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Research Report

Timing matters: Age-related changes in episodic retrieval control as revealed by event-related potentials



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Volker Sprondel*, Kerstin H. Kipp, Axel Mecklinger

Department of Psychology, Saarland University, Germany

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ABSTRACT

The retrieval of information from episodic memory involves the engagement of preretrieval control processes that facilitate the recovery of task-relevant information. The development of these processes was investigated here by comparing neural correlates of retrieval orientation between 13-14-year-old adolescents and young adults. In each age group, event-related potentials (ERPs) elicited by new test pictures were contrasted across two recognition memory tasks (specific vs. general retrieval tasks), which were designed to place greater demands on the recovery of perceptual information associated with each picture in the specific than in the general task. Memory accuracy was higher in the general than in the specific task but did not differ between age groups. In adults, new item ERPs at anterior sites were more positive going in the specific than in the general task from 400 to 1200 ms. In adolescents, the onset latency of this effect was delayed by 300 ms relative to adults, even though no age differences in response speed were obtained in either task. The magnitude of the ERP new item effect in adults correlated with response accuracy, consistent with the view that pre-retrieval processes facilitate the recovery of taskrelevant information. For adolescents, this relationship was only obtained for a subset of participants with early onsetting ERP effects, supporting the claim that the influence of pre-retrieval processes depends upon their temporal onset. Together, the findings suggest age-related changes in the efficiency of using control processes to facilitate successful retrieval while highlighting the role of onset latency in mediating these changes.

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1. Introduction

Recent accounts of episodic memory development have emphasized the view that the development of cognitive control processes plays a fundamental role in episodic remembering throughout childhood and adolescence (Ghetti et al., 2012; Ofen, 2012; Shing et al., 2010). These control processes enable the increasing use of memory strategies with age, such as children's more frequent and efficient use of semantic organization during the formation of episodic memories. Equally important, however, is the influence of control processes on the development of strategies engaged during retrieval.

^{*}Correspondence to: Experimental Neuropsychology Unit, Saarland University, P.O. Box 151150, D-66041 Saarbrücken, Germany. Fax: +49 681 302 6510.

E-mail address: v.sprondel@mx.uni-saarland.de (V. Sprondel).

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Several models of episodic memory retrieval assume that there are functionally distinct processing stages at which cognitive control can support the implementation of different kinds of retrieval strategies (e.g., Moscovitch and Winocur, 2002; Schacter et al, 1998). A critical assumption of these models is that the specific contributions of retrieval control processes differ depending on whether they occur before or after the recovery of information. In the present report, the focus will be on the development of processes engaged before retrieval, because these processes have been conceived as one of the key determinants of the degree to which retrieval is successful (Burgess and Shallice, 1996; Mecklinger, 2010). In particular, pre-retrieval processes are assumed to be responsible for constraining and maintaining task-dependent representations of the retrieval cue, in order to specify which parts of the memory trace that is related to the cue should be accessed. These constraints in retrieval cue processing have also been described in terms of retrieval orientations, which are cognitive sets that are maintained according to the specific demands of the retrieval task and can be initiated before a memory judgment is made (Rugg and Wilding, 2000).

Evidence from neuropsychological and functional neuroimaging research indicates that retrieval control processes depend on an ensemble of prefrontal cortex (PFC) regions and their interactions with the medial temporal lobe (MTL) memory system (Simons and Spiers, 2003). Structural brain maturation within the PFC, in turn, has been shown to follow a protracted developmental course, with the evidence suggesting that critical changes occur through adolescence in the form of synaptic pruning and myelination (O'Hare and Sowell, 2008). This is consistent with neuroimaging findings showing that the functional development of the networks that underlie cognitive control continues through adolescence (Luna et al., 2010). As there is no evidence about developmental changes in pre-retrieval processing during adolescence available to date, in the present study we addressed these changes by means of event-related potentials (ERPs).

Evidence about the development of controlled retrieval processing is scarce, yet there are a few studies in which ERPs were used to make inferences about the development of processes that occur at retrieval and post-retrieval stages of episodic recollection (for reviews see: Mecklinger et al., in press; Friedman, 2012). The critical ERP data for these inferences were acquired in memory exclusion paradigms, in which participants were required to discriminate between target and nontarget items depending on the study context in which the items were learned (see Jacoby, 1991, for details). This paradigm has been employed, for example, in studies in which an ERP index of recollection – the parietal old/new effect – was compared across groups of 8-11-year-old children and young adults (Czernochowski et al., 2009; Czernochowski et al., 2005; Sprondel et al., 2011). A key observation from these studies was that ERP old/new effects elicited by non-targets were present in adults but virtually absent in the children groups, which has been taken to suggest that the processes that underlie the strategic control of recollection are still immature in late childhood and develop during adolescence.

Evidence consistent with the role of adolescent development comes from a recent exclusion paradigm, in which young adults and 13-year-old adolescents made target/non-target judgments depending on the color of previously studied words (Sprondel et al., 2012). A critical aspect in which that paradigm differed from the aforementioned exclusion tasks was the emphasis on only one class of diagnostic information distinguishing between targets and non-targets, because this can be assumed to increase the degree to which it is useful to rely on a selective retrieval strategy by which recollection of target information is prioritized over non-target recollection. In line with this was the finding that the adults showed reliable parietal ERP old/new effects for targets only, whereas for adolescents, these effects were reliable for targets and non-targets. Alongside the observation that the adults showed higher levels of target/non-target discrimination than adolescents, this pattern of results was interpreted as evidence for age-related changes in the selective control of recollection, in so far as the absence of non-target ERP old/new effects in adults suggested greater success in prioritizing target content (Sprondel et al., 2012). Of additional interest to those data are findings from studies in which ERP correlates of post-retrieval control processes were reported to be absent in adolescents or less refined compared to those observed in adults (de Chastelaine et al., 2007; Sprondel et al., 2011, 2012). Findings such as these were taken to indicate that control processes that operate downstream from the recovery of information also develop over the adolescent years.

