Differentiation of functional networks during long-term memory retrieval in children and adolescents

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A B S T R A C T

The processes that characterize the neural development of long-term memory (LTM) are largely unknown. In young adults, the degree of activation of a single large-scale memory network corresponds to the level of contextual detail involved; thus, differentiating between autobiographical, episodic, and semantic retrieval. In contrast to young adults, children and adolescents retrieve fewer contextual details, suggesting that they might not yet engage the entire memory circuitry and that this brain recruitment might lack the characteristic contextual differentiation found in adults. Twenty-one children (10–12 years of age), 20 adolescents (14–16 years of age), and 22 young adults (20–35 years of age) were assessed on a previously validated LTM retrieval task, while their brain activity was measured with functional magnetic resonance imaging. The results demonstrate that children, adolescents, and adults recruit a left-lateralized subset of the large-scale memory network, comprising semantic and language processing regions, with neither developmental group showing evidence of contextual differentiation within this network. Additionally, children and adolescents recruited occipital and parietal regions during all memory recall conditions, in contrast to adults who engaged the entire large-scale memory network, as described previously. Finally, a significant covariance between age and brain activation indicates that the reliance on occipital and parietal regions during memory retrieval decreases with age. These results suggest that both children and adolescents rely on semantic processing to retrieve long-term memories, which, we argue, may restrict the integration of contextual detail required for complex episodic and autobiographical memory retrieval.

1. Introduction

Declarative memory allows us to re-experience the past, learn about the world, develop a sense of self, and make predictions about the future. Three types of long-term memory (LTM) are commonly distinguished: semantic memory (SM; general knowledge), episodic-laboratory memory (EM; non-personal, event-related), and autobiographical memory (AM: personal, event-related; Cabeza and St Jacques, 2007; Tulving, 1972). There has been considerable debate whether SM, EM, and AM engage independent neural systems (Cipolotti and Maguire, 2003; Nyberg et al., 2002; Tulving, 1987; Yonelinas, 1994) or whether all three types of declarative memory are subserved by a single system (Baddeley, 1984; Burianová and Grady, 2007; Burianová et al., 2010; Maguire and Mummery, 1999; Rajah and McIntosh, 2005; St-Laurent et al., 2011).

Evidence for the single system view comes from functional magnetic resonance imaging (fMRI) studies that have demonstrated that SMs and EMs recruit functionally overlapping regions of the brain (Cabeza and Moscovitch, 2013; Nyberg et al., 2003; Rajah and McIntosh, 2005) and that the retrieval of AMs, EMs, and SMs is subserved by the same functional brain network, known as the common memory network (Burianová and Grady, 2007; Burianová et al., 2010; St-Laurent et al., 2011). The common memory network comprises activations in the middle temporal gyrus (MTG), inferior frontal gyrus (IFG), angular gyrus (AG), and caudate nucleus, bilaterally, as well as the left superior temporal gyrus (STG), middle frontal gyrus (MFG), lingual gyrus (LG), posterior cingulate gyrus, supplementary motor area (SMA), hippocampus, and thalamus. The neural overlap is reflected in a conceptual overlap among the subtypes of declarative memory, as SM is rarely context-free, EM is seldom devoid of personal relevance, and both EM and AM require the recall of semantic content (Baddeley, 1984; Gilboa, 2004; Rajah and McIntosh, 2005; Westmacott and Moscovitch, 2003).

In line with this view, it has been shown that declarative memories

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can be differentiated by the amount of contextual detail that is retrieved and that their recall can be characterized along a continuum of contextualization (Levine et al., 2002; Marian and Neisser, 2000). On this continuum, EMs and AMs are located towards the highly contextualized end because their recall involves the integration of more contextual detail and complex features (*e.g.*, emotion and social context). In contrast, SMs form the weakly contextualized end of the continuum because their recall mainly involves context independent facts, general knowledge, and objective features. Evidence shows that healthy young adults exhibit significant contextual differentiation in the recruitment of the common memory network, *i.e.*, neural activity within the memory network increases as the memory involves more contextual details (Burianová and Grady, 2007). Critically, studies from healthy ageing further demonstrate that this contextual differentiation is functionally relevant; whilst older adults do recruit the common memory network during AM, EM, and SM retrieval, they show significant contextual *de*differentiation, *i.e.*, they recruit the common memory network to the same degree across all three memory subtypes, regardless of their contextual complexity (St-Laurent et al., 2011). This lack of contextual differentiation within the common memory network is related to a reduction in contextual detail of the retrieved memories and increased reliance on the semantic content of autobiographical and episodic memories during recall (Davidson and Glisky, 2002; Levine et al., 2002; St Jacques and Levine, 2007).

The deficits associated with contextual *de*differentiation observed in healthy ageing resemble the developmental issues in long-term memory retrieval observed in children and adolescents. Evidence shows that performance on verbal episodic memory tasks is significantly poorer in 10-year-old children compared to adults (Finn et al., 2016). Additionally, although accurate autobiographical retrieval has been demonstrated in children as young as 8 years, children aged 4–8 years are generally not able to accurately retrieve the temporal order of autobiographical memories (Friedman, 1992). More recent evidence further demonstrates that, in children, age is associated with increased specificity of autobiographical content and a higher number of memories recalled (Nuttall et al., 2014). Together, this evidence demonstrates that children show specific difficulties recalling declarative memories that are highly contextualized and that the ability to integrate contextual detail with semantic content during AM and EM recall increases with age. Declarative memory involves the integration of many cognitive processes, including attention, language, visual and spatial perception, mental imagery, emotion, and error monitoring (Burianová et al., 2010; Levine et al., 2002; Grady et al., 2015; Ullman, 2004). Developmentally, these cognitive processes have heterogeneous trajectories (Erikson, 1965; Inhelder and Piaget, 1964; Vygotsky, 1978), which viably restrict the binding and integration of high levels of contextual detail during long-term memory recall. We suggest that low-context SMs, or schemas, provide a foundation for EM and AM retrieval. Schemata are hierarchically organized units of knowledge that start with a specific object, idea, or thought, and become more generalized through the process of assimilation and accommodation of new information (Bartlett and Kintsch, 1995; Piaget, 1973). Similarly, SM is memory of specific facts and isolated features, whereas EMs and AMs require the integration and assimilation of greater contextual detail. Just as the development of schemata is driven by experience and prior knowledge, so too is long-term memory. Thus, similarly to older adults who show context *de*differentiation in AM and EM recall, we suggest that in children, the common memory network is as yet *un*differentiated by context and that functional differentiation is associated with age and higher-level cognitive development.

To date, no research has investigated whether children and adolescents engage the common memory network to the same extent as young adults and whether their retrieval of SM, EM and AM is accompanied by a differential recruitment of the common memory network. While previous studies have shown that semantic recall in children and adults relies on the same brain structures, such as the left inferior frontal gyrus and left middle and superior temporal gyri (Gaillard et al., 2000; Moore-Parks et al., 2010), very little is known about the brain activation underlying AM and EM prior to adulthood. The purpose of the present study was to investigate the functional organization of declarative memory and contextual differentiation in children and adolescents, compared to young adults.

