculum in a systematic way and are required to process and remember a lot of information. It has been argued that schooling, at least in countries such as Germany, places greater demands on children's executive control than kindergarten does, which contributes to the rapid development of executive functions observed between 5 and 7 years of age (Brod et al., 2017). At the same time, the way that children learn new information, i.e., memory processes, may also be altered by schooling. Thus far, it is unclear to what extent observed changes in memory abilities at 5-7 years of age are due to normative brain development and/or formal schooling.

The school-cutoff design (e.g., Morrison et al., 1997) aims to disentangle the effects of schooling and brain maturation. In this design, children who are in their first year of school are compared to children who are still in kindergarten. Importantly, both groups of children are of similar age at the time of testing. This procedure is possible since many educational systems have a cutoff date for school entrance, so that children born around that cutoff date are similar in age, but those children who are born shortly before the cutoff date go to school one year earlier than those born shortly after.

The school-cutoff logic was applied in the HippoKID study, a longitudinal study where 5-6 year old children from Berlin, Germany, were tested in kindergarten at baseline, and one year later at followup, when roughly half of them had entered school while the others had remained in kindergarten. The children completed a variety of tasks including memory tasks and cognitive control tasks. For cognitive control, it has been shown that children who transitioned to school ("transition group) showed greater

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE increase in blood oxygen level dependent (BOLD) signal from baseline to follow-up in posterior parietal cortex during a a go/no go task of inhibitory control, compared to children who remained in kindergarten ("non-transition group). This increase in BOLD signal in a region implicated in cognitive control was correlated with improvement in accuracy on an independent behavioral task of cognitive control (Brod et al., 2017).

The overarching goal of the current investigation was to examine the neural mechanisms of memory formation in 5-7 year old children. Using fMRI to study the neural substrates of memory formation in such young children is clearly charting novel territories. We, therefore, aimed to characterize both the general neural substrates of successful memory formation in this age group as well as longitudinal changes across one year. We used data of the HippoKID study, which further allowed us to investigate the factors that might lead to these changes, including schooling. In the following sections, we will first introduce research on the development of the neural mechanisms of memory formation. This is followed by a discussion of the potential forces that drive this development.

Age differences in memory formation

The subsequent memory approach is commonly used to investigate memory formation and its neural underpinnings (Brewer et al., 1998; Davachi, 2006; Paller et al., 1987; Wagner et al., 1998). Here, a sequence of stimuli is presented to the participants (encoding phase) which they have to remember later (retrieval phase), e.g., in a recognition test. Brain activity during encoding is compared between stimuli that were subsequently remembered or forgotten. In adults, subsequent memory effects in the BOLD signal were revealed in the medial temporal lobe (MTL), particularly in the hippocampus, and in the PFC (see Kim, 2011; Spaniol et al., 2009, for a meta-analyses), suggesting that these areas play a critical role for successful memory formation. Interestingly, greater BOLD signal in forgotten than in remembered trials (negative subsequent memory effects) is usually found in brain areas such as posterior midline and temporoparietal areas. These areas are often discussed as being part of the so-called default network, and a disengagement of these areas may support encoding (Daselaar et al.,

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE 2004; De Chastelaine & Rugg, 2014; Otten & Rugg, 2001; White et al., 2013).

The subsequent memory effect has also been investigated in younger participants (see Ghetti & Fandakova, 2020, for an overview). For example, in a cross-sectional study, children, adolescents, and young adults from 8-24 years of age participated in an fMRI study (Ofen et al., 2007; see also Fandakova et al., 2019; Geng et al., 2019; Ghetti et al., 2010). During encoding, participants saw scenes that they categorized as indoor or outdoor scenes. In a later recognition test, participants saw the studied scenes alongside new scenes, and they had to respond whether they had seen the scenes before ("old") or not ("new"). Positive subsequent memory effects were observed in MTL, i.e., in hippocampus and parahippocampal gyrus (PHG), but the positive subsequent memory effects in MTL did not vary with age. In PFC, on the other hand, there was a linear relation between age and positive subsequent memory effects. More specifically, the youngest participants hardly showed any positive subsequent memory effect in left PFC (BA 46) and only a comparably small positive subsequent memory effect in right PFC (BA 9). Activity in these regions was the greater the older the participants were. These results suggest a shift in neural memory mechanisms towards a higher involvement of PFC during development, which goes along with immaturity of PFC in early school age (Ofen et al., 2007; see also Tang et al., 2018).

Negative subsequent memory effects, which are associated with greater deactivation of the default mode network for remembered versus forgotten trials, seem to develop from childhood to early adulthood: Children do not show deactivation of the default network to the same extent as adults (Chai et al., 2014; Tang et al., 2018; see also de Chastelaine et al., 2011, 2015; Mattson et al., 2014 for negative subsequent memory effects in older adults).

Two component framework of episodic memory development

Developmental changes in neural mechanisms underlying episodic memory have also been suggested in the two-component framework (Shing et al., 2008, 2010; Shing & Lindenberger, 2011). According to this framework, episodic memory is supported by two interacting components: an

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE associative component which binds the different aspect of an episode together, and a strategic component which is related to memory control processes. In a cross-sectional lifespan study, different age-groups ranging from 10 to 75 years of life were compared regarding differences between the associative and strategic component (Shing et al., 2008), and the results suggested different developmental trajectories for the two components. While the associative component develops faster in childhood than the strategic component, both components start to decline at similar times in older age. Hence, young children's deficits in episodic memory, compared to young adults, seem to be due to the later development of the strategic component. This is also in line with studies showing increased mnemonic strategy use over the course of childhood and adolescence (Kron-Sperl et al., 2008; Schneider et al., 2004; Schwenck et al., 2009).

Importantly, the two-component framework suggests also that the two memory components differ regarding their neural correlates. The authors suggest that the associative component is more strongly related to activity in MTL while the strategic component is more strongly related to activity in PFC. This is in line with the protracted development of the PFC compared to the MTL (Giedd et al., 1999; Gogtay et al., 2006; Huttenlocher, 1979; Sowell et al., 2002, 2004). In addition, dissociative patterns of age-related positive subsequent memory effects have been observed in the MTL vs. the PFC (Ofen et al., 2007). To date, however, little is known about the influence of formal schooling on the development of the two components of episodic memory and their neural correlates.

Increase in prior knowledge as a driver of memory development

As mentioned above, in school, children acquire new knowledge in a structured way. This may affect the use of mnemonic strategies, depending on the teachers' way of communication (Coffman et al., 2008; Ornstein et al., 2010; Schneider & Ornstein, 2019). In addition, a strong increase in knowledge can be observed in middle childhood (Hudson et al., 1992; Vosniadou & Brewer, 1992). New information is assimilated into existing knowledge (i.e., knowledge begets knowledge), thereby, knowledge plays a major role in memory differences over the lifespan (Brod et al., 2013, for a review).

