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Developmental changes in memory encoding: insights from event-related potentials

Leslie Rollins and Tracy Riggins

Department of Psychology, University of Maryland, USA

Abstract

The aim of the present study was to investigate developmental changes in encoding processes between 6-year-old children and adults using event-related potentials (ERPs). Although episodic memory ('EM') effects have been reported in both children and adults at retrieval and subsequent memory effects have been established in adults, no previous ERP studies have examined subsequent memory effects in children. This represents a critical gap in the literature because encoding processes, and changes in neural correlates supporting encoding, partially account for age-related improvements in children's memory performance. Results revealed that subsequent memory effects differed between children and adults temporally, directionally, and topographically. These findings lend support to the hypothesis that encoding processes and their neural correlates are an important source of change in memory development.

Introduction

Memory shows pronounced development during childhood (Bauer, 2006) and has widespread effects on cognitive and social behavior (e.g. Crick & Dodge, 1994; Piaget & Inhelder, 1973). Age-related changes at each stage of the memory process (i.e. encoding, consolidation, storage, and retrieval) are thought to contribute to improvements in memory performance (see Bauer, 2006). The eventrelated potential (ERP) methodology is well suited to the assessment of memory and its neural bases across development due to its high temporal resolution, non-invasive nature, and relative ease of implementation. ERPs are segments of the electroencephalogram (EEG) that reflect postsynaptic activity of neural populations that are timelocked to the presentation of stimuli (e.g. pictures/words). ERPs associated with successful and unsuccessful memory performance can be compared to assess the neural activity during encoding and/or retrieval portions of memory paradigms.1

ERP responses associated with *retrieval* have been extensively investigated in adults (see Friedman &

Johnson, 2000; Rugg & Curran, 2007, for reviews). These studies have revealed differences between ERP waveforms that are generated to old versus new stimuli (referred to as old/new or episodic memory (EM) effects). Typically old items have been found to generate larger amplitudes compared to new items (Friedman & Johnson, 2000). EM effects have been used to address the long-standing debate as to whether single or dual process models of memory provide a more accurate description of episodic memory retrieval (Wixted, 2007; Yonelinas, 2002). Studies using a variety of paradigms (e.g. subjective and objective memory tasks) have shown that neural responses at retrieval differ as a function of the qualitative nature of the memory, which is consistent with dual process models of memory that propose that two processes underlie recognition memory (i.e. recollection and familiarity; Yonelinas, 2002; cf. Wixted, 2007).

Based on this work, many investigations have utilized ERPs to examine the development of retrieval processes in infants (see de Haan, 2007, for review) and children (Cycowicz, Friedman & Duff, 2003; Czernochowski, Mecklinger, Johansson & Brinkmann, 2005; Marshall, Drummey, Fox & Newcombe, 2002; Mecklinger, Brunnemann & Kipp, 2010; Riggins, Miller, Bauer, Georgieff & Nelson, 2009; Spondrel, Kipp & Mecklinger,

Address for correspondence: Leslie Rollins or Tracy Riggins, Department of Psychology, University of Maryland, 1147 Biology/Psychology Building, College Park, MD 20742, USA; e-mail: rollins@umd.edu, riggins@umd.edu

¹ In contrast, consolidation and storage are more difficult to assess in vivo, particularly using ERPs, since they are continuous/prolonged processes.

2011) typically employing objective memory tasks, which are easier for children to complete. Consistent with the adult literature, most studies have reported that old items elicit a more positive ERP response than new items (Cycowicz et al., 2003; Czernochowski et al., 2005; Marshall et al., 2002; Mecklinger et al., 2010; cf. Riggins et al., 2009). These studies have allowed for greater specificity in describing developmental changes in memory performance (Cycowicz et al., 2003; Marshall et al., 2002; Czernochowski et al., 2005; Mecklinger et al., 2010; Riggins et al., 2009). For example, age-related differences in contributions of frontal regions supporting accurate memory performance have been shown by variations in the spatial topography of EM effects between children and adults (Cycowicz et al., 2003; Czernochowski et al., 2005; Mecklinger et al., 2010; Spondrel et al., 2011). In addition, age-related changes in processing efficiency have been suggested by shorter latencies (Czernochowski et al., 2005; Marshall et al., 2002; Riggins et al., 2009) and decreased amplitude (Riggins et al., 2009) of EM effects with age.