Typically, the study of autobiographical and episodic memory in children involves paradigms that are based on recognition (Cabeza et al., 2003; Naveh-Benjamin et al., 2003) or autobiographical interviews (Levine et al., 2002; Crane and Goddard, 2008). Autobiographical interviews are useful in determining whether children *can* recall autobiographical memories, but do not allow for a comparison of memories with different contextual detail. Similarly, recognition-based assessments involve simple, isolated (*e.g.*, yes/no) judgments during semantic, object, or face recognition, which do not require retrieval or integration of contextual detail and are not typical of day-to-day semantic retrieval. Thus, in this study, we used a previously validated long-term memory task (Burianová and Grady, 2007; Burianová et al., 2010; Grady et al., 2015; St-Laurent et al., 2011), which was designed specifically to allow for a direct comparison of SM, EM and AM retrieval, and adapted it for use with children and adolescents.

The aim of this study was to examine whether and how children and adolescents engage the common memory network during AM, EM, and SM retrieval in comparison to young adults. Children and adolescents differ significantly from each other in their ability to understand emotions and think introspectively, which may be a result of differences in social independence (Nelson et al., 2005; Steinberg, 2008). It could be argued that independence encourages introspection, self-reflection, emotion regulation, and social competency (McRae et al., 2012; Steinberg, 2005; Yurgelun-Todd, 2007); thus, facilitating the differentiation of declarative memory subtypes by context. Adolescence is also a critical time for cognitive development and maturation of key limbic structures (*i.e.*, amygdala, hippocampus, parahippocampus, entorhinal cortex, and cingulate cortex), which are thought to have a critical role in processing emotional and social stimuli (Adolphs, 2003; Smith et al., 2013). Due to the interaction of functional and structural development, it is thus feasible to suggest that adolescents, compared to children, would show stronger activation of and contextual differentiation within the common memory circuitry.

We hypothesized that both children and adolescents would engage the common memory network during LTM retrieval. Due to their reliance on semantic content in AM and EM retrieval, we further expected that children would not demonstrate contextual differentiation, in contrast to adolescents who would show signs of contextual differentiation (*i.e.*, engagement of the memory network significantly more during AM than SM retrieval). Finally, investigating the relationship between functional brain activation during declarative memory retrieval and age as a covariate, we predicted that increased age would be associated with greater bilateral activation of top-down components (*e.g.*, fronto-parietal regions) and reduced activity in semantic and verbal components (*i.e.*, temporal lobes) of the common memory network.

2. Methods

2.1. Participants

Sixty-three right-handed participants were recruited from the general public in three age brackets: children aged 10–12 years (n = 21; M_{age} = 10.90 years; 8 females), adolescents aged 14–16 years (n = 20; M_{age} = 15.25 years; 11 females), and young adults aged 20–35 years (n = 22; M_{age} = 26.71 years; 11 females). One adult was excluded due to a technical issue with the response collection. All participants were healthy, screened for MRI compatibility and presented with no visual impairments or history of mental illness, disease, or trauma. Informed consent was obtained from all participants or, in the case of participants under 18 years of age, consent was additionally obtained from their parent/legal guardian. The study was approved by the University of

Queensland Human Research Ethics Committee. All participants were reimbursed $30 AUD.

2.2. Procedure

Participation in the study involved a 15-min training session, a 1-h magnetic resonance imaging (MRI) session, and a 30-min session, during which participants filled out a questionnaire pertaining to the retrieval of specific autobiographical memories in the scanner. To confirm that they engaged with the task and to gauge the content of each retrieved memory, participants were asked to briefly describe each autobiographical memory retrieved during the scanning session. Participants were asked to recall which response they selected inside the scanner and write a few sentences describing the memory, when it occurred and where it took place. During the training session, the experimenter explained the task and provided examples of each experimental condition. During the imaging session, a structural MRI, three fMRIs, and a diffusion weighted image (DWI) were obtained. The results of the diffusion imaging data will be reported elsewhere. The fMRI task was presented using E-Prime (Version 2), standard edition. Responses were made on a bimanual 2 × 2 fibre optic response pad. Participants were instructed to use their right index finger for button one, right middle finger for button two, and left index finger for button three.

2.3. Experimental design

The declarative memory task used in this study was originally developed by Burianová and Grady (2007), but was adapted for the use with children. The task design generally involves the presentation of a cue image for 4 s, followed by a 1 s inter-stimulus interval, a retrieval cue screen for 8 s, during which participants retrieve different long-term memories, and a jittered 800–1200 ms inter-trial interval (jitter average = 1 s) (see Fig. 1). Twenty-five images of everyday life events (e.g., the beach or a classroom) were used as visual cues for memory retrieval. The stimuli used in this study were different from the original task to ensure that children from the age of 10 years could relate to them

with their everyday experience. Furthermore, the stimuli were culturally specific to the Australian population that was tested (see Supplementary Table 1). For the control stimuli, 5 images were randomly selected from the set of 25 and scrambled using Adobe Photoshop. This rendered the image meaningless whilst keeping the perceptual input similar to the memory retrieval images. A description of all images and associated questions and response options can be viewed in Supplementary Table 1.

The task was presented across three functional runs, in each run the same 25 stimulus images and 5 control images were presented. However, the type of memory retrieval was manipulated by adjusting the response screen to cue the retrieval of either an AM (run 1), SM (run 2) or EM (run 3). In the autobiographical run, participants were asked to think about their own personal experience and then rate their AM based on the clarity of their memory retrieval (1 = very clear, 2 = somewhat clear, or 3 = not at all clear). A response of "1" or "2" was categorized as successful retrieval. The questions in the semantic run related to general knowledge and factual information and the episodic run required participants to answer questions about the content of the photographs presented as cue images (see Fig. 1). In the control trials, the presentation of a scrambled stimulus was followed by an arbitrary instruction unrelated to the stimulus itself (e.g., "Press the button for 'Y'"). During semantic, episodic, and control trials either button 1 or 2 was used for the correct answer and 3 corresponded to "I don't know". Response latency (defined as the start of the question screen) and successful retrieval were recorded, and only successfully retrieved responses were included in the analysis.

In the original declarative memory task (Burianová and Grady, 2007), the type of memory and stimulus order were randomized within each run. In this study, the stimulus order, but not the type of memory, was randomized within each run and all participants retrieved AM, SM, and EM in the first, second, and third run respectively (see Fig. 1). This adaptation not only reduced the complexity of the task for the children, but also had several important implications. Presenting the episodic condition last ensured that the images were encoded into long-term rather than working memory. The instructions for the autobiographical condition differed slightly from the semantic and episodic conditions; hence, it was important to present this condition first for clarity.