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE Consequently, schooling may act as a memory catalyst, not only by potentially changing memory mechanisms, but also by providing knowledge which facilitates further learning. Knowledge can be represented in so-called schemas, which can be understood as associative network structures that contain extracted commonalities across multiple episodes and thus allow inference beyond already experienced situations (Bartlett, 1932; Ghosh & Gilboa, 2014). A classical example for the effect of prior knowledge on memory is the so-called "memory congruency effect", which denotes a memory advantage for schema-congruent as opposed to schema-incongruent new information. This effect has been attributed to congruent new information being integrated more easily and allowing a more elaborate encoding (Bein et al., 2015; Craik & Tulving, 1975).

The memory congruency effect has also been investigated in recent fMRI studies. The congruency effect has been linked to the ventromedial prefrontal cortex (vmPFC), which displays enhanced activation for successfully encoded and retrieved schema-congruent information (Brod & Shing, 2018, 2019; van Kesteren et al., 2013; Van Kesteren et al., 2010). Furthermore, activity in the vmPFC for successfully memorized course-related information has been shown to predict course performance in university students (Van Kesteren et al., 2014). The memory congruency effect thus seems to be a suitable index for facilitated encoding through prior knowledge.

The current study

The current study comprised two memory tasks as assessed in the HippoKID study described above. We aimed to reveal the neural mechanisms of episodic memory encoding in 5-year-olds as well as their longitudinal development across one year. We further aimed to unravel the extent to which this development is shaped by formal schooling. To this end, we investigated fMRI subsequent memory effects at two time points. At baseline, all tested children were still in kindergarten. Roughly half of the children had transitioned to school one year later while the rest had remained in kindergarten. Based on the two-component framework (Shing et al., 2010) and the fMRI study by Ofen et al. (2007), we expected that children would show reliable positive subsequent memory effects in MTL. Those should

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE be similar at baseline and follow-up, and not differ between the two groups. In PFC, on the other hand, we expected a greater increase in positive subsequent memory effects over time in the transition group than in the non-transition group. This is because schooling as a structured learning environment may strengthen the strategic component of episodic memory more than the associative component.

We further investigated the role of schematic knowledge that was acquired during the first year of schooling on memory encoding. At the second measurement point, we added a second fMRI task in which we presented objects alongside schema-congruent or schema-incongruent scenes. Importantly, the themes of the scene stimuli were selected based on the first grade curriculum. The transition group was thus familiar with the topics and we expected a greater congruency effect for the transition group than for the non-transition group in memory performance. In addition, we expected a greater congruence-dependent positive subsequent memory effect in vmPFC in the transition group than in the non-transition group.

Method

General study approach

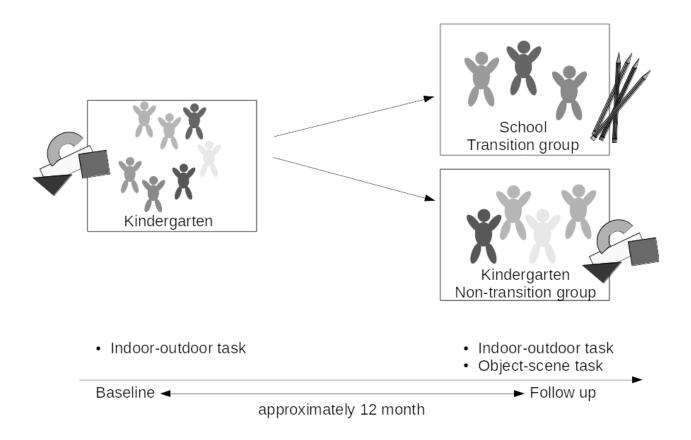
We aimed to recruit children who were similar in age but who differed systematically in the age of entering school. Five- and 6-year old children born between October and March were recruited through advertisements in kindergartens, newspapers, and Internet forums for parents. The children's birthdays were close to the official cutoff date for school entrance in Berlin which was the 31st of December. Children born between the beginning of October and the 31st of December were supposed to enter school roughly at the age of five and a half, whereas children born between the 1st of January and the end of March were supposed to enter school roughly at the age of six and a half. However, some parents of children born before the cutoff date decided to defer school entry, such that these children would also enter school at the age of six and a half, contrary to the cutoff date rule. As a result, school entrance of a few of our participants who were supposed to be in the transition group was delayed, and they ended up in the non-transition group. The children attended various (predominantly state-funded)

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE kindergartens and schools in Berlin.

The sample was divided into two groups. Both groups were tested twice during two consecutive summers, at the age of 5 and at the age of 6 (baseline and follow-up). The first group, the "non-transition group", were attending kindergarten during both years. The second group, the "transition group", were in kindergarten at the age of 5, however, they had already been in school for almost a year when they were tested again at the age of 6 (see Fig. 1).

Figure 1.

School cutoff-logic.



Note. Children who were born around the official school cutoff date were recruited for this study. Hence, they were all similar in age. At baseline, all children were still in kindergarten. At follow-up, some of the children had transitioned to school (transition group) while the others had remained in kindergarten (non-transition group).

Children were tested in two waves in order to reach larger sample sizes, one from 2013 till 2014 and one from 2014 till 2015. The settings were identical for the two cohorts. Testing took place every year in summer time with three testing sessions on three different days. The number of days between sessions varied depending on the participants' schedule, but were kept as short as possible. Each session took approximately 90 minutes and consisted of behavioral tasks and neuroimaging. The time in the scanner lasted about 20 minutes each time, excluding preparation.

Participants

Ninety-three children were tested in total. Fifty-three children (25 females) did their baseline testing in 2013, 49 (22 females) of them returned for the follow-up in 2014. Forty children (23 females) did their baseline testing in 2014, 34 (21 females) returned for the follow-up in 2015. Thus, longitudinal data from baseline and follow-up was available from 83 children in total. Overall dropout across both waves was 10.3%. Forty-two children were in the non-transition group, 22 children were in the transition group (see Fig. 1). Nineteen children did not fit into any of the two groups because they were already around 6 years old at baseline. All children were native German speakers and did not suffer from psychiatric and neurological disorders according to their parents. Children were paid 10 € per hour for their participation and additionally received a small gift after each testing session. Informed consent was obtained from the children's parents or legal guardians. All procedures were approved by the ethics committee of the German Psychological Society (DGPs). Some children's data were not included in the data analyses due to poor data quality (for details see below). The final sample sizes differed for the two tasks, as some children had good data quality in one task but not in the other.

Selected participants for indoor-outdoor task. Only data from the non-transition group and the transition group was considered. The data were analyzed for children of whom data of at least 5 trials per condition existed (remembered versus forgotten trials), who did not have more than 15% of missing data (due to e.g., movement artifacts, see data analysis for further details; or the child did not

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE finish the entire task), and who did not exhibit more than 3 mm of mean absolute motion and 1 mm of mean relative motion (between consecutive volumes). One child was excluded because of unusual brain anatomy. These exclusion criteria were applied to the individual timepoints, and exclusion at either timepoint resulted in exclusion of the entire data. The data of 16 children of the non-transition groups and the data of 7 children of the transition group were excluded. Taken together, the data of 41 children were analyzed. The final non-transition group consisted of 26 children (12 girls; mean age at baseline: 5.3 years; mean age at follow-up: 6.4 years). The final transition group consisted of 15 children (8 girls; mean age at baseline: 5.5 years; mean age at follow-up: 6.5 years).