The evidence reviewed here argues for a critical role of adolescence in the development of controlled retrieval processing. However, because these changes have only been demonstrated for processes that operate in parallel to or after successful recollection, one question that arises from this data is whether maturation also affects processes that are set in train at pre-retrieval stages of episodic retrieval. The experiment described here, therefore, was designed to determine whether comparable evidence would be obtained by investigating age-related changes in the neural correlates of retrieval orientation.

ERP correlates of retrieval orientation have typically been investigated in paradigms in which contrasts were limited to new (unstudied) items from tasks with distinct retrieval requirements (Rugg and Wilding, 2000; for reviews see: Mecklinger, 2010; Wilding and Ranganath, 2011). It is typically assumed that, because new item ERPs bear no relation to studied items, they provide an uncontaminated index of retrieval cue processes engaged before retrieval success occurs. Consistent with this assumption is the finding that differences between new item ERPs often emerge as early as 200-300 ms post-stimulus, suggesting that these differences reflect processes engaged prior to item recognition (Hornberger et al., 2006; Robb and Rugg, 2002). It should be noted, however, that there is considerable variability in the timing of ERP new item effects across studies, and that more extended time courses of these effects may index periods during which cue processing continues in the face of retrieval failure (Hornberger et al., 2004).

An important related finding is that ERP indices of preretrieval processing predict response accuracy, consistent with the assumption that these processes facilitate the recovery of task-relevant information (Bridger et al., 2009; Bridger and Mecklinger, 2012). For example, Bridger and Mecklinger (2012) contrasted the differences between new item ERPs in distinct retrieval tasks and observed that the magnitudes of these differences – reflecting the degree to which pre-retrieval processes were engaged – correlated positively with response accuracy. The fact that these correlations with response accuracy were observed from 400 to 800 ms but were no longer evident from 800 to 1600 ms is interesting, because evidence from a number of ERP studies indicates that recollection occurs by 800 ms post-stimulus (for reviews see: Friedman and Johnson, 2000; Rugg and Curran, 2007). These findings are therefore consistent with the view that new item ERP effects index cue specification processes engaged at pre-retrieval stages toward the successful recovery of task-relevant information. With this in mind, the major interest of the present study was on whether the ability to engage these influential operations changes during adolescence.

Retrieval orientation in the present experiment was operationalized in line with a series of experiments where new item ERPs were contrasted according to the degree to which information about perceptual detail had to be retrieved (Benoit et al., 2009; Ranganath and Paller, 1999, 2000; Werkle-Bergner et al., 2005). For example, Ranganath and Paller (1999) contrasted ERPs across two recognition memory tasks (general vs. specific), for which the task relevance of perceptual information was manipulated by a change in response requirements. Each task comprised picture items, some of which were modified in aspect ratio across the study and test phases, some of which were unchanged, and some of which were new. Whereas the general task required old/new judgments irrespective of changes in aspect ratio, the specific task required endorsing only unchanged pictures as old and to reject all other pictures as new.

In manipulations of this kind, the specific task is assumed to place greater demands on the recovery of perceptual details than the general task, and in keeping with this assumption, memory accuracy was lower in the specific task across several previous reports of this paradigm (Benoit et al., 2009; Ranganath and Paller, 1999; Werkle-Bergner et al., 2005). The ERPs elicited by new test items in these studies were more positive-going in the specific than in the general task, an effect that onset around 200-300 ms post-stimulus. The scalp distribution of these effects indicated a maximum over anterior-frontal recording sites. This can be paralleled with data from an fMRI paradigm that used an analogous manipulation, and in which hemodynamic activity in a region located in left-anterior PFC was greater during specific than during general test trials (Ranganath et al., 2000). Collectively, these effects were taken to reflect changes in the engagement of pre-frontally based cue specification processes across tasks, such that participants engaged these processes to a greater extent in the task where there was a greater emphasis on the recovery of perceptual information.

These considerations motivated the present experiment, in which young adults and 13–14-year-old adolescents completed specific and general retrieval tasks similar to those employed in previous studies (e.g., Ranganath and Paller, 1999, 2000). In the present study, the general task required old/new judgments for studied pictures, whereas in the specific task old/ new judgments differed depending on whether the color of the pictures was modified across the study and test phases. For the young adults, this manipulation was expected to result in ERP retrieval orientation effects with similar time course and anterior topography compared to those reported earlier. The key questions were (a) whether these effects would also be present in adolescents and (b) whether the effects would be differentially related to response accuracy across age groups.

The first issue was addressed by evaluating ERP new item effects within each age group, in addition to exploring agerelated differences in onset latency, magnitude, and scalp topography of the effects. For example, in line with the critical role of the temporal characteristics of pre-retrieval processes, one possibility is that the development of these processes translates into longer onset latencies of these effects in adolescents relative to adults. In addition, changes in the magnitudes of the effects would provide evidence of changes in the degree with which pre-retrieval cue processes can be engaged, whereas differences in topography would allow inferences with regard to changes in the underlying functional activity.

Correlations with response accuracy were examined using an approach similar to that employed by Bridger et al. (2009) and Bridger and Mecklinger (2012). Specifically, the magnitudes of the current ERP new item effects were plotted against response accuracy in the specific task separately for each age group. The critical assumption here was that these effects reflect processes engaged toward the recovery of information in the specific task, and that larger amplitudes of these effects should therefore be associated with increased performance in this task. Evidence that these amplitudes correlate positively with behavioral accuracy in the specific task for adults but not for adolescents, therefore, would provide support for the view that young adolescents are less efficient in engaging pre-retrieval operations in the service of successful retrieval.

2. Results

2.1. Behavior

Table 1 displays mean probabilities and RTs of hits and correct rejections (CRs) in both retrieval tasks for both age groups. Memory accuracy was operationalized using the discrimination index Pr, which is obtained by subtracting the probability of false alarms from that of hits (p[hit]-p[false alarm (FA)]; Snodgrass and Corwin, 1988). As a necessary step in keeping Pr comparable across the two retrieval tasks and consistent with an approach employed by Werkle-Bergner et al. (2005), hits and FAs were defined in line with the separate response requirements in each task. Hits in the specific task were defined as correct responses to old-same items, whereas hits in the general task were collapsed across correct responses to oldsame and old-different items. Conversely, FAs in the specific task were collapsed across incorrect responses to old-different and new items, whereas FAs in the general task were defined as incorrect responses to new items.