This task was adapted from Burianová & Grady (2007)
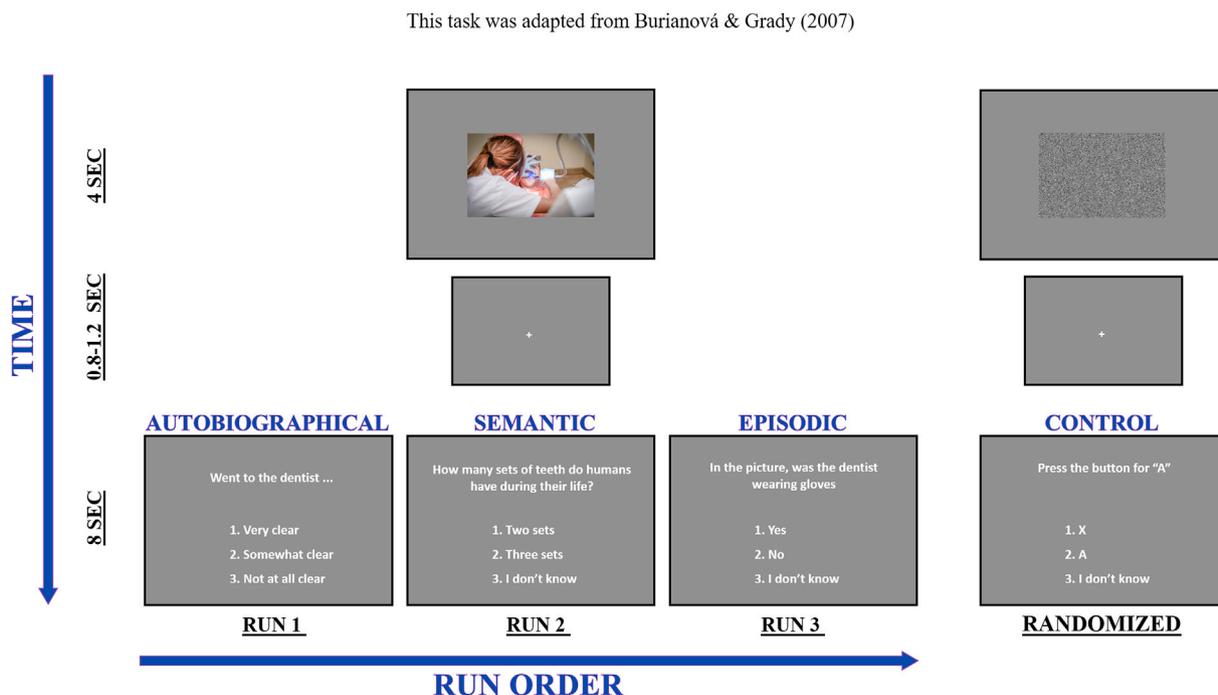
Fig. 1. In each trial participants viewed one image (4 s) followed by a fixation cross (jittered: 800–1200 ms, average of 1 s) and were then asked a question with three responses options (8 s). Each run of the task contained different types of memory questions; however, the same stimuli were presented. This task was adapted from Burianová & Grady, (2007).

Additionally, because the same images were used for all three conditions, it was important that participants would not prepare responses to the autobiographical condition in advance.

2.4. Image acquisition and analysis

A T1-weighted volumetric anatomical MRI was acquired for each participant (MP2-RAGE). The following parameters were used: 176 slices sagittal; 1 mm^3 isotropic volume; repetition time (TR) = 4000 ms; echo time (TE) = 2.89 ms; FOV = 256 mm. Further, diffusion-weighted images along 64 gradient directions were obtained (60 slices; $2.3 \times 2.3 \times 2.4$ mm; TR = 8600 ms; TE = 109 ms; FOV = 240 mm; b-value = 3000 s/mm^2). Functional MRIs were acquired using a T2*-weighted echo-planar image pulse sequence (45 slices, 2.5 mm slice thickness; voxel size 2.5 mm^3, TR = 3000 ms; TE = 30 ms; FOV = 190 mm; flip angle = 90°). All images for the children and adults were acquired on a 3T Siemens Magnetom Trio scanner. The images for the adolescents were acquired on an upgraded 3T Siemens Magnetom Prisma scanner (*i.e.*, the testing location remained constant, but scanner hardware was upgraded). A 32-channel head coil was used and all scanning parameters remained identical across the three age groups.

Brain activation was assessed using the blood oxygenation level-dependent (BOLD) effect (Ogawa et al., 1990). All functional images were preprocessed with Statistical Parametric Mapping software (SPM8; http://www.fil.ion.ucl.ac.uk/spm). The images were slice-time corrected, realigned to a mean image for head motion, spatially normalized to the Montreal Neurological Institute (MNI) template (voxel size 2 mm^3), and spatially smoothed with a 6 mm full width half maximum Gaussian kernel. Head motion did not exceed 2 mm in any of the data. Normalization to the MNI template has been used in numerous developmental fMRI studies with children as young as 7 years of age (Booth et al., 2005; Crone et al., 2006; Dekker et al., 2011; Howard et al., 2017; Lee et al., 2017; Schulz et al., 2004; Siffredi et al., 2017). This method has been deemed acceptable, as total cerebral volume does not significantly change after the age of 5 years (Klingberg et al., 2002; Passarotti et al., 2007; Reiss et al., 1996). Furthermore, after 6 years of age, standard normalization procedures do not lead to artefacts and the method of comparing child and adult fMRI data within a common space has been validated (Kang et al., 2003; Muzik et al., 2000).

Following preprocessing, whole-brain fMRI data from all three groups were analyzed together, using Partial Least Squares (PLS; https://www.rotman-baycrest.on.ca/index.php?section=84) analysis. Onsets were defined from the beginning of the response/question screen (Fig. 1); *i.e.*, six 3-sec TRs of data, starting at the onset of the question screen, were isolated for each condition and analyzed using event-related PLS. PLS is a model-free, multivariate analysis tool similar to principal component analysis (McIntosh et al., 2004) and based on the assumption that the neural activity underlying cognitive processes is best analyzed as the coordinated activity of groups of voxels rather than the independent activity of any single voxel (Krishnan et al., 2011; McIntosh and Lobaugh, 2004). Furthermore, one of the advantages of using an event-related PLS analysis, which also makes it highly suitable for a comparison between groups with potentially different BOLD responses, is that PLS does not model the HRF (Krishnan et al., 2011; McIntosh and Lobaugh, 2004; McIntosh et al., 2004). For this reason, any issues with age-related differences in BOLD, and by extension in HRF, would not impact the results. In brief, PLS mean-centers and then decomposes the covariance matrix between brain activity and the experimental design (or an external variable such as age) for all participants in a single analytic step, using singular value decomposition (SVD). SVD results in separate, mutually orthogonal latent variables (LVs), which describe patterns of brain activity related to the experimental design (McIntosh et al., 2004; Krishnan et al., 2011). SVD maximizes covariance in the partial least squares sense and generates a weight for each voxel, which designates its degree of covariance with the whole brain activity pattern. PLS then assesses the statistical significance of each LV using permutation testing with 500

permutations (McIntosh et al., 1996) and the reliability of the brain activity patterns for each voxel by using a bootstrapping procedure with 100 bootstraps, resulting in an estimate of the standard error, which is used to calculate the bootstrap ratio (Efron and Tibshirani, 1985). Peak voxels with a minimum bootstrap ratio of 3 are considered to be reliable (Sampson et al., 1989). In PLS, computation of LVs and corresponding brain images is conducted in a single analytic step across all voxels and participants; therefore, no correction for multiple comparisons is required (McIntosh and Lobaugh, 2004). Finally, a brain score, indicating how strongly each resulting pattern is expressed in each individual participant, is calculated by multiplying each individual data set with the whole-brain activation loadings.

2.5. Data and code availability statement

The raw data and results of this study are publicly available under a Creative Commons Attribution-ShareAlike 4.0 International Public License (CC BY-SA 4.0) in compliance with approval by the University of Queensland Human Research Ethics Committee. The raw data are available at https://openneuro.org/datasets/ds001748 and the result files are available at https://neurovault.org/collections/MFCNFLGC/.