The two groups (excluding four participants of the transition group and five participants of the non-transition group whose parents did not report family income) did not differ regarding mean family income at baseline, t < 1. In addition, the two groups (excluding two participants from the non-transition group with missing data) did not differ in working memory at baseline, t < 1 (combined score of corsi block and colors backward, taken from AGTB 5-12, Hasselhorn et al., 2012).

Selected participants for object-scene task. Cross-sectional data were collected during the follow-up session for both the transition group and the non-transition group. Criteria for data exclusion were the same as for the indoor-outdoor task. Again, one child was excluded because of unusual brain anatomy. The data of 10 children of the non-transition groups and the data of 4 children of the transition group were excluded. Additional data came from four kindergarten children (three girls and one boy) who participated at the second wave baseline (which coincided with the first wave follow-up). They were already around 6 years old and hence matched the non-transition group in age and were still in kindergarten (due to deferred school entry). At baseline of the first wave, the task had not been included yet. Because these four participants matched the non-transition group (both in terms of age and education), they were added to this group to provide a slightly bigger sample size. Taken together, the data of 54 children was analyzed. The final (combined) non-transition group consisted of 36 children (21 girls; mean age: 6.35 years). The final transition group consisted of 18 children (10 girls,

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE mean age: 6.53 years).

The two groups (excluding four participants of the transition group and eight participants of the non-transition group whose parents did not report family income) did not differ regarding mean family income at baseline, t < 1. In addition, the two groups (excluding one participant from the non-transition group with missing data) did not differ in working memory at baseline, t < 1 (combined score of corsi block and colors backward, taken from AGTB 5-12, Hasselhorn et al., 2012).

Paradigms

Indoor-outdoor task. The indoor-outdoor task took place on the second day of testing each year. This task was a non-incidental, intentional memory task consisting of an encoding phase which took place inside the scanner and a retrieval phase which took place outside the scanner. During the encoding phase (see Figure 2a), photographs of 30 indoor and 30 outdoor scenes as well as 5 filler items were presented via a mirror which was placed on top of the MR coil. Participants indicated via key presses with their right and left hand if the scenes were indoor or outdoor scenes. Response versions were counterbalanced across participants. Filler items were cartoons of a hippopotamus, the mascot of the study. Children were told that the hippopotamus would occur when they did well in the task and that more occurrences of the hippopotamus meant better performance. Unbeknownst to participants, the same number of filler items was shown to each participant. Each picture was presented for 3 seconds, with an inter-trial interval of 2, 3, 4, 5, or 6 seconds between the key press and the next trial. A fixation cross was shown during the inter-trial interval. The order of the scenes and the filler items was randomized and kept constant across subjects.

In the retrieval phase, the same 30 indoor and 30 outdoor scenes were shown again, together with 15 new indoor and 15 new outdoor scenes. Children's task was first to indicate verbally if the objects were old or new, hence, if they had seen them before during the encoding phase of the task. The experimenter pressed the corresponding key for them. After every trial, a binary confidence rating (sure, unsure, see Hembacher & Ghetti, 2014) appeared and the experimenter asked the child if it was

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE sure or unsure about the answer (see Fig. 2a). Different sets of stimuli were used during baseline and follow-up. Three sets of stimuli were used in total, and the sets and their order were counterbalanced across participants such that each participant saw two of the sets.

Object-scene task. The object-scene task took place on the first day of testing. The task was an incidental learning task, i.e., children were not told that their memory would be tested later on. It consisted of an encoding phase that took place inside the scanner and a retrieval phase that took place outside the scanner (see Figure 2b). During the encoding phase, 88 objects were presented and paired with one of 22 different scenes. Each scene was, thus, paired with 4 different objects. The objects and scenes were chosen based on pilot studies with 10 teachers and 10 first-grade pupils. First, the teachers selected scenes (e.g., farms, forests, fields) and objects that were typical for the topics discussed in first grade. Second, the pupils rated congruency of scenes and objects.

In the actual study, objects and scenes were presented simultaneously next to each other on a black background for 5 s. Object and scene frames were of identical size and presented on two screen locations, respectively (left and right of the centre). The location (left/right) of the object and scene was randomized across trials. Half of the objects were paired with congruent and the other half with incongruent scenes, as rated in the pilot studies. Participants indicated via key presses if the objects were congruent or incongruent with the scenes. For example, a field that was paired with wheat grains would be congruent. A white fixation cross followed. 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). In addition to the object-scene pairs, 5 filler items were presented, as in the indoor-outdoor task. The order of the object-scene pairs and the filler items was randomized.

In the retrieval phase, the 88 objects were shown again, alongside 44 new objects. The objects were presented centrally. Children's task was first to indicate verbally if the objects were old or new, hence, if they had seen them before during the encoding phase of the task (i.e., object recognition). The experimenter pressed the corresponding key for them. If children indicated that the object was old, they

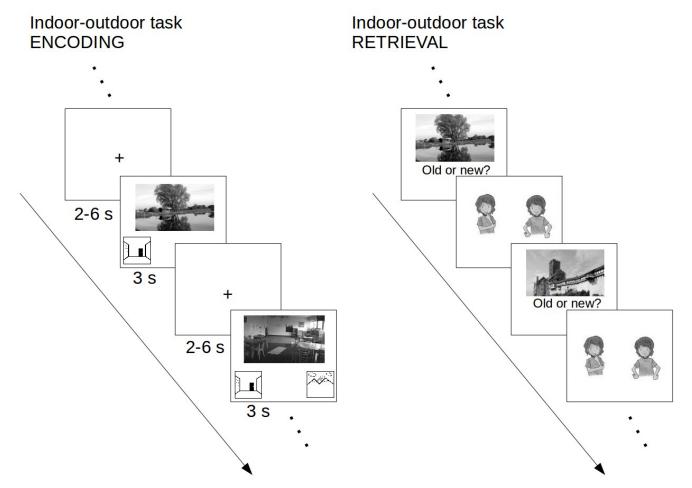
NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE were shown three scene options and were asked to indicate which scene had been previously paired with the object (i.e., associative memory). Each of the scenes had been presented during encoding. There were always one congruent and two incongruent scene options. The order of the three scenes on the screen was random. If the object had indeed been presented during the encoding phase, the paired scene was always among the three scenes. Finally, after their response, children were asked to recall whether the object was presented on the right or on the left of the screen during encoding (i.e., location memory). The order of trials at test was randomized (see Fig. 2b).

Data of the first graders has also been reported in a cross-sectional lifespan comparison performed with this task (Brod & Shing, 2019). We only report the results of the object recognition measures here to ensure comparability with the indoor-outdoor task. Results of the associative memory and location memory measures are reported in Brod & Shing (2019).