Memory accuracy was analyzed by submitting Pr values to an ANOVA with factors of Task (specific vs. general) and Age (adults vs. adolescents). A main effect of Task [F(1, 47)=44.11, p<.001] indicated that, across age groups, memory performance was worse in the specific than in the general task. However, because of the fact that FAs in the specific task

Table 1 – Memory performance data for both age groups in both retrieval tasks.

Adults		Adolescents			
Specific	General	Specific	General		
.71 (.14)	.75 (.12)	.71 (.10)	.75 (.08)		
.85 (.08)	.89 (.09)	.80 (.08)	.89 (.07)		
.56 (.17)	.64 (.15)	.52 (.14)	.63 (.11)		
.46 (.18)	-	.41 (.15)	-		
845 (137)	746	876 (126)	795		
	(139)		(139)		
818 (145)	719	887 (132)	784		
	(125)		(136)		
	Adults Specific .71 (.14) .85 (.08) .56 (.17) .46 (.18) 845 (137) 818 (145)	Adults Specific General .71 (.14) .75 (.12) .85 (.08) .89 (.09) .56 (.17) .64 (.15) .46 (.18) - 845 (137) 746 (139) 818 (145) 719 (125)	Adults Adolescent Specific General Specific .71 (.14) .75 (.12) .71 (.10) .85 (.08) .89 (.09) .80 (.08) .56 (.17) .64 (.15) .52 (.14) .46 (.18) - .41 (.15) 845 (137) 746 876 (126) (139) 818 (145) 719 887 (132) (125)		

^a Hits=items correctly classified as "old"; CRs=items correctly classified as "new"; Note that Hits and CRs were defined according to the separate response requirements in the specific and general retrieval tasks (see text). Pr values were obtained by subtracting the probability of FAs from that of Hits (Snodgrass and Corwin, 1988).

^b Pr = p[Hit] - p[FA].

^c Pr_Specific=p[Hit]-p[old-different FA].

were collapsed across new and old-different items, Pr values alone do not allow determining whether this performance decrement resulted from the requirement to discriminate old-same from old-different items. We therefore conducted an additional analysis in which memory accuracy in the specific task was operationalized using an index of each participant's ability to discriminate old-same from olddifferent items (Pr_Specific=p[hit]-p[old-different FA]; see Table 1). These Pr_Specific scores were directly contrasted with Pr scores from the general task using again an ANOVA with factors of Task (specific vs. general) and Age (adults vs. adolescents). A main effect of Task [F(1, 47)=148.10, p<.001] indicated that, across age groups, discriminations between oldsame and old-different items in the specific task were less accurate than old/new discriminations in the general task. This outcome supports the view that the relatively poorer old/new discriminations in the specific task (as indexed in Pr values) resulted from the requirement to distinguish old-same from old-different items.

Finally, in line with the critical comparisons between new item ERPs across the two retrieval tasks, a further analysis was conducted on mean probabilities of correct responses to new items in the two retrieval tasks for adults (specific: M=.95, SD=.06; general: M=.89, SD=.09) and adolescents (specific: M=.91, SD=.08; general: M=.89, SD=.07). These probabilities were submitted to the same ANOVA employed for Pr and revealed a main effect of task [F(1, 47)=10.89], p < .01], reflecting a smaller likelihood of correctly rejecting a new item in the general than in the specific task. One explanation of this decrease in new item accuracy in the general task follows directly from the response requirements underpinning this task, in which concordance between study and test items might be best achieved on a conceptualsemantic rather than on a perceptual level. That is, it is possible that participants in the general task were more likely to endorse new items as old on the basis of their conceptual familiarity, because the parameters of this task encouraged the engagement of a strategy that emphasized conceptual rather than perceptual cue features.

Mean response times were submitted to an ANOVA with factors of Task (specific vs. general), Response (Hit vs. CRs), and Age (adults vs. adolescents). A main effect of Task [F(1, 47)=72.65, p<.001] indicated longer RTs in the specific than in the general task across response types and age groups.

In summary, participants in both age groups showed less accurate old/new discriminations and longer response times in the specific than in the general task. The poorer accuracy in the specific task resulted from poor discriminations between old-same and old-different items. In contrast, response accuracy for new items was greater in the specific than in the general task. Critically, there was no evidence of changes in accuracy and response times between age groups.

2.2. ERP results

Fig. 1 shows the grand average waveforms for ERPs elicited by new items in the specific and general tasks for adults and adolescents. A first set of time course analyses aimed to identify the time-windows that encapsulated reliable differences between the critical new item ERPs in each age group, and which could be used for subsequent analyses of ERP task effects within and across age groups. The following procedure was employed. In each group, mean amplitudes were quantified for 100 ms bins from 200 to 1200 ms and were submitted to separate paired t tests (specific vs. general) in each bin at each of the 12 electrodes specified in Section 4.5. p Values were considered significant only if adjacent electrodes and time-windows showed reliable effects at $p \le .02$ (see Rosburg et al., 2011, for a similar approach). For adults, these contrasts revealed more positive-going ERPs in the specific than in the general task from 400 to 1200 ms. For adolescents, the corresponding effects were reliable only from 800 to 1200 ms. Notably, none of the intervals before 400 ms in adults and 800 ms in adolescents showed reliable effects at any electrode (p values >.05). Therefore, following the constraint that the selected time-windows should be of equal duration in each group, two time-windows for adults (400-800 and 800-1200 ms) and one time-window for adolescents (800-1200 ms) were selected for subsequent analyses.