3. Results

3.1. Behavioural performance

Successful retrieval and mean reaction time (RT) on successfully retrieved trials were analyzed using a one-way between groups (children, adolescents, adults) analysis of variance (ANOVA) on each condition of the task independently. While previous research showed differences between the conditions (Burianová and Grady, 2007), in this study only differences between groups were of interest. All means and standard deviations are presented in Table 1.

3.1.1. Reaction times

A one-way between groups ANOVA revealed no difference among the groups in RT for AM retrieval ($F_{(2,59)} = 0.57$, $p = .569$, $\eta^2 = 0.019$), suggesting that all groups spent a similar amount of time retrieving autobiographical memories. For SM retrieval, a main effect of group was identified ($F_{(2,59)} = 7.5$, $p = .001$, $\eta^2 = 0.203$). Post-hoc pairwise t-tests, using the Bonferroni correction for multiple comparisons, revealed that RTs were significantly slower during semantic retrieval for children, compared to adolescents ($t_{(39)} = 2.023$, $p < .001$, Bonferroni corrected) and to adults ($t_{(40)} = 2.021$, $p = .02$, Bonferroni corrected). Adolescents and adults did not differ significantly in RT during SM retrieval ($t_{(39)} = 2.023$, $p = 1.00$, ns, Bonferroni corrected). A main effect of group was identified for EM retrieval ($F_{(2,59)} = 8.1$, $p < .001$, $\eta^2 = 0.216$). Post-hoc pairwise t-tests revealed that children were significantly slower than adolescents ($t_{(39)} = 2.023$, $p < .001$, Bonferroni corrected) and adults ($t_{(40)} = 2.021$, $p = .045$, Bonferroni corrected). The analysis did not reveal any significant differences between adolescents and adults for EM ($t_{(39)} = 2.023$, $p = .405$, ns, Bonferroni corrected). Finally, the ANOVA also revealed a main effect of group for the baseline control condition ($F_{(2,59)} = 19.4$, $p < .001$, $\eta^2 = 0.396$). Post-hoc pairwise t-tests revealed that children were significantly slower to respond during the baseline control condition than adolescents ($t_{(39)} = 2.023$, $p = .024$, Bonferroni corrected) and adults ($t_{(40)} = 2.021$, $p = .024$, Bonferroni corrected). In addition, adolescents responded significantly faster than adults in the baseline control condition ($t_{(39)} = 2.023$, $p = .024$, Bonferroni corrected).

3.1.2. Successful retrieval

A one-way between groups ANOVA on AM retrieval success revealed that there was no significant difference among the groups in the number of successfully retrieved AM, ($F_{(2,59)} = 2.72$, $p = .074$, $\eta^2 = 0.084$). A

Table 1
Task reaction time and retrieval success means & standard deviations (ms) for each group.

	Semantic		Episodic		Autobiographical		Control	
	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD
				Reaction Time (ms)				
Group	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD
Children	4196	571	3188	636	2827	757	2078	374
Adolescents	3365	858	2490	512	2922	818	1280	534
Adults	3570	707	2755	522	3155	1372	1729	295
Total	3710	786	2811	618	2968	1008	1696	516
				Successful Retrieval (%)				
Group	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD	Mean	+/− SD
Children	85.33	4.95	88	4.20	91.81	5.72	99.36	2.01
Adolescents	95.20	6.44	93.40	4.36	90.20	8.85	100	0.00
Adults	92.57	7.08	91.81	7.85	95.43	7.30	100	0.00
Total	90.97	7.42	91.03	6.09	92.52	7.58	99.78	1.19

one-way between groups ANOVA also revealed that retrieval success did not differ significantly among the groups in the baseline control condition ($F(2,59) = 2.80$, $p = .137$, $\eta^2 = 0.065$). In the semantic condition, the one-way ANOVA revealed a significant main effect of group ($F(2,59) = 13.97$, p .001, $\eta^2 = 0.321$). Post-hoc pairwise t-tests revealed that children were significantly less accurate than adolescents ($t(39) = 2.023$, p .001, Bonferroni corrected) and adults ($t(40) = 2.021$, $p = .001$, Bonferroni corrected). No other comparisons were significant. In the episodic condition, the one-way ANOVA revealed a significant main effect of group ($F(2,59) = 4.82$, $p = .011$, $\eta^2 = 0.141$). Post-hoc pairwise t-tests revealed that children were significantly less accurate than adolescents ($t(39) = 2.023$, $p = .011$, Bonferroni corrected), but no other group comparisons differed significantly.

3.2. Functional analysis

3.2.1. Whole-brain analysis: group similarities

The whole-brain analysis, including all experimental conditions (autobiographical, episodic, semantic) and the control (baseline) condition, and the three groups (children, adolescents, and adults), yielded one significant LV that accounted for 39% of covariance in the data ($p < .001$). The spatiotemporal pattern of brain activity differentiated all three memory conditions from the control condition across the three age groups, demonstrating significant activations in the inferior and superior frontal gyri, and middle and superior temporal gyri (see Fig. 2A, Table 2).

The confidence intervals for the mean brain scores overlapped for all memory conditions in children and adolescents, demonstrating that there were no significant differences in network salience among semantic, episodic, and autobiographical conditions for either group (see Fig. 2B). In adults, the confidence intervals for the autobiographical and episodic conditions did not overlap with the semantic condition; thus, demonstrating that the salience of the network is significantly stronger in EM and AM retrieval compared to SM retrieval.

3.2.2. Whole-brain analysis: group differences

The whole-brain analysis, after the removal of the baseline condition, yielded two significant LVs (both p-values $< .001$). The first LV accounted for 57% of covariance in the data and differentiated brain activity in children and adolescents from that of adults across all memory conditions. Children and adolescents show stronger recruitment of visual areas, including the fusiform gyrus, lingual gyrus, middle occipital gyrus, and precuneus bilaterally during LTM retrieval (Table 3, Fig. 3A). In addition, non-overlapping confidence intervals reveal that activation of these regions is significantly stronger during SM and EM, compared to AM retrieval (Fig. 3C). In contrast, adults show significantly more activity in bilateral regions in the frontal, temporal, and inferior parietal lobes, as well as the insula, cingulate gyrus, and thalamus during LTM retrieval (Table 3, Fig. 3B). Furthermore, non-overlapping confidence intervals reveal that activation of these regions is significantly stronger during AM
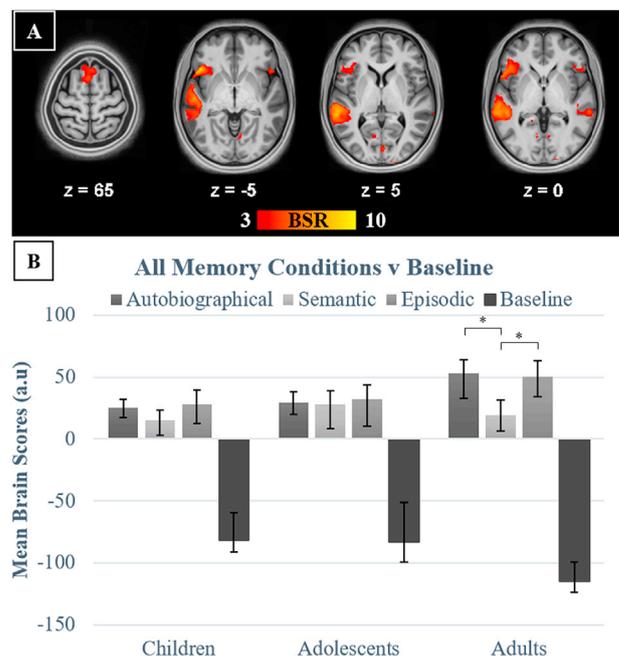
Fig. 2. (A) Activations (overlaid on MNI-average brain template; left = left hemisphere; z = axial slice number) common to all memory retrieval conditions vs. baseline, shared among children, adolescents, and adults. (B) Mean brain scores (a.u. = arbitrary units) in children, adolescents, and adults, in each of the memory conditions (positive values), compared with baseline (negative values). The values for autobiographical, semantic, and episodic recall represent the contribution of each group to the network displayed in A. Error bars reflect confidence intervals from the bootstrap analysis. BSR = bootstrap ratio.