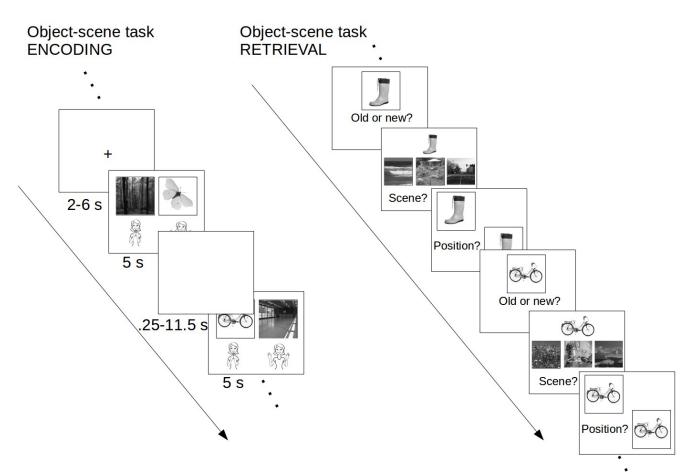
Figure 2.

Memory tasks.

A.



Β.



Note.

a. Indoor-outdoor task. During encoding, scenes were classified as indoor or outdoor scenes. During retrieval, old or new scenes were presented and participants responded whether they remember seeing the scenes ("old") or not ("new"). Children also indicated if they were confident in their decision. Encoding was done inside the scanner, retrieval was done outside the scanner.

b. Object-scene task. During encoding, object-scene pairs were classified as "congruent" or "incongruent" to each other. During retrieval, old or new objects were presented and participants responded whether they remember seeing the objects before ("old") or not ("new"). If children responded "old", they were also asked to remember and select the scene paired with the object, as well as the encoding position of the object on the screen. Encoding was done inside the scanner, retrieval was done outside the scanner.

MRI data acquisition

To keep the children engaged in the tasks while in the MR scanner, we told them that they were like little astronauts going for a journey into their own brains in a machine which resembles a space shuttle. Before they went into the MR scanner, children explored a mock scanner to get familiarized with the MR procedure. They were also trained to not move too much in the mock scanner. While children were in the real MR scanner, there was always an experimenter standing next to the scanner. This was done to help the children feel comfortable throughout the tasks, stay engaged, and not move too much.

For the two tasks, T2*-weighted echo-planar images were acquired using a 3-T Siemens TIM Trio MRI scanner with a 12-channel head coil (transverse slice orientation, interleaved ascending scanning direction, field of view = 216 mm, repetition time = 2,000 ms, echo time = 30 ms, 36 slices, slice thickness = 3 mm, matrix = 72 × 72, voxel size = 3 × 3 × 3 mm, distance factor = 10%). 238 volumes were acquired in the indoor-outdoor task, while 281 volumes were acquired in the objectscene task. In addition, anatomical scans were obtained with a T1-weighted 3-D magnetizationprepared rapid gradient-echo sequence (repetition time = 2,500 ms, echo time = 2,500 ms, sagittal slice orientation, spatial resolution = 1 × 1 × 1 mm).

Behavioral data analyses

Pr-values (discrimination measure: hits minus false alarms) and d' were calculated for each participant at each timepoint, respectively for each condition in each task. For the indoor-outdoor task, the data were submitted to a 2x2 ANOVA with the within-subject variable timepoint (baseline, follow-up) and the between-subject variable group (non-transition group, transition group). For the object-scene task, the data were submitted to a 2x2 ANOVA with the within-subject variable congruency (congruent, incongruent) and the between-subject variable group (non-transition group (non-transition group, transition group). Congruency was determined based on children's judgments from the encoding phase.

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE congruency ratings from the pilot studies and from children's judgments in the encoding phase were mostly overlapping. For all ANOVAs, we used Type III sums-of-squares calculations along with effect coding, as recommended for mixed-effects designs with unequal group sizes.

fMRI data analyses

Preprocessing. Functional MRI data was analyzed using FSL's FEAT (FMRIB's Software Library; Smith et al., 2004) and using ART, a Matlab-based tool for detecting motion artifacts (cos.northeastern.edu/whitfield-gabrieli/software/art/). In both tasks, the first four volumes were acquired to reach a stable signal and were discarded from the analysis. The data was first corrected for slice acquisition time (interleaved) and motion (MCFLIRT in FSL), high-pass filtered at 90 Hz, and spatially smoothed using a 5-mm full-width half-maximum Gaussian filter.

Afterwards, the fMRI data were submitted to ART, alongside motion parameters derived from MCFLIRT, for detecting outliers in the time series. These outliers were determined based on both global signal and motion measures. Threshold for absolute global signal outlier was 3.0. Composite motion measures, i.e., voxel displacement resulting from the combined effect of the individual translation and rotation displacement measures, were used. Threshold for motion estimates was 1.0 mm, and scan-to-scan motion was used to determine specific time points in the time series that have outlying values.

The two groups (separately tested for baseline and follow-up of the indoor-outdoor task as well as the object-scene task) were compared regarding motion parameters (mean relative and mean absolute motion and number of artifacts detected by ART). The two groups did not differ in any of the motion parameters (all |t| < 1.1, p > .29).

General linear modeling: First level analysis. Individual first-level analyses were then conducted (separately for each task) using general linear modeling (FSL FEAT). Time-series were modeled with a gamma hemodynamic response function. The list of outliers derived from ART were modeled as confound events in the first-level analyses. In the indoor-outdoor task, a separate model

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE was calculated for baseline and follow-up. For each time point, 3 types of events were modeled: remembered scenes (duration: 3 s from stimulus onset), forgotten scenes (duration: 3 s from stimulus onset), and responses (duration: 0 s from response onset). Contrasts for positive subsequent memory effects (greater activation for remembered than for forgotten trials) and for negative subsequent memory effects (smaller activation for remembered than for forgotten trials) were calculated. Second-level analyses were conducted to contrast baseline and follow-up for longitudinal changes in positive subsequent memory and negative subsequent memory effects using fixed effects. This analysis was conducted within-participant.

For the object-scene task, 5 types of events were modeled: remembered congruent scenes (duration: 3 s from stimulus onset), remembered incongruent scenes (duration: 3 s from stimulus onset), forgotten congruent scenes (duration: 3 s from stimulus onset), forgotten incongruent scenes (duration: 3 s from stimulus onset), and responses (duration: 0 s from response onset). As in the indooroutdoor task, contrasts for positive subsequent memory effects (greater activation for remembered than for forgotten trials) and for negative subsequent memory effects (smaller activation for remembered than for forgotten trials) were calculated separately for congruent and incongruent trials. Second-level analyses were conducted to assess differences in positive subsequent memory for congruent versus incongruent object-scene pairs using fixed effects. This analysis was conducted within-participant.