2.2.1. Task effects within age groups

For adults, initial ANOVAs conducted separately for each of the two time-windows revealed main effects of task [400–800 ms: F(1, 17)=9.24, p<.01; 800–1200 ms: F(1, 17)=5.39, p<.05] as well as reliable interactions between Task and AP [400–800 ms: F(1, 17)=4.55, p<.05; 800–1200 ms: F(1, 17)=5.85, p<.05]. For each time-window, these interactions indicated reliable task effects across anterior locations [400–800 ms: F(1, 17)=12.04, p<.01; 800–1200 ms: F(1, 17)=8.39, p=.01] but not across posterior sites (both p values >.25). For adolescents, the analysis conducted for the 800–1200 ms interval revealed a main effect of Task [F(1, 30)=5.31, p<.05], indicating a topographically widespread ERP task effect.

The topographies of the ERP effects revealed in the two time-windows for adults were directly contrasted to one



Fig. 1 – Grand average ERP waveforms elicited by new items in the general and specific retrieval tasks for adults (top) and adolescents (bottom).

another to determine whether these effects reflect functionally distinct processes (Wilding, 2006). Task effects were quantified as difference amplitudes (specific minus general), sampled from a larger set of 15 electrodes that permitted a more thorough analysis of changes in topography across time (F7, F3, FZ, F4, F8, T7, C3, CZ, C4, T8, P7, P3, PZ, P4, and P8). These amplitudes were submitted to an ANOVA with factors of time-window (400-800 vs. 800-1200 ms), AP (anterior vs. central vs. posterior), and Laterality (left-inferior vs. left-lateral vs. midline vs. right-lateral vs. right-inferior). To remove overall changes in these difference amplitudes across time-windows, all subtraction data were rescaled prior to analysis using the vector length method (McCarthy and Wood, 1985). The ANOVA revealed no reliable interaction between time-window and either of the topographical factors (p values >.25). Overall, therefore, the present analyses suggest the presence of a single ERP task effect in adults that remained stable from 400 to 1200 ms, whereas the effect in adolescents was present only from 800 to 1200 ms.

2.2.2. Between-group analyses

2.2.2.1. Onset latency. Onset latencies were calculated in the grand average waveform of each age group using a jackknifebased scoring method (Miller et al., 1998; Ulrich and Miller, 2001). In this procedure, standard errors of grand average latencies are estimated using an iterative procedure by which each participant is temporarily omitted and the ERP onset is calculated in the grand average waveform computed from the remaining n-1 participants. In line with a previously recommended approach (Kiesel et al., 2008), in each group onset latency was defined as the time-point at which the amplitude of the critical ERP difference waveform (specific minus general) reached a relative threshold criterion, which was set to 50% of the peak amplitude in the grand average waveform. To increase the signal-to-noise ratio of the critical average waveforms, these were collapsed across the six anterior electrodes used in the initial analyses of reliable ERP task effects (FP1, FP2, F7, F3, F4, and F8). As already suggested by outcomes of these initial analyses, a one-way ANOVA revealed that mean onset latencies were reliably shorter in adults (M=365 ms) than in adolescents (M=665 ms): F(1, 47)=4.18, p<.05.

2.2.2.2. Magnitude. The magnitudes of the ERP task effects were compared between age groups at anterior electrode locations in those time-windows where reliable task effects were obtained in each group (adults: 400–1200 ms, adolescents: 800–1200 ms). Because task effects revealed in each group did not vary between hemispheres and electrode sites, mean ERP difference amplitudes (specific minus general) were again collapsed across the six anterior electrodes used in the preceding analyses (FP1, FP2, F7, F3, F4, and F8). A oneway ANOVA revealed no reliable difference between age groups in the magnitudes of the anterior task effects (p=.90).

2.2.2.3. Topography. Fig. 2 depicts the scalp distributions of the ERP task effects identified in each age group. The ERP subtraction data from the age-specific time-windows (adults: 400–1200 ms, adolescents: 800–1200 ms) were sampled from the 15 electrodes used in the topographic analysis reported above (F7, F3, FZ, F4, F8, T7, C3, CZ, C4, T8, P7, P3, PZ, P4, P8). These data were rescaled using the vector length method (McCarthy and Wood, 1985) and were then submitted to an



Fig. 2 – Topographic maps showing the scalp distributions of the ERP task effects for adults (400–1200 ms) and adolescents (800–1200 ms). These maps were computed by subtracting mean amplitudes associated with ERPs elicited by new items in the general task from those associated with new item ERPs in the specific task.

ANOVA with factors of Age (adults vs. adolescents), AP (anterior vs. central vs. posterior), and Laterality (left-inferior vs. left-lateral vs. midline vs. right-lateral vs. right-inferior). No reliable interaction between Age and either of the topographical factors was revealed (p values >.39). Thus, even though the within-group analyses reported above suggested stronger anterior focus of the ERP task effect in adults than in adolescents, the present comparisons revealed no reliable evidence of differences in scalp distribution after amplitude normalization across groups.

2.2.3. Correlation analyses

Correlations between ERP new item effects and response accuracy were analyzed using the subtraction amplitudes from the previously specified six anterior electrodes (FP1, FP2, F7, F3, F4, and F8). The time-windows used for these analyses were selected within the constraints that they were of equal duration and showed reliable task effects in each age group (adults: 400-800 ms, adolescents: 800-1200 ms). The 400-800 ms time-window selected for adults is consistent with the approach reported by Bridger and Mecklinger (2012) and was considered to best encompass those epochs that map onto the engagement of pre-retrieval processes. In each age group, the critical ERP difference amplitudes were plotted against Pr scores from the specific task, in line with the assumption that these amplitudes reflect the degree to which pre-retrieval processes are engaged toward the recovery of task-relevant information in this task. As shown in Table 2, strong positive correlations were obtained for adults across locations, whereas for adolescents no such relationships were evident. The scatterplots shown in Fig. 3 depict this pattern of relationships at electrode F3, for which the largest correlation was obtained for adults. The figure shows that only in adults response accuracy in the specific task increased with the magnitude of the ERP task effect.