Table 2
Activations during all memory conditions (children, adolescents, and adults) vs. baseline.

			Similarities			
				MNI Coordinates		
Region	Hem	BA	x	y	z	BSR
IFG	L	47	−48	20	−4	9.19
MTG	L	21	−56	−2	−10	9.04
STG	L	22	−60	−38	4	8.85
SFG		6	0	20	64	7.99

Hem = Hemisphere, L = left. BA = Brodmann area. BSR = bootstrap ratio where values > 3 indicate significance of $p < .001$. IFG = inferior frontal gyrus, MTG = middle temporal gyrus, STG = superior temporal gyrus, SFG = superior frontal gyrus.

Table 3
Group differences.

	Children and Adolescents > Adults					
			MNI Coordinates			
Region	Hem	BA	x	y	z	BSR
Inferior TG	R	19	46	−72	0	10.52
Cuneus	L	18	−12	−98	10	9.90
	R	18	20	−92	20	8.16
Thalamus	L	-	−22	−30	0	4.79
	R	-	22	−30	2	4.60
SOG	R	19	38	−76	24	8.01
MOG	L	18/19	−30	−86	10	6.67
	R	18/19	14	−96	16	8.89
Fusiform Gyrus	L	37	−32	−46	−12	7.04
	R	37	42	−56	−10	7.53
Lingual Gyrus	L	18	−30	−72	−10	6.99
	R	18	30	−72	−10	10.04
Precuneus	R	7	22	−68	42	5.05

	Adults > Children and Adolescents					
			MNI Coordinates			
Region	Hem	BA	x	y	z	BSR
MTG	L	22	−60	−42	4	7.09
	R	21/22	56	−34	−2	8.19
IPL	L	40	−56	−18	22	12.35
	R	40	50	−42	40	10.89
Cingulate Gyrus	L	32	−2	22	34	10.32
IFG	L	44	−56	8	18	9.80
	R	47	52	20	−6	9.45
Insular	L	13	−38	12	4	9.67
	R	13	40	6	2	8.70
Cuneus	M	19	0	−80	30	8.62
Putamen	L		−28	−16	8	8.51
Thalamus	L		−16	−20	12	8.14
	R		12	−2	8	10.02
SFG	L	9	−34	40	30	7.23
	R	9	26	46	30	7.38
MFG	L	8	−34	22	42	6.35
	R	8	36	36	40	6.46

Hem = Hemisphere, L = left, R = Right. BA = Brodmann area. BSR = bootstrap ratio where values > 3 indicate significance of p < .001. TG = temporal gyrus, SOG = superior occipital gyrus, MOG = middle occipital gyrus, MTG = middle temporal gyrus, IPL = inferior parietal lobe; IFG = inferior frontal gyrus; SFG = superior frontal gyrus; MFG = middle frontal gyrus.

and EM, compared to SM retrieval (Fig. 3D). As predicted, adults show more activity than children and adolescents in regions of the previously identified common network (Burianová and Grady, 2007; Burianová et al., 2010).

The second LV accounted for 11% of covariance in the data and revealed a pattern of activity that was shared between adolescents and children during autobiographical retrieval and adult episodic retrieval. This network included the left inferior parietal lobe, medial frontal gyrus and bilateral precuneus, as well as several limbic structures, such as bilateral parahippocampus and hippocampus, and left posterior cingulate gyrus (see Fig. 4 & Table 4).

3.2.3. Covariance of brain activity with age
To explore the relationship between brain activity and age during each task condition, brain activity during the three memory conditions was covaried with age. The resulting whole-brain pattern accounted for 75% of covariance in the data ($p < .001$) and showed that age correlated positively with increased activation in a bilateral and widespread network of brain regions, including bilateral inferior parietal lobe, middle temporal gyrus, and inferior frontal gyrus, as well as the cingulate gyrus, left amygdala, bilateral thalamus, and insula (Table 5, Fig. 5A). Furthermore, age was negatively correlated with activity in the bilateral lingual gyrus, middle occipital gyrus, cuneus, fusiform gyrus, and parahippocampal gyrus. These correlations were similarly strong for AM ($r = 0.84$), SM ($r = 0.77$), and EM ($r = 0.74$) retrieval (Fig. 5B–D).

4. Discussion

In the present study, we examined whether children and adolescents engage the same brain regions and show similar contextual differentiation as adults during declarative memory retrieval. Our results demonstrate that for all three memory subtypes (autobiographical, episodic-laboratory, and semantic) children, adolescents, and adults recruit a set of left fronto-temporal areas, which only partially overlap with the common memory network identified previously in young adults and adults (Burianová and Grady, 2007; Burianová et al., 2010; St-Laurent et al., 2011). Unlike adults who engage these regions more strongly for AM and EM compared to SM, neither children nor adolescents show evidence of contextual differentiation. Furthermore, our results demonstrate that children and adolescents engage visual-semantic processing, face and object recognition, and word association areas (fusiform gyrus, lingual gyrus, middle occipital gyrus, and inferior temporal gyrus) more strongly than adults who, in turn, show greater activation of the common bilateral, large-scale memory network. In addition, while the adults show contextual differentiation in these areas (i.e., stronger activation for AM and EM compared to SM), children and adolescents engage the semantic regions more strongly during SM and EM than during AM. Our results further demonstrate that children and adolescents recruit a set of medial and lateral parietal, as well as posterior cingulate and medial temporal regions during AM retrieval, which are activated by adults during EM retrieval. Finally, our results reveal that age is positively correlated with the degree to which the common memory network is engaged during LTM retrieval.

Our findings reveal differences and commonalities between adults, children, and adolescents. With respect to commonalities, children and adolescents showed activation in fronto-temporal components of the common memory network (Burianová and Grady, 2007; Burianová et al., 2010; St-Laurent et al., 2011). This set of regions was left lateralized and overlapped with semantic and language processing areas of the brain (Bishop, 2013; Gaillard et al., 2000; Moore-Parks et al., 2010). We predicted that children and adolescents would recruit the common memory network similarly to adults, but that children would show a lack of differentiation of the memory subtypes, whereas adolescents would show some level of contextual differentiation. Our findings suggest that declarative memory is undifferentiated in children and, contrary to our expectations, also in adolescents. In adults, our results replicate previous findings (Burianová and Grady, 2007) and provide evidence for the differentiation of AM and EM from SM. Our results are in line with the idea that higher-order, top-down processing might be responsible for the differentiation of AM, EM, and SM during retrieval. During childhood, recruitment of top-down processing is restricted (Bunge et al., 2015; Durston et al., 2006; Luna et al., 2010) and the structural connectivity of cognitive control networks is not fully developed until late adolescence (Casey et al., 2005; Luna et al., 2001; Uddin et al., 2011). In contrast, language and semantic memory are developed early in life (Favarotto et al., 2014; Gaillard et al., 2000; Gathercole et al., 1992), which might explain the reliance on these networks for declarative memory processing during childhood. However, the results of this study show conflicting findings in the adolescents age group. In adolescents (aged 14–16 years), behavioural performance was comparable to adults, but their pattern of neural activation was more similar to children. Our results suggest that the development of the common memory network and its contextual differentiation may be protracted, occurring during late adolescence or even early adulthood.