The functional data of each child were coregistered to her or his structural image (boundarybased registration in FSL) and then coregistered with a sample-specific common space (12 degrees of freedom in FSL FLIRT). This sample-specific template was created from T1 images of our sample using the nonlinear-registration ANTS program (Avants et al., 2011), following the iterative procedures of Sanchez et al., (2012).

General linear modeling: Group analysis. Group analyses were conducted using betweensubject mixed-effects analyses (FLAME1 in FSL FEAT) on the second-level contrasts described above. We tested for greater activation in the transition group than in the non-transition group, and vice versa.

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE Z-statistic images were thresholded at a voxel-wise threshold of z > 2.6, with a FWE-corrected cluster threshold of p < 0.05. Finally, cluster maps from group analyses were registered to Montreal Neurological Institute (MNI) space in order to better compare the sample-specific activation maps with the literature and to provide the coordinates of peak voxels in the zstat maps.

Results

Behavioral results

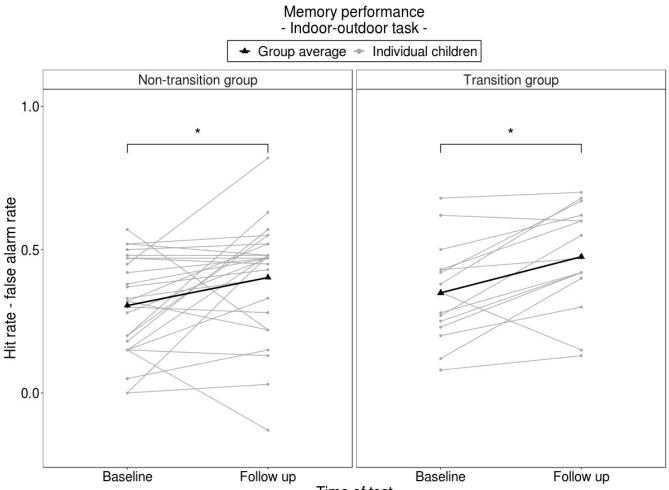
Indoor-outdoor task. The time x group ANOVA on Pr-values showed that children's memory performance increased from baseline (average Pr = .32; SD = .17) to follow-up (average Pr = .43; SD = .20). This was reflected in a significant main effect of time, F(1, 39) = 14.33, p < .001, $\eta_p^2 = .08$. There were no differences between the transition and the non-transition group, F(1, 39) = 1.30, p > .26, $\eta_p^2 = .02$, neither was there an interaction, F < 1 (see Fig. 3a). No significant differences were revealed in the analysis of d' (all F < 1).

Object-scene task. The congruency by group ANOVA on Pr-values showed that children's memory performance was higher for congruent object-scene pairs (average Pr = .56; SD = .14) than for incongruent object-scene pairs (average Pr = .50; SD = .14). This was reflected in a significant main effect of congruency, F(1, 52) = 18.70, p < .001, $\eta_p^2 = .04$. There were no differences between the transition and the non-transition group, F(1, 52) = 1.71, p > .19, $\eta_p^2 = .03$, neither was there an interaction, F(1, 52) = 2.20, p > .14, $\eta_p^2 = .01$ (see Fig. 3b). The congruency by group ANOVA on d' showed again that children's memory performance was higher for congruent object-scene pairs (average d' = 1.86; SD = 0.54) than for incongruent object-scene pairs (average d' = 1.71; SD = .58). This was reflected in a significant main effect of congruency, F(1, 52) = 17.75, p < .001, $\eta_p^2 = .02$. There were no differences between the transition and the non-transition group, F(1, 52) = 1.245, p > .12, $\eta_p^2 = .04$, neither was there an interaction, F(1, 52) = .02.

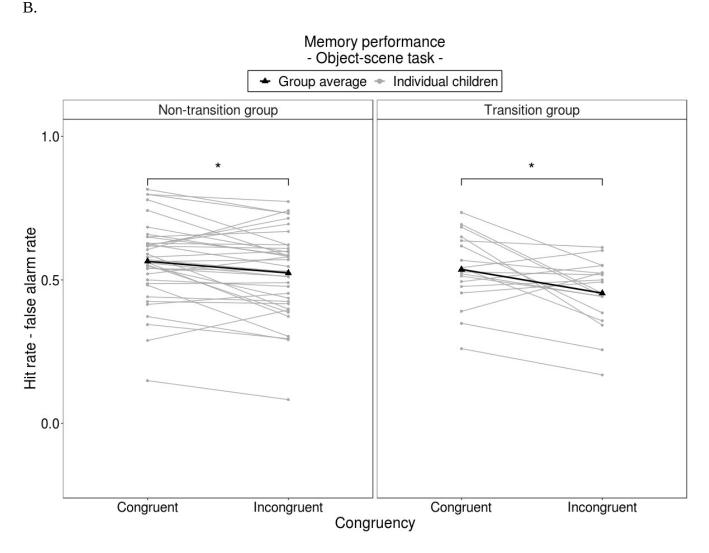
Figure 3.

Behavioral performance (hits-false alarm rates).

A.



Time of test



Note.

a. Indoor-outdoor task performance is depicted for baseline and follow-up, separated by group. In both groups, memory performance increased over time (approximately one year). The two groups showed similar levels of memory performance across time.

b. Object-scene task performance is depicted for congruent and incongruent items, separated by group.In both groups, congruent objects were better remembered than incongruent objects. The two groups showed similar levels of memory performance across conditions.

fMRI results

Positive subsequent memory effects. In the indoor-outdoor task, positive subsequent memory effects were assessed at baseline and follow-up. At baseline, positive subsequent memory effects were

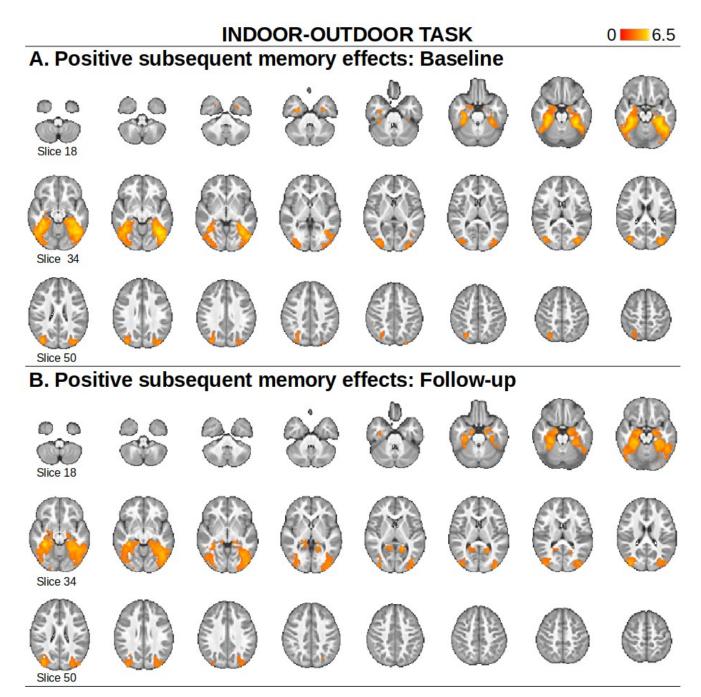
NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE identified in bilateral medial temporal lobe including hippocampus and parahippocampal gyrus, as well as lateral occipital cortex (see Fig. 4a and Table 1a). The pattern at follow-up was very similar to the pattern at baseline (see Fig. 4b and Table 1b). A whole-brain analysis examining the effect of time (baseline vs. follow-up) on positive subsequent memory revealed no clusters that survived the predefined threshold. There was also no difference between the transition group and the non-transition group at either time point.