2.2.4. Post-hoc analysis of ERP-behavior relationships in adolescents

The preceding ERP analyses revealed two major differences between the age groups. First, reliable age differences were observed in the onset latencies of the ERP task effects, indicating that the effect occurred by 300 ms later in adolescents than in adults. Second, the amplitudes of these effects were correlated positively with response accuracy in adults but not in adolescents. One possible explanation of this pattern of results

Table 2 – Pearson's R values relating ERP new item difference amplitudes (specific minus general) at anterior electrodes to Pr scores in the specific task in both age groups.

Site	Adults	Adolescents
FP1 FP2 F7 F3 F4 F8	.61** .72** .75** .79** .65**	07 .06 10 01 .05 .00
*** =p<.01.		

is that the neural index of retrieval orientation in adolescents did not relate to response accuracy because the processes reflected in this index were engaged too late in time. This account is consistent with the findings reported by Bridger and Mecklinger (2012), suggesting that the time point at which preretrieval processes are engaged is a key determinant of the degree to which these processes can influence the success of retrieval. The present analysis tested this account by separating subgroups of adolescents on the basis of the onset of their ERP task effects. Specifically, if the foregoing account is correct, then ERP task effects should be more likely to correlate with response accuracy in individuals with early onset latencies than in those with late onset latencies.

Classifying participants according to their ERP onset latencies made it necessary to determine these onset latencies in each individual ERP difference waveform of adolescents. Because these waveforms showed lower signal-to-noise ratios than the group averages employed in the jackknife procedure reported above, a 12-Hz low-pass filter was applied to each individual difference waveform prior to analyses. Moreover, onset latency in the current approach was defined as the first time point after which the threshold criterion (i.e. 50% of the peak amplitude) was exceeded for a period of at least 100 ms (see Johansson et al, 2002, for a comparable approach).

Onset estimates were again derived from the ERP waveforms collapsed across the six anterior electrodes used in the preceding analyses (FP1, FP2, F7, F3, F4, and F8). Five particiants were excluded from this analysis, either because they did not show positive-going task effects at all, or because the critical period was shorter than 100 ms. The remaining 26 participants were split into two subgroups, depending on whether their onset latency fell above or below the median (735 ms). The mean latencies were 532 and 911 ms for the subsequent early and late onset subgroups, respectively. In each subgroup, Pr scores from the specific task were plotted against mean ERP difference amplitudes, sampled from those time-windows during which task effects were largest in each subgroup (600–1000 ms and 800–1200 ms for the early and late onset subgroups, respectively). Consistent with an approach employed by Sprondel et al. (2012), one further participant whose Pr score deviated from the group mean by more than 1.5 SDs was excluded from each group. Notably, in the early onset subgroup, significant positive correlations were obtained at FP1, FP2, F3, and F4 (n=12; r values >.61; p values <.05). By contrast, no such correlations were obtained in the late onset subgroup (n = 12; |r| values < .54; p values > .08). The finding that only in the early onset subgroup response accuracy in the specific task increased with the amplitude of the ERP task effect is illustrated in Fig. 4. This outcome supports the claim that the degree to which the engagement of pre-retrieval operations in adolescents was related to response accuracy depended upon the time point when this engagement occurred.

3. Discussion

To our knowledge, this is the first study that investigates developmental changes in pre-retrieval control processes during adolescence. This was achieved by comparing ERP



Fig. 3 – Scatterplots showing the relationships between old/new discrimination scores in the specific task and ERP difference score amplitudes (specific ERPs minus general ERPs) for adults and adolescents at electrode F3. These relationships were computed from the earliest 400 ms time-windows during which ERP task effects were reliable in each group (adults: 400–800 ms, adolescents: 800–1200 ms). The relationship was significant for adults (r=.79, p<.01) but not for adolescents (r=.01).



Fig. 4 – Scatterplots showing the relationships between old/new discrimination scores in the specific task and ERP difference score amplitudes (specific ERPs minus general ERPs) for subgroups of adolescents, separated according to the onset of their ERP task effects, at electrode F3. Each subgroup comprised 12 subjects, and relationships were computed from those time-windows during which ERP task effects were maximal in each subgroup (early onset subgroup: 600–1000 ms, late onset subgroup: 800–1200 ms). Reliable positive relationships were obtained for the early onset subgroup (r=.64, p<.05) but not for the late onset subgroup (r=-.53, p=.08).

correlates of retrieval orientation between adolescents and young adults. Retrieval orientation was operationalized by means of contrasting ERPs elicited by new items across specific and general retrieval tasks, which were designed to vary the requirements of recovering perceptual information. These contrasts are assumed to provide indices of cue specification strategies, because they should reflect processes engaged toward the specification and maintenance of cue features necessary for recovering task-relevant information in the specific task.

3.1. Behavioral findings

There were lower behavioral estimates of retrieval accuracy alongside longer response times in the specific than in the general task for participants in both age groups. These results replicate findings from previous experiments in which perceptual detail was used to manipulate retrieval orientation and are in line with the assumption that the specific task placed greater demands on the engagement of retrieval control processes than did the general task (Ranganath and Paller, 1999; Werkle-Bergner et al., 2005). In contrast to these behavioral differences across tasks, however, there were no reliable differences in the accuracy and the speed of behavioral responses between the two age groups. That is, although there was a consistent pattern of higher discrimination indices and shorter response times for adults than for adolescents (see Table 1), these differences failed to reach significance level in any of the statistical tests performed here (all p values >.14). This is an important aspect of the data, because it means that there were no definite behavioral indicators of differences in task difficulty or processing speed between age groups. In line with this are findings

from previous developmental ERP paradigms, which indicate that young adolescents can reach mature levels of memory performance even under circumstances that place high demands on retrieval control processes (de Chastelaine et al., 2007; Sprondel et al., 2011; see also discussion below).