In addition to demonstrating the commonalities between children, adolescents, and adults, our findings also revealed group differences. The results show that, for all types of memory retrieval, children and adolescents recruited regions involved in visual-semantic processing, word association, face and object recognition, and mental imagery (Cavanna and Trimble, 2006; Ghosh et al., 2010; Zhen et al., 2013). In contrast, adults engaged the common memory network, which was identified in previous research, for all retrieval conditions (Burianová and Grady,
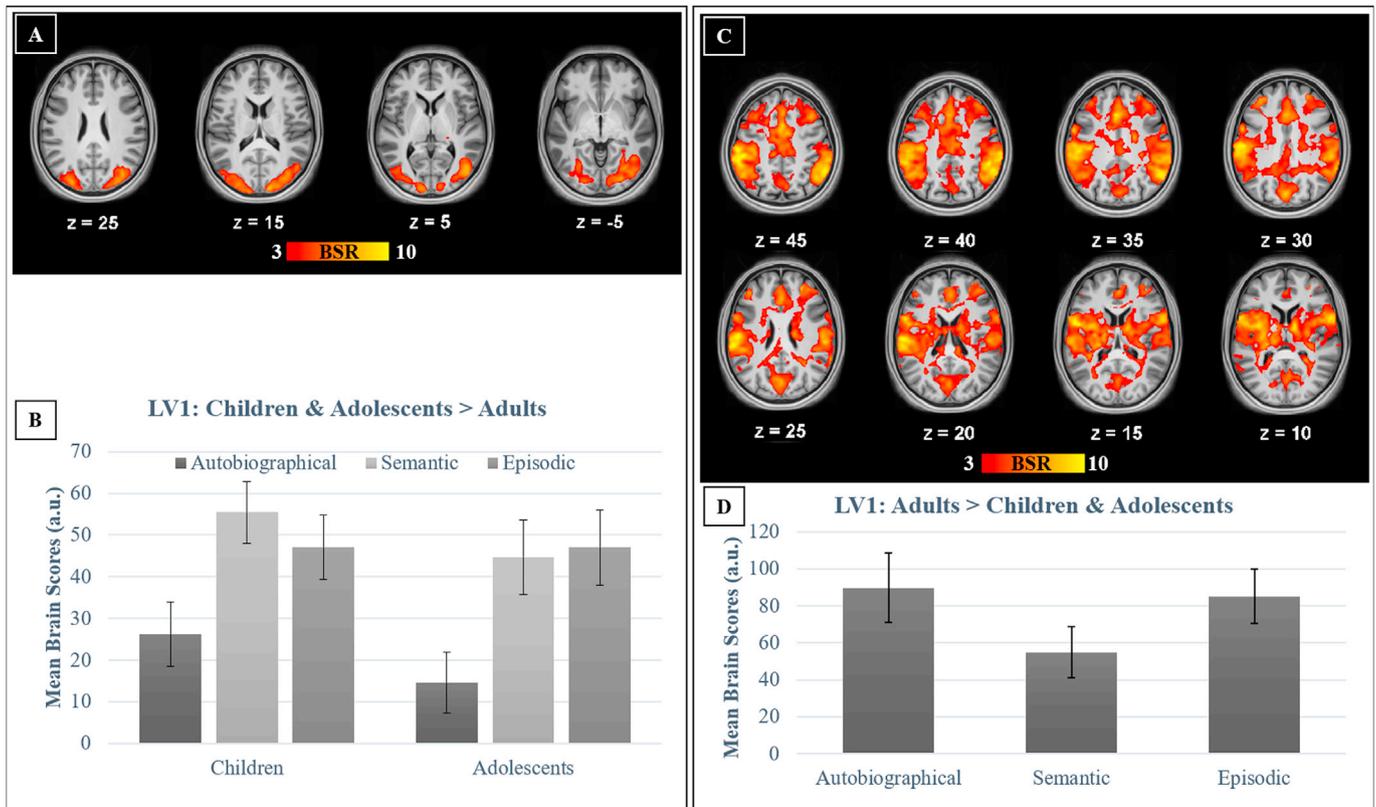
Fig. 3. Activations are overlaid on the MNI-average brain template (left = left hemisphere; z = axial slice number) (A) Activations, greater for children and adolescents compared to adults, and common to autobiographical, semantic, and episodic retrieval conditions. (C) Activations that are greater for adults compared to children and adolescents for all memory retrieval conditions. Mean brain scores (a.u. = arbitrary units) for each condition of LV1 for (B) children and adolescents and (D) adults. Brain scores for children and adolescents (B) correspond to pattern (A) and mean brains cores for adults (D) corresponds with pattern (C). Error bars indicate confidence intervals from the bootstrap ratio. The two activation patterns (A & C) and associated bar plots (B & D) are anti-correlated. For display purposes we have separated these two patterns of activation and displayed both using absolute values. BSR = bootstrap ratio.
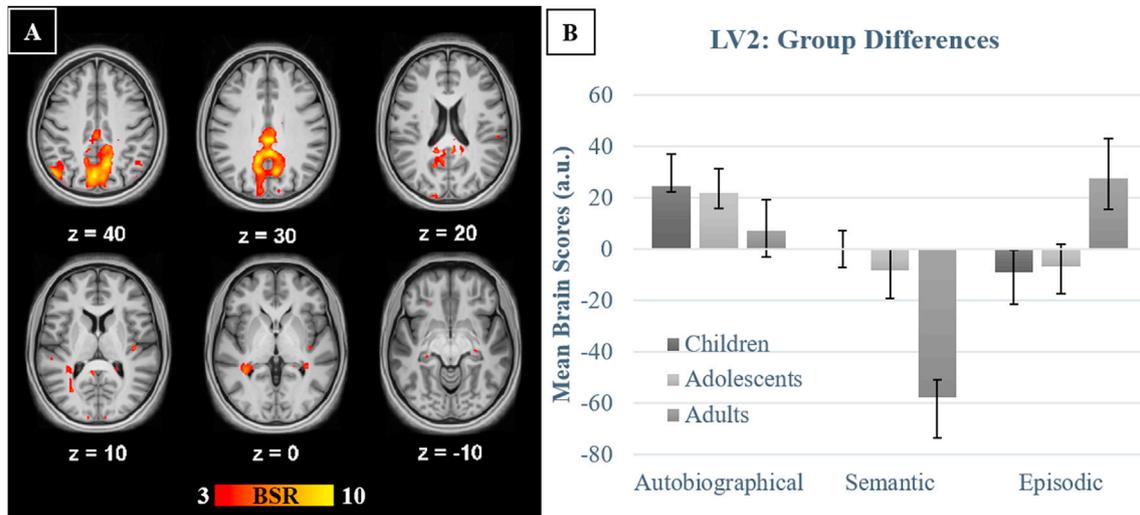
Fig. 4. (A) Activations (overlaid on MNI-average brain template; left = left hemisphere; z = axial slice number) in the inferior parietal lobe, posterior cingulate gyrus, hippocampus, and parahippocampus from LV2 group differences analysis. The relationship between these activations and task conditions are displayed in the mean brain scores graph (B). Mean brain scores (a.u. = arbitrary units) demonstrate that the autobiographical (children and adolescents) and episodic (adults) retrieval conditions share a common pattern of activity that relates to increased activation of in regions displayed in (A). Error bars indicate confidence intervals from the bootstrap ratio. BSR = bootstrap ratio.