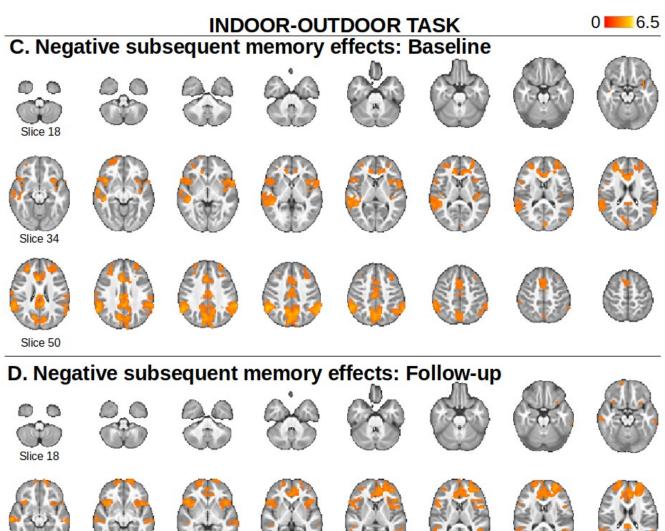
These results were complemented by the data of the object-scene task. Positive subsequent memory effects, for both groups combined, were similar to the results of the indoor-outdoor task, with enhanced activation in bilateral medial temporal lobe including hippocampus (see Fig. 5a and Table 1c), as well as lateral occipital cortex (see Fig. 5a and Table 1c). There was no significant difference between the transition group and the non-transition group.

Figure 4.

Positive subsequent memory effects and negative subsequent memory effects of the indoor-outdoor task

(*n* = 41, threshold *z* > 2.6, *p* < 0.05).







Note. The clusters are depicted in the sample-specific template space (see details in Table 1 and 2). The left hemisphere is depicted right, and the right hemisphere is depicted left. Every second slice was selected so that the slices depict the activation maps most clearly.

a. Positive subsequent memory effects (remembered > forgotten) at baseline, collapsing across groups.

b. Positive subsequent memory effects (remembered > forgotten) at follow-up, collapsing across

c. Negative subsequent memory effects (remembered < forgotten) at baseline, collapsing across groups.

d. Negative subsequent memory effects (remembered < forgotten) at follow-up, collapsing across

groups.

Table 1

Positive subsequent memory effects and memory congruency effects with threshold z > 2.6, p < 0.05.

Area	Hemis- phere	Number of voxels	Peak z- value	Cluster peak (MNI space)				
				х	у	Z		
A. Positive subsequent memory effects. Indoor-outdoor task at baseline.								
Hippocampus, parahippocampal gyrus, fusiform cortex, lateral occipital cortex	right	4629	6.06	30	-12	36		
Hippocampus, parahippocampal gyrus, fusiform cortex, lateral occipital cortex	left	4303	6.48	-25	-3	-38		
B. Positive subsequent memory effects. Indoor-outdoor task at follow-up.								
Hippocampus, parahippocampal gyrus, lingual gyrus, fusiform cortex, lateral occipital cortex	left	4874	5.04	-29	-32	-27		
Hippocampus, parahippocampal gyrus, lingual gyrus, fusiform cortex, lateral occipital cortex	right	3969	6.07	36	-16	-29		
C. Positive subsequent memory effects. Object-scene task.								
Hippocampus, inferior temporal gyrus	left	1073	5.12	-27	-3	-38		
Hippocampus, temporal fusiform gyrus	right	707	4.97	30	-12	-36		
Inferior temporal gyrus, lateral occipital cortex	right	316	4.17	49	-50	-19		
D. Memory congruency effects. Object-scene task	•							
Lingual gyrus, cuneus, precuneus	left, right	574	3.80	-1	-63	-8		
Postcentral gyrus	left, right	555	3.83	-5	-36	52		
Paracingulate gyrus, anterior cingulate gyrus	left, right	231	3.87	6	29	22		
Precentral gyrus, superior frontal gyrus	left, right	208	3.79	2	-19	57		

Note. Overview over fMRI results. The cluster sizes are based on the sample-specific template. For

better comparison with the adults literature, the coordinates of the cluster peaks in the z-values are

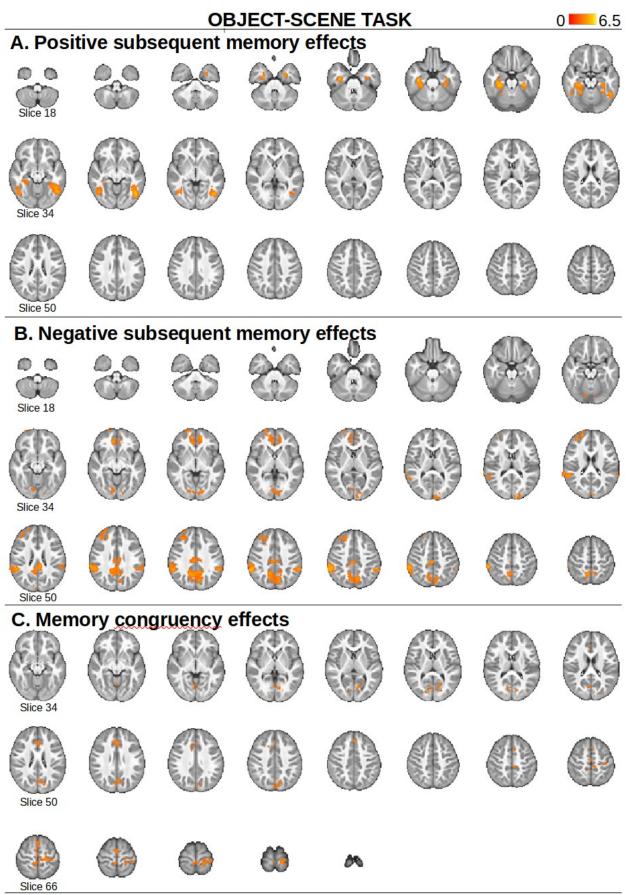
reported in MNI space.