3.2. ERP findings

Important insights into the way how pre-retrieval processes functionally mature during adolescence follow from the comparisons of the ERP new item effects across age groups. For both age groups, new item ERPs from the specific task demonstrated a greater bilateral anterior positivity compared to those from the general task. The ERP new item effect observed in adults is similar to the retrieval orientation effects observed in several previous reports (e.g., Benoit et al., 2009), in terms of both its anterior distribution and time course, which comprised a period from 400 ms until the end of the recording epoch. Adolescents did not differ from adults in magnitude and scalp distribution of these ERP new item effects, but reliable age differences were evident in the temporal characteristics of the effects. The fact that the effects were topographically indistinguishable between groups is worthy of comment, given that the within-group analyses revealed some evidence for a stronger anterior focus of the effects in adults than in adolescents. One possibility is that there was a greater degree of interindividual variability of topographies in adolescents than in adults, consistent with findings that adolescence is characterized by a considerable degree of heterogeneity in brain development across individuals, which may be related to differences in pubertal status (Blakemore et al., 2010).

Age differences in the timing of ERP new item effects were demonstrated by (a) the outcomes of the time course analyses, which indicated that the epochs over these effects were reliable started at 400 ms in adults and at 800 ms in adolescents and (b) the comparison of ERP onset latencies, which revealed reliable evidence that the critical new item ERP differences emerged later in adolescents than in adults. Of additional importance is the fact that there were no age differences in behavioral response times, suggesting that the differences in ERP onset latency are unlikely to result from a general age-related delay in cognitive processing related to myelination (Picton and Taylor, 2007). In this way, the present pattern of data suggests that the processes indexed in the critical new item ERP effects were engaged later in adolescents than in adults, potentially reflecting a developmental change in the speed with which retrieval control processes can be engaged. Consistent with this conclusion are data reported by de Chastelaine et al. (2007), where an index of post-retrieval processing measured in the response-locked ERP of children, adolescents, and adults was found to occur at increasingly earlier time points with increasing age, whereas response times did not vary between age groups. One account of the pattern of data, therefore, is that the neural networks underlying retrieval control, though available for young adolescents, become more efficient with age in engaging task-dependent retrieval strategies.

These findings are also significant with regard to the developmental implications that follow from the outcomes

of the correlation analyses. These analyses revealed that the magnitude of the ERP new item effect measured from 400 to 800 ms in adults correlated with response accuracy, whereas no such relationship was observed for the magnitude of the effect measured from 800 to 1200 ms in adolescents. This pattern of relationships suggests that response accuracy benefitted from the engagement of retrieval control processes in adults only and therefore provides support for the view that the group of adolescents as a whole was less efficient in using these processes to facilitate successful retrieval. Notably, as outlined above, these data can be accommodated within accounts that claim that pre-retrieval processes benefit successful retrieval only when these processes occur sufficiently early in time. Consistent with this view, Bridger and Mecklinger (2012) recently reported a paradigm in which ERP new item effects correlated with response accuracy over an early time interval from 400 to 800 ms but were no longer linked to response accuracy over a later, post-retrieval epoch from 800 to 1600 ms. Similar to the present study, the occurrence of recollection was not assessed directly in the Bridger and Mecklinger (2012) study, but the data reported are consistent with findings from several ERP studies which indicate that recollection occurs by 800 ms post-stimulus (see Rugg and Curran, 2007). A notable observation from the present study is that response times of adolescents were in the range of 780-890 ms post-stimulus. Given that (a) response selection would have occurred some 100-150 ms earlier and (b) ERP new item effects in adolescents were reliable from 800 ms onward only, it follows that the processes indexed in these effects were engaged after the point when successful retrieval has occurred (see Hayama et al. (2008), for similar arguments).

Additional evidence that can speak to this issue follows from the outcomes of the post-hoc correlation analyses, which showed that the magnitude of the ERP new item effect in adolescents was in fact linked to response accuracy, but that this was only the case for subgroup of adolescents with early ERP onset latencies. While caution is necessary when interpreting data from subsets of participants only, this pattern of relationships is consistent with the view that retrieval control processes in adolescents influenced response accuracy only for those participants who engaged these processes early in time. It is also noteworthy that the two subgroups of adolescents did not show any differences in behavioral performance in the specific task [Pr: early onset group, M=.50, late onset group, M=.55; RT (collapsed across hits and CRs): early onset group, M=912 ms, late onset group, M=908 ms]. As is the case with the absence of behavioral differences between the adult and adolescent age groups, this additional data point suggests that the temporal onset of retrieval control processes had little influence on mean accuracy and the speed of retrieval judgments. As a whole, therefore, the outcomes of the present post-hoc analyses provide additional evidence consistent with the claim proposed here, which is that the differences in the efficiency of pre-retrieval processing between adolescents and adults were mediated by changes in the onset latency of these processes.

The present findings thus provide electrophysiological evidence that the mechanisms that underlie the successful engagement of pre-retrieval cue specification processes functionally mature during adolescence. The data therefore fit with and extend recent accounts of memory development, which postulate protracted developmental changes for those memory functions that depend on strategic control (e.g., Friedman, 2012; Mecklinger et al., in press; Shing et al., 2010). The current findings confirm and extend those accounts, because they highlight that one aspect of what characterizes adolescent development is improvements in the functional efficiency of control processes that occur prior to successful retrieval. Of additional importance here is that there was no evidence of changes in mean behavioral accuracy, neither between the two age groups, nor between the two subgroups of adolescents. Notably, the absence of reliable group differences in mean accuracy runs counter to the prospect that any changes in the efficiency of pre-retrieval processing across groups reflect a simple difference in the effort with which participants completed the task. Nonetheless, the tendency toward higher mean discrimination indices for adults relative to adolescents discussed above is still worthy of note, because this raises the possibility that there were at least some, albeit small, behavioral improvements associated with the developmental changes in pre-retrieval processing observed here. Therefore, in determining conclusive evidence about the functional outcomes of developmental changes in pre-retrieval processing, it will be important in future studies to identify the circumstances under which these changes are associated with improvements in mean behavioral performance.