2007; Burianová et al., 2010; St-Laurent et al., 2011). Our results clearly demonstrate a robust inverse relationship between these two sets of regions and further show that the transition from the visual-semantic to the

common memory network is correlated with age. In other words, the older the participant is the less he/she engages the visual semantic network and the more he/she engages the common memory network.

Table 4
Overlapping activations for autobiographical retrieval in children and adolescences, and episodic retrieval in adults.

Region	Hem	BA	MNI Coordinates			BSR
			x	y	z	
Precuneus	L	7	−8	−68	36	9.34
	R	7	9	−65	36	9.06
IPL	L	39	−46	−72	44	7.69
Cingulate Gyrus	R	23/31	3	−31	30	7.67
Pos Cingulate	L	30	−30	−68	8	5.56
STG	R	13	42	−20	8	5.48
Parahippocampus	L	19	−35	−46	0	5.23
	R	19	35	−41	0	4.19
Medial FG	R	6	16	−6	50	4.47
Hippocampus	L		−31	−30	−8	3.49
	R		29	−25	−8	3.62

Hem = Hemisphere, L = left, R = Right. BA = Brodmann area. BSR = bootstrap ratio where values > 3 indicate significance of p < .001. IPL = inferior parietal lobe; STG = superior temporal gyrus; FG = frontal gyrus.

Table 5
Covariance with age.

Greater activity in younger individuals						
Region	Hem	BA	MNI Coordinates			BSR
			x	y	z	
Lingual Gyrus	L	18	−28	−70	−6	−8.18
	R	18	28	−70	−8	−14.01
MOG	L	18	−28	−92	22	−8.61
	R	19	14	−96	16	−10.53
Cuneus	L	18	−12	−98	10	−9.65
	R	18	20	−92	20	−10.74
Fusiform Gyrus	L	37	−30	−48	−10	−6.67
	R	37	43	−58	−6	−5.95
Parahipp. G	L	37	−26	−46	−9	−5.95
	R	37	30	−42	−8	−6.19
Thalamus	R	-	22	−30	2	−4.21
Precuneus	R	7	14	−82	46	−3.60

Greater activity in older individuals						
Region	Hem	BA	MNI Coordinates			BSR
			x	y	z	
IPL	L	40	−58	−22	46	19.09
	R	40	56	−20	24	11.45
STG	L	22	−56	14	0	16.79
Medial FG	M	6	2	0	50	16.31
Inferior FG	L	47	−46	22	−6	7.66
	R	47	52	19	−8	10.98
MTG	L	22	−64	−42	4	10.90
	R	21	60	−34	−2	9.42
Cingulate Gyrus	M	32	0	24	32	11.35
Amygdala	L	-	−22	−1	−10	7.32
Thalamus	L	-	−16	−14	14	8.36
	R	-	12	−4	10	11.57
Insular	L	13	−40	14	2	11.13
	R	13	36	16	4	7.64

Hem = Hemisphere, L = left, R = Right. BA = Brodmann area. BSR = bootstrap ratio where values > 3 or < −3 indicate significance of p < .001. Negative values should be interpreted from 0 (no activation) to lower numbers (greater activity). MOG = middle occipital gyrus, Parahipp. G = parahippocampal gyrus, IPL = inferior parietal lobe, STG = superior temporal gyrus, FG = frontal gyrus, MTG = middle temporal gyrus.

Together with the finding that the common memory network is undifferentiated in children and adolescents, these results suggest that the functional organization of declarative memory during development is characterized by a lack of engagement with the higher-order cognitive systems that are typically involved in the adult common memory network (Burianová and Grady, 2007). This finding is consistent with several working memory studies, which implicate the involvement of the posterior cortices during memory retrieval in children (Ciesielski et al.,

2006; Yaple and Arsalidou, 2018). We propose that children and adolescents do not have a strong ability to retrieve and integrate complex contextual details, but instead recall complex AMs as a series of visual-semantic features. Children and adolescents are not incapable of *experiencing* highly complex contextualized events evident in the fact that, behaviourally, they perform with about 85% accuracy across all memory conditions of the task; but their ability to integrate complex features during memory retrieval seems restricted.

Intriguingly, our assessment of between-group differences revealed a second pattern of brain activity in areas, which children and adolescences recruited only during autobiographical retrieval, but which were recruited by adults during episodic-laboratory retrieval. This pattern of activations includes the posterior cingulate gyrus, precuneus, hippocampus, parahippocampus, and left inferior parietal lobe, and overlaps with key nodes of the default mode network (Greicius et al., 2009), which is involved in autobiographical and episodic retrieval (Burianová and Grady, 2007; Irish and Piguet, 2013). Assuming that declarative memory is separated along a context continuum, these results suggest that retrieval of highly contextualized, autobiographical memories in children and adolescents might be similar to retrieval of somewhat contextualized episodic-laboratory memories in adults. This conjecture is further supported by the other finding in this study that children and adolescents are unable to engage the memory network to the same extent as adults when recalling memories at the high end of the context continuum.

Complex episodic and autobiographical memory retrieval relies on higher-order cognitive mechanisms, such as emotion regulation and processing, the integration and binding of contextual features, as well as metacognition (*e.g.*, introspection or reflection). Developmentally, many of these processes mature during adolescence or early adulthood (Casey et al., 2000, 2005; Schneider, 2008; Weil et al., 2013). Previous research indicates that the common network is *de*differentiated in older adults, meaning that older adults retrieve less contextual detail (St-Laurent et al., 2011); together with the results of this study, we suggest that the differentiation of long-term memory may follow an inverted U-shaped trajectory across the lifespan. Interestingly, such a lifespan trajectory of within network differentiation seems to mirror the differentiation between large-scale networks across the lifespan. Resting state studies show that in children and older adults, the default mode network is co-activated with, and, therefore, not fully differentiated from the task-positive network (Chai et al., 2014; Geerligs et al., 2015). An interesting question for future research would be whether both within and between network differentiation across the lifespan are dependent on the same factors or whether they constitute two separate phenomena. An additional area for future research would be to investigate whether children and adolescents also have a restricted capacity to encode complex declarative memories. Perhaps complex contextual details are encoded, but the immaturity of neural network connectivity prevents the integration of these details during memory acquisition. This possibility is supported by evidence showing that adults have difficulties remembering events and personal memories from their childhood years, a phenomenon known as childhood amnesia (Bauer and Larkina, 2014; Eacott, 1999). If children encode the building blocks of their memories, but fail to integrate them into a full autobiographical or episodic memory, one would expect that childhood memories would lack complexity and high levels of contextual detail. A full understanding of declarative memory retrieval will, in future, require further investigations of how memories are encoded as well as retrieved during development.