Negative subsequent memory effects. In the indoor-outdoor task, negative subsequent memory effects were assessed at baseline and follow-up. At baseline, negative subsequent memory effects were isolated in a large cluster along the midline (from occipital pole to bilateral frontal pole), as well as bilateral activation in supramarginal and angular gyrus and bilateral activation in clusters including the insula and the inferior frontal gyrus (see Fig. 4c and Table 2a). The pattern at follow-up was again very similar to the pattern at baseline, with activation along the midline, as well as bilateral activation in supramarginal and bilateral activation in clusters including the insula and the inferior frontal gyrus and bilateral activation in clusters including the insula and the inferior frontal gyrus and bilateral activation in clusters including the insula and the inferior frontal gyrus (see Fig. 4d and Table 2b). A whole-brain analysis examining the effect of time (baseline vs. follow-up) on negative subsequent memory revealed no clusters that survived the predefined threshold. There was also no difference between the transition group and the non-transition group at either time point.

These results were complemented by the data of the object-scene task. Negative subsequent memory effects, for both groups combined, were similar to the results of the indoor-outdoor task, with activation along the midline and frontal poles, as well as bilateral activation in supramarginal and right angular gyrus (see Fig. 5b and Table 2c). There was no significant difference between the transition group and the non-transition group.

Figure 5.

Positive subsequent memory effects, negative subsequent memory effects, and memory congruency effects of the object-scene task (n = 54, threshold z > 2.6, p < 0.05). Participants did this task only at follow-up.



Note. The clusters are depicted in the sample-specific template space (see details in Table 1 and 2). The

left hemisphere is depicted right, and the right hemisphere is depicted left. Every second slice was

selected so that the slices depict the activation maps most clearly.

a. Positive subsequent memory effects (remembered > forgotten), collapsing across groups.

b. Negative subsequent memory effects (remembered < forgotten), collapsing across groups.

c. Memory congruency effects (positive subsequent memory effects for congruent object scene pairs >

positive subsequent memory effects for incongruent object-scene pairs), collapsing across groups.

Table 2

Negative subsequent memory effects.

Area	Hemis- phere	Number of voxels		Cluster peak (MNI space)					
				X	У	Z			
A. Negative subsequent memory effects. Indoor-outdoor task at baseline.									
Precuneus, cuneus, occipital pole, cingulate cortex, paracingulate cortex, frontal pole	left, right	7101	5.03	34	53	-9			
Supramarginal gyrus, angular gyrus, superior temporal gyrus	right	3142	5.34	62	-24	-13			
Supramarginal gyrus, angular gyrus	left	1567	4.92	-61	-67	15			
Insula, inferior frontal gyrus, operculum	left	988	4.13	-35	5	-15			
Insula, inferior frontal gyrus, operculum	right	673	4.68	45	5	-10			
B. Negative subsequent memory effects. Indoor-outdoor task at follow-up.									
Anterior cingulate cortex, paracingulate cortex, frontal pole	left, right	4360	4.59	-18	63	-10			
Precuneus, cuneus, occipital pole, posterior cingulate cortex	left, right	3722	5.18	2	-93	16			
Supramarginal gyrus, angular gyrus, superior temporal gyrus	right	2800	4.82	64	-23	-16			
Supramarginal gyrus, angular gyrus, middle temporal gyrus	left	2644	5.60	-66	-32	-18			
Insula, inferior frontal gyrus, operculum	left	965	4.29	-29	18	-19			
Middle frontal gyrus, frontal pole	right	912	4.27	25	58	17			
Insula, inferior frontal gyrus, operculum	right	850	4.40	36	18	-14			
Frontal pole	right	338	3.67	14	64	-15			

Precuneus, posterior cingulate cortex	left, right	2344	4.51	-3	-43	22		
Supramarginal gyrus, angular gyrus	right	1135	5.04	67	-40	9		
Frontal pole	right	599	3.96	36	47	21		
Lingual gyrus, occipital fusiform gyrus	left, right	477	3.75	15	-80	-18		
Anterior cingulate gyrus, paracingulate gyrus, frontal pole	right	439	4.10	10	42	-7		
Supramarginal gyrus	left	393	4.06	-65	-45	20		
Anterior cingulate gyrus, paracingulate gyrus	left	216	4.48	-5	39	-4		
<i>Note</i> . Overview over fMRI results. The cluster sizes are based on the sample-specific template. For								

C. Negative subsequent memory effects. Object-scene task

better comparison with the adults literature, the coordinates of the cluster peaks in the z-values are reported in MNI space.

Memory congruency effect. In the object-scene task, we were further interested in the modulation of positive subsequent memory effects by congruency. For both groups combined, greater positive subsequent memory effects for congruent than for incongruent object-scene pairs were revealed in a variety of frontal and parietal midline clusters (see Fig. 5c and Table 1d). There was no significant difference between the transition group and the non-transition group.

Discussion

In the current study, we aimed to investigate the development of episodic memory and its neural substrates between the ages of 5 and 6. Since this is the age range when many children transition to formal schooling, we also investigated the influences that schooling might have on episodic memory development. We found a significant increase of memory performance across those 12 months. However, this increase was not influenced by schooling. In line with these data, we found evidence that congruent object-scene pairs were remembered better than incongruent object-scene pairs in both groups, indicating a beneficial effect of prior knowledge that is independent of schooling.

Regarding the neural correlates of children's episodic memory, our results reveal a similar

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE pattern of positive subsequent memory effects across both tasks and time points. In line with our hypotheses, we found consistent positive subsequent memory effects in the MTL. However, in contrast to findings in older children and adults (e.g., Kim, 2011), we did not find any positive subsequent memory effects in the PFC. We also did not find the expected increase in PFC activation over time, which we hypothesized to be stronger for the transition group than for the non-transition group. Our results, thus, suggest that successful memory formation in 5-6-year-olds relies heavily on the MTL, and less on the PFC than previously thought. This finding held whether or not children went to school.

While behavioral memory performance improved, we did not observe a significant change in the underlying neural signature. We thus interpret the data such that encoding mechanisms did not qualitatively change within the tested time, even though participants doubtlessly acquired a lot of new knowledge during this period. The performance improvement on the behavioral level may also be due to differences in retrieval, during which we did not collect fMRI data. Alternatively, the performance improvement may also be related to a more efficient use of the encoding mechanisms (in other words, no qualitative changes) at follow-up compared to at baseline (see also Brod et al., 2016). Interestingly, the findings dovetail with data reported by Ofen et al. (2007) that show little engagement of the PFC for positive subsequent memory in slightly older children, with similar involvement of the MTL across age groups..