The present findings also prompt several further considerations, one of which is what mechanisms might be responsible for the age-related changes in controlled retrieval processing observed here. One possibility follows from functional accounts of the current ERP contrasts, which have identified working memory (WM) as a candidate mechanism for the processes reflected in these contrasts. For example, Mecklinger (2010) argued that cue specification mechanisms are likely to involve the maintenance of task-relevant cue features in WM, such that they are more likely to interact with some memory contents than with others (see Ranganath and Paller, 1999, for similar arguments). This possibility would be consistent with correlational findings from a recent ERP paradigm, in which adults were reported to exert a greater degree of selective control of recollection than young adolescents (Sprondel et al., 2012; see Introduction). A critical additional finding in that study was that the ERP index of selective retrieval control was correlated with increases in a behavioral index of WM capacity in adults but not in adolescents. This was taken to suggest that the adults were more successful in allocating WM resources available for cognitive control to the processes underlying selective recollection. The present pattern of associations converges with this account, in so far as it suggests age-related changes in the extent to which successful recollection benefitted from the engagement of the mechanisms underlying preretrieval processing.

A further consideration concerns the neural basis of the current changes in retrieval control. Neuroimaging research has shown that the transition into adult-level cognitive functioning is supported by different developmental processes that describe distinct patterns of change in functional brain organization (Edin et al., 2007; Luna et al., 2010). One such process, and the one that might account for the age differences revealed here, has been described as a refinement in the functional

connectivity among distributed brain systems. For example, Ofen et al. (2012) described changes in functional connectivity on the basis of changes in the degree to which hemodynamic activity in left PFC correlates with activation in left and right MTL during the successful retrieval of scenes. Specifically, the functional coupling between MTL and prefrontal regions increased from 8 to 21 years of age, as did behavioral estimates of retrieval success, a pattern that highlights the development of functional retrieval connectivity throughout childhood (Ofen et al., 2012). Hence the finding of earlier onsetting ERP retrieval orientation effects in adults than in adolescents, alongside the differences in their relationship with behavioral performance, could be a reflection of changes in the connectivity of a prefrontal-MTL network underlying pre-retrieval control. In line with this account would be data from a recent fMRI connectivity analysis, suggesting that inhibitory control of retrieval in the adult system can best be modeled as a modulatory influence of the dorsolateral PFC on processes supported by the hippocampus (Benoit and Anderson, 2012). As such, greater connectivity in preretrieval control networks might enable the faster and more efficient allocation of cognitive control to downstream processes associated with the successful recovery of information. We acknowledge, however, that reasoning along these lines remains somewhat speculative, and that more conclusive evidence for any account of this kind would follow from approaches that combine the high spatial and temporal resolutions of the fMRI and ERP techniques.

3.3. Conclusion

In conclusion, the present findings provide, for the first time, insights into the development of pre-retrieval cue processing underlying retrieval orientation during adolescence. The ERP contrasts performed here revealed age-related changes in the timing of these processes, alongside changes in the degree with which their engagement is functionally related to retrieval success. Together, these findings are in line with models that emphasize the role of distinct processing stages involved in episodic retrieval and highlight age-related immaturities in the efficiency with which pre-retrieval processes can be engaged.

4. Experimental procedure

4.1. Participants

Twenty adults and 40 adolescents participated in the study. The inclusion of a larger number of adolescents was motivated by our interest in individual differences in retrieval processing, given that the adolescents can be expected to show a relatively high variability in ERP amplitude, which might in turn dilute the relationship between the ERP and behavioral measures in adolescents (DeBoer et al., 2005). The data of two adults and nine adolescents were excluded from the final analyses, because of low response accuracy in at least one of the two retrieval tasks (as indicated by $p(correct) \le .5$; 2 adults, 3 adolescents), a large number of EEG artifacts (5 adolescents), or technical problems during measurement (1

adolescent). The final samples included 18 adults (mean age=23.44 years, range: 19–30; 8 male) and 31 adolescents (mean age=13.61 years, range: 13–14; 12 male). Adults were recruited from the student population of Saarland University. Adolescents were recruited from local schools. All participants were right-handed, had normal or corrected-to-normal vision, and reported not suffering from color blindness. Participants (and adolescents' parents) gave informed consent and were compensated €8/h for participation.

4.2. Materials and design

Stimuli were taken from a set of pictures used in a previous experiment (Ecker and Zimmer, 2008). This set consisted of 320 colored and black/white photographic image pairs depicting every-day objects. From each of these pairs, one picture was selected for the present experiment and manipulated subsequently to create a complementary, color-changed version. These manipulations consisted of either removing all color information from colored images or adding color to black/white images. This procedure resulted in 320 image pairs, each of which comprised two complementary versions of the same object picture (color vs. black/white). Fig. 5 shows an example sample of these pairs. Pictures were presented on a white background in the center of a monitor 1 m from participants.

The experiment was split into two separate study-test cycles so that each cycle comprised 160 pictures. Each cycle began with a study phase, in which 50 colored pictures were intermixed with 50 black/white pictures. The following test phase comprised one specific and one general retrieval task, administered in a fixed order (specific-general), and each containing 80 pictures. In each of these tasks, new pictures were randomly intermixed with two classes of old pictures: pictures that were repeated in the same color status as in the

preceding study phase (old-same items) and pictures that were repeated in their complementary, color-changed version (old-different items). In the specific task, participants were required to respond "old" to old-same pictures only, whereas in the general task, "old" responses were required for both old-same and old-different pictures.

The number of old-same, old-different, and new pictures in each retrieval task were set at levels that ensured that the ratio between old and new responses was constant across both tasks. To this end, the 80 pictures in each retrieval task were allocated to the following groups: 40 old-same, 20 olddifferent, and 20 new pictures in the specific task and 20 oldsame, 20 old-different, and 40 new pictures in the general task. Each of these groups comprised an equal number of color and black/white pictures. Table 3 illustrates the distribution of these groups across the experimental conditions. Rotating pictures across groups, counterbalancing color status within each group, and counterbalancing image pairs across the two study-test cycles created 20 experiment lists. These lists ensured that, across participants, all pictures served equally often in all the possible testing conditions of the two retrieval tasks and that each picture was encountered in both study-test cycles.