5. Conclusions

In summary, we argue that the network subserving declarative memory retrieval in adults is preceded by regions engaged in semantic processing during childhood and early adolescence. Our findings clearly demonstrate that age is correlated with the recruitment of higher-order cognitive systems. Critically, we suggest that this age-related change in
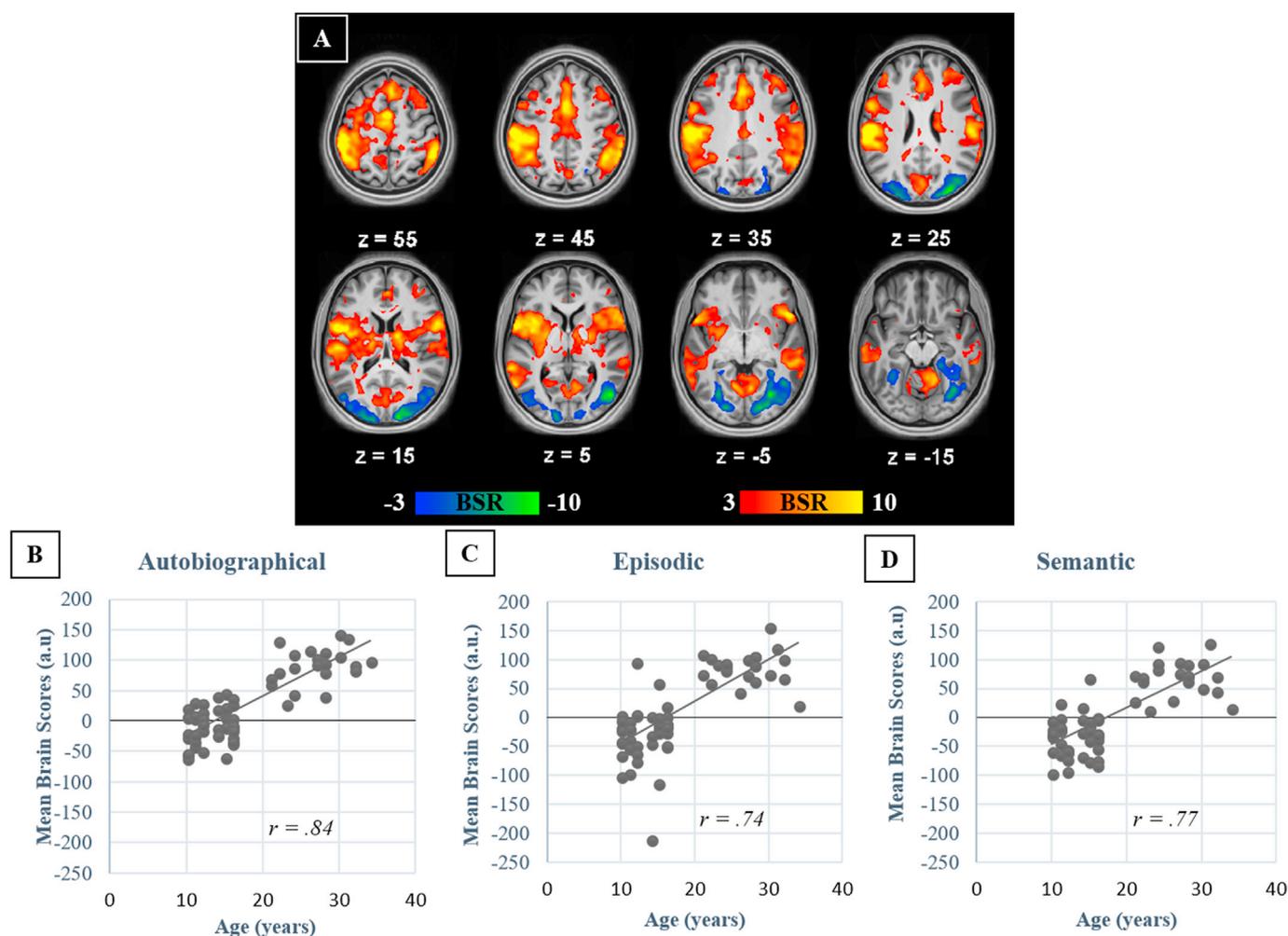
Fig. 5. (A) Activations (overlaid on MNI-average brain template; left = left hemisphere; z = axial slice number) that positively correlated with age (red-yellow) and negatively correlated with age (blue-green). These two patterns were anti-correlated, meaning that recruitment of the yellow-red regions relates to decreased recruitment in the blue-green regions. (B–D) Correlation between age and mean brain scores (below 0 = blue-green activations; above 0 = yellow-red activations). Correlations between AM and age (B) = 0.84, EM and age (C) = 0.74 and SM and age (D) = 0.77. BSR = bootstrap ratio.

the organization of declarative memory also underlies the contextual differentiation of SM, EM, and AM. Our results reveal that retrieval of declarative memories is restricted in children and adolescents by the immature ability to integrate contextual details. We argue that both age groups (children and adolescents) retrieve semantic features of AMs and EMs, but do not integrate them into complex memory constructs during recall. In future, systematic longitudinal studies of declarative memory across development are needed to better understand the relationship between functional change and age, brain-behaviour interactions, and the relationship between the structure and function of the brain. The delayed maturation of neural structures supporting the large-scale bilateral common network for declarative memory may be restricting the integration of complex contextual features in the younger age groups. While our research provides the first evidence for the functional organization of declarative memory in the brains of children and adolescents, future research is needed to identify the underlying patterns of change.

6. Limitations

There are a few limitations to the present study that should be considered when interpreting the results. As mentioned, the task was designed so that the youngest participants (aged 10 years) could achieve successful retrieval on greater than 85% of trials for all conditions. One effect of this design decision is that the task was less cognitively

demanding for adults. Despite this limitation, our results demonstrate that adults do recruit the common network found in – and thereby replicating the findings of – previous studies (Burianová and Grady, 2007; Burianová et al., 2010; St-Laurent et al., 2011). In addition, adolescent participants were scanned after a hardware upgrade of the MRI machine. The upgrade from a Magnetom Trio Trim to Magnetom Prisma scanner involved switching from TQ gradients 45 mT/m at 200 T/m/s simultaneously to XR gradients 80 mT/m at 200 T/m/s simultaneously, on all three axes. This change increased the signal-to-noise ratio (SNR) and long-term stability, whilst minimizing acoustic noise during scanning. All other changes would only affect the data if we adjusted the scanning parameters to utilize the increases resolution capabilities of the Prisma scanner. We kept all scanning parameters constant across all groups to decrease any effect that this may have had on data. It is possible that the SNR of the BOLD signal may have been better in adolescent data, compared to data from adults and children. However, if the scanner upgrade had caused a boost in SNR in adolescents, we would have expected to observe a strong difference between children and adolescents, but no difference was observed between these groups. Participant age groups also differed in range. The adult age group range was 15 years, whereas the range of ages for children and adolescents was only 3 years. We could not increase the range in children and adolescents because of the extreme developmental change in these groups. Future studies should consider this issue in their participant

sampling. Finally, the paradigm involved a memory cue consisting of a question and participants were required to read the question, retrieve the memory, and respond to one of three options. We tested across three different developmental age brackets, each of which could have had different reading capabilities, meaning that response times and temporal patterns of brain activity could relate to the length of time taken to read the questions. A suggestion for future studies would be to use auditory memory cues, so that the timeframe taken for the question to be delivered remains constant across all groups.

Conflicts of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.01.065.

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