Testing subsequent memory effects in 5-6-year-old children is a relatively novel undertaking. Findings of our study, thus, constitute an important building block to further understand the development of episodic memory mechanisms in children. They suggest that, already at age 5, the hippocampus has reached a state of relative functional maturity. These results are in line with the propositions of the two-component framework of episodic memory (Shing et al., 2010). According to this framework, the strategic component of episodic memory is related to activity in the PFC and develops later in childhood than the associative component which is related to activity in the MTL. This corroborates also findings on the anatomical development of the PFC which happens later than the

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE development of the MTL (Giedd et al., 1999; Gogtay et al., 2006; Huttenlocher, 1979; Sowell et al., 2002, 2004). The current data also complement nicely the cross-sectional findings in older children by Ofen et al. (2007). They did not find an age trend for the MTL, which is consistent with our stable MTL activation across time. Note that the same type of explicit item-encoding task was used in both the current study and the study by Ofen et al. (indoor-outdoor task), while age-related increases in hippocampal activation were found for associative memory in different tasks (Geng et al., 2019; Ghetti et al., 2010). Such differences across studies may reflect differences in encoding of item and associative information. The youngest children tested by Ofen et al. (2007) were 8 years old and they showed much smaller positive subsequent memory effects in PFC compared to younger adults. The children we tested here were 5-6 years old and our data did not reveal increased PFC activation for remembered items (while showing robust positive subsequent memory effects in the MTL). Our data is, thus, in line with the notion of a linear relationship between age and positive subsequent memory effects in PFC. Of course, one has to be careful when interpreting the null finding in the PFC. Our total sample sizes were comparably high (n = 41 in the indoor-outdoor task, n = 54 in the object-scene task), however, and we observed robust effects in the MTL which stand in contrast to the absence of activation in the PFC..

In addition to positive subsequent memory effects, we also investigated negative subsequent memory effects. In line with previous research, the contrast revealed several brain areas, such as midline, temporal, and parietal areas. These brain areas are often discussed as being part of the default network. The pattern of results is in line with what has been found in young adults and suggests that successful memory encoding may be facilitated when the activation of the default network is decreased (Daselaar et al., 2004; Otten & Rugg, 2001). We neither found a change from baseline to follow-up here nor an effect of schooling in these brain regions. Negative subsequent memory effects have been shown to increase with age from childhood to adulthood in a cross-sectional study (Chai et al., 2014). Here, we did not find a change from 5 to 6 years of age. This may be due to the comparably small time

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE span used in the current study. Changes in negative subsequent memory effects may change more strongly later in development.

We did not find a significant effect of schooling on memory performance nor on its neural correlates in the current study. In general, the increase in memory performance from baseline to followup was rather small, and no significant changes over time were observed in the fMRI data. While one can assume that children acquire an impressive amount of knowledge and skills from 5 to 6 years of age, the way they learn, including its neural underpinnings, does not seem to undergo drastic changes. This has to be seen in the specific context of the study, as the subsequent memory effects investigated here target encoding of new information and thus highlight only one of many aspects of learning and memory. Our study suggests that at 5 years of age, children are already equipped with a memory system that allows them to encode a wide range of new information, including the contents of the school curriculum in the first year. Put differently, one could interpret that teaching in school, as formal and different it seems from the way children learn before, matches the encoding abilities that children already have when they enter school. It remains unclear, however, if formal schooling alters memory mechanisms at an older age. The school cutoff-design is a useful tool for investigating the role of schooling during the first year of school, but unfortunately it cannot help to disentangle the role of brain maturation and schooling at older ages without further longitudinal follow up.

We also investigated the role of knowledge on episodic memory. Our data suggest that congruent scene-objects pairs are better remembered than incongruent ones, and this is also reflected in greater positive subsequent memory effects for congruent than for incongruent items. The memory congruency effect was supported by brain areas along the midline. This finding is in line with a considerable amount of data on memory congruency effects and suggests that prior knowledge plays a strong, beneficial role already in young children (see Brod & Shing, 2019). Even though we carefully selected material that was part of the first year curriculum, the transition group and the non-transition group showed similar behavioral and fMRI results. A potential explanation for this null finding is that

NEURAL CORRELATES OF MEMORY ENCODING IN KINDERGARTEN AND FIRST GRADE the advance in knowledge through schooling in the first grade may not have been strong enough for the selected topics, or that our task did not tap sufficiently into the increased knowledge in school.

The current results suggest that episodic memory and its neural substrates do not undergo dramatic changes from 5-6 years of age, and that they are not characterized by schooling. This result stands in some contrast to findings on cognitive control (see Brod et al., 2017; Burrage et al., 2008; Roebers et al., 2011). Brod and colleagues (2017) found schooling to have a positive impact on the longitudinal increase in task-related activity in PPC, a region implicated in attentional control, and the extent of increase in PPC was related to behavioral improvement in an independent cognitive control task. Importantly, however, the schooling-related increases were restricted to PPC, and not observed in PFC where effects would be expected based on the adult literature (Brod et al., 2017). This is in line with the current results such that we did not find activity in PFC to be altered due to schooling. At this young age, hence, PFC may still be relatively immature and thus not respond plastically to changes in the environment.

Considering the findings on cognitive control and memory together, results provide a more comprehensive picture of the role of one year of schooling on changes in children's cognitive and neural mechanisms. While children show clear increases in their cognitive control abilities, their item memory does not seem to be substantially altered due to schooling. A potential reason for this is that, in Germany, kindergartens are play-oriented, which means that children are not required to sit still and sustain their attention to a teacher for a longer period of time. Entering formal schooling, thus, means a strong increase in cognitive control demands for children, which sculpts the corresponding neural mechanisms. Conversely, children may already learn at high rates while in kindergarten despite being play-oriented, which means that memory demands might not be altered due to school entry. Memory encoding, including its neural underpinnings, may, thus, change rather gradually across the first years of schooling, at least in settings such as those of the current study.

Limitations

The results of the current study have to be carefully evaluated regarding some limitations. Most notably, even though the overall sample size was relatively high for an fMRI study with children (n = 41 in the indoor-outdoor task, n = 54 in the object-scene task), splitting the participants into the two groups resulted in small sample sizes. This means that the study was underpowered when it comes to detecting differences between the transition and non-transition groups. The null findings regarding schooling effects obtained in the current study have to be interpreted with caution since they might be detected with larger samples. The small and unequal group sizes partly resulted from the fact that some parents wanted their children to stay in kindergarten one more year even though the children were born shortly before the cut-off date. This resulted in a small transition group (n = 15 in the indoor-outdoor task, n = 18 in the object-scene task). To compensate for the low power of detection a group difference or interaction, a relatively liberal threshold for voxel-level statistics was used. With a more stringent threshold (z = 3.1), the results remain similar, except for the congruency by memory interaction in the object-scene task which resulted in smaller clusters being below threshold. However, the results reported in this study were largely consistent with previous findings in children (Brod & Shing 2019).

In addition, school structures and curricula vary significantly between countries, which means that it is unclear whether the results generalize beyond Germany. One should also keep in mind that we tested for memory encoding of relatively simple material that did not require much binding. More complex material may have recruited additional brain areas (e.g., Geng et al., 2019; Ghetti et al., 2010). In addition, other mnemonic processes such as cued-based recall were not assessed either.

Conclusion

In sum, our results show that memory encoding at the age of 5-6 years is strongly supported by the MTL. Unlike adults, the children at this age rely less on PFC than on MTL for successful memory encoding, suggesting that the linear relationship between age and PFC reported in the developmental literature kicks in at a later age. Finally, at least in the first school year, formal education does not seem to have a strong effect on episodic memory and the neural substrates of memory formation.

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