4.3. Procedure

Participants were initially fitted with an EEG cap for approximately 1 h. To familiarize participants with the task requirements in both the study and test phases, the experiment began after a short practice phase with an additional set of 16 pictures. Participants were asked to repeat each set of instructions for the two retrieval tasks back to the experimenter to ensure that they understood the separate task requirements.

In each study phase, participants were required to make a binary response depending upon whether each picture was



Fig. 5 - Example sample of image pairs derived from originally colored pictures (A) and originally black/white pictures (B).

Table 3 – Distribution of old and new items across the experimental conditions in each of the two study-test cycles.				
Study	Test	Test		
	Specific Task	General Task		
60 old-same (30/30)	40 old-same (20/20)	20 old-same (10/10)		
40 old-different (20/20)	20 old-different (10/10) 20 new (10/10)	20 old-different (10/10) 40 new (20/20)		

Items to which participants were required to respond "old" in each retrieval task are highlighted in bold. Numbers in parentheses represent the ratio between color and black/white pictures.

presented in color or in black/white. Responses were made with left and right index fingers on a computer keyboard. Study trials began with a fixation cross (300 ms), followed by a blank screen period (200 ms). Pictures were presented for 1100 ms, after which the screen was blanked for 1900 ms and the following trial began.

In each test phase, participants made old/new responses depending upon the particular task instructions (see Table 3). All pictures for which participants were not required to make an "old" response had to be rejected as "new". Responses were made with left and right index fingers on a response pad. Hand-to-response mappings were counterbalanced across participants. Test trials began with a fixation cross (300 ms), followed by a 200 ms baseline blank screen period. Test pictures were presented for 600 ms before the screen was blanked. Responses were recorded within 2500 ms after stimulus onset, and the following trial began 1000 ms after the response.

In each test phase, participants always completed the specific before the general retrieval task. This was because participants performed particularly poorly when the specific task was completed after the general task, as revealed by extensive behavioral pilot testing. Task sequence was held constant, therefore, in order to circumvent the exclusion of too many data sets because of low performance and a low number of trials included in the ERP averages from the specific task.

4.4. Electrophysiological recording

Continuous EEG was recorded from 27 Ag/AgCl-electrodes located at the following sites (adapted from the standard 10–20 system): FP1, FP2, F7, F3, FZ, F4, F8, FC5, FC3, FCZ, FC4, FC6, T7, C3, CZ, C4, T8, CP3, CP2, CP4, P7, P3, PZ, P4, P8, O1, and O2. EEG was acquired referenced to the left mastoid and rereferenced offline to the average of the left and right mastoids. EEG signals were digitized at a sampling rate of 500 Hz and band-pass filtered from DC-250 Hz. Electrode impedance was kept below 5 k Ω . EOG activity was assessed using four additional electrodes above and below the right eye and on the outer canthi. Trials containing EOG blink and movement artifacts were corrected using a linear regression approach (Gratton et al., 1983) embedded in the pre-processing software package. Epochs were defined beginning 200 ms before and ending 1200 ms after stimulus onset. All mean amplitudes were computed relative to a 200 ms prestimulus baseline interval.

Averaged ERPs were collapsed across the two study-test cycles and were formed for correct responses to all items, but in the following only ERPs elicited by new items will be reported.¹ For adults, the mean trial numbers (range) for new items in the specific and general tasks, respectively, were 27 (19–40) and 50 (30–76). The equivalent values for adolescents were 24 (16–35) and 48 (25–71).

4.5. ERP data analysis

All ERP analyses were restricted to contrasts between new item ERPs from the general and specific retrieval tasks (in the following: *task effect*). Mean amplitudes were collected from a 4×3 electrode grid that sampled equally from anterior and posterior as well as left and right hemisphere locations and, as suggested by visual inspection, best encompassed the majority of ERP task effects within each age group. These electrodes comprised three left-anterior (FP1, F7, F3), three right-anterior (FP2, F8, and F4), three left-posterior (O1, P7, and P3), and three right-posterior (O2, P8, and P4) sites.

To evaluate ERP task effects within age groups, initial ANOVAs including factors of Task (specific vs. general), AP (anterior vs. posterior), Hemisphere (left vs. right), and Site

¹The ERP waveforms elicited by old-same and old-different items are depicted in Supplementary data (see Figure S1). These data allowed addressing a further issue of potential interest here, which is whether there were age-related changes in familiarity or recollection-based processing, as indexed in early mid-frontal and late parietal ERP old/new effects, respectively (see Rugg and Curran, 2007). To this end, mean amplitudes associated with oldsame, old-different, and new items from both retrieval tasks were collected from nine electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) from two subsequent time-windows in each age group (adults: 200-400 and 500-800 ms; adolescents: 300-500 and 500-800 ms) and were then submitted to one of two ANOVAs, each designed to assess age-related differences in the critical ERP old/ new effects in one of the two intervals. Overall, the outcomes of these analyses indicated that both classes of old items elicited reliable early mid-frontal and late parietal ERP old/new effects in each retrieval task for both age groups. In this way, the present data are in line with previous studies that have reported reliable such effects in adolescents and young adults (Friedman et al., 2010; Sprondel et al., 2012). This suggests that the ERP correlates of familiarity and recollection were unaffected by the age-related changes in pre-retrieval processing reported here.

(inferior vs. lateral vs. mid-lateral) were conducted for each group. Only effects involving the task factor are of concern, and these were followed-up with subsidiary ANOVAs in cases where significant interactions with at least one of the topographical factors were obtained.

Comparisons of onset latency, magnitude, and topography of the ERP task effects across age groups were conducted using mean amplitudes of ERP difference waveforms, which were obtained by subtracting new item ERPs associated with the general task from those associated with the specific task. These difference amplitudes were also used in the analyses of correlations between the magnitude of the ERP task effects in either age group and response accuracy in the specific task.

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Appendix A. Supplementary meterial

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.brainres. 2013.09.005.

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