In adults (see Friedman & Johnson, 2000; Johnson, 1995; Wagner, Koutstaal & Schacter, 1999, for reviews), ERPs recorded at encoding have been shown to differentiate between items that are subsequently remembered and those that are subsequently forgotten. Later remembered items are often associated with a larger positive amplitude response compared to items subsequently missed (Friedman & Johnson, 2000; Johnson, 1995; Sanquist, Rohrbaugh, Syndulko & Lindsley, 1980; Smith, 1993; Wagner et al., 1999). These 'subsequent memory effects' have been identified early in the waveform (~200 ms) across frontal leads and later (400-900 ms) across frontal, central and parietal leads (Friedman, Ritter & Snodgrass, 1996; Johnson, 1995; Smith, 1993; Wagner et al., 1999). The specific cognitive processes that underlie these effects have not been identified. Since the subsequent memory effects span multiple components previously identified in the literature (e.g. the P300 which has been implicated in novelty detection), encoding may be eliciting a unique ERP effect or encoding may be modulating multiple components that each reflect a different cognitive process (see Friedman et al., 1996, and Wagner et al., 1999, for discussion). The latter suggestion is supported by the variety of factors that have been shown to influence the subsequent memory effect including (but not limited to) stimulus type, encoding conditions (i.e. shallow vs. elaborative), and allocation of attention (Paller & Wagner, 2002; Wagner et al., 1999). Although some research supports the neural dissociation of recollection and familiarity at encoding in adults (Duarte, Ranganath, Winward, Hayward & Knight, 2004; Friedman & Trott, 2000; Mangels, Picton & Craik, 2001; Yovel & Paller, 2004), inconsistencies are present (Friedman & Trott, 2000; Guo, Duan, Li & Paller, 2006; Smith, 1993). Some of this discrepancy is related to the utilization of subjective versus objective measures of memory performance. Differences between recollection and familiarity have been shown consistently by studies employing paradigms that allow participants to make subjective memory judgments (i.e. remember/know paradigm; Tulving, 1985; Duarte et al., 2004; Friedman & Trott, 2000; Mangels et al., 2001; Yovel & Paller, 2004, cf. Smith, 1993). In contrast, studies that have utilized objective paradigms which require the inference of recollection from participants' accurate retrieval of a contextual detail (i.e. memory of the list in which a word was studied) report either less robust or null findings (Duarte et al., 2004; Friedman & Trott, 2000; Guo et al., 2006).

Despite this body of literature on encoding processes in adults, to our knowledge, no studies in childhood have investigated whether ERPs at encoding are able to differentiate between items that are subsequently remembered and forgotten (see Friedman, 2012, for preliminary results). This represents a critical gap in the literature because age-related changes during the initial encoding of information likely contribute to the observed increase in memory accuracy for items, events, and contextual details across development (Ackerman, 1984; Bauer, 2006; Carroll, Byrne & Kirsner, 1985; Cycowicz, Friedman, Snodgrass & Duff, 2001; Dirks & Neisser, 1977; Ghetti & Angelini, 2008; Ghetti, DeMaster, Yonelinas & Bunge, 2010; Ghetti, Mirandola, Angelini, Cornoldi & Ciaramelli, 2011: Ofen, Kao, Sokol-Hessner, Kim, Whitfield-Gabrieli & Gabrieli, 2007).

Behavioral and neuroimaging studies suggest that increased encoding efficiency contributes to these developmental changes. For example, the duration of stimulus exposure necessary for successful memory performance decreases with age (Ghetti & Angelini, 2008; Morgan & Hayne, 2006). Specifically, when 6-, 8-, and 10-year-old children were exposed to stimuli for 1500 ms, 6-year-olds showed lower levels of item familiarity (Ghetti & Angelini, 2008). However, when encoding time was increased to 4500 ms 6-year-olds performed similarly to older children (Ghetti & Angelini, 2008). In conjunction with these behavioral studies, recent fMRI investigations have shown changes in the activation of the prefrontal cortex and medial temporal lobes from middle childhood to adulthood during encoding tasks which are related to behavioral performance (Ghetti et al., 2010; Menon, Boyett-Anderson & Reiss, 2005; Ofen et al., 2007). This research collaboratively suggests that encoding undergoes development during childhood. However, the neural correlates of encoding processes have yet to be examined in children younger than 8 years old, a task for which ERP methodology is well suited. Although studies have reported collecting ERPs during encoding portions of memory paradigms, these data have not been reported as these papers focused on the development of retrieval (Cycowicz et al., 2003; Marshall et al., 2002). Only one study in the infant literature has attempted to examine memory processes during encoding using ERPs (Bauer, Wiebe, Carver, Lukowski, Haight, Waters & Nelson, 2006). In a 9- and 10-month-old infant sample, Bauer and colleagues (2006) found evidence that neural activity recorded near the time of encoding could account for differences in subsequent memory performance. However, given the engaging and behavioral nature of the memory paradigm (i.e. a live experimenter demonstrated action sequences to the infant in realtime), ERPs to static images of the action sequences were obtained after the initial encoding experience.

The aim of this investigation was to examine ERP responses at encoding as a function of subsequent memory performance in children and adults. An exploratory aspect of the current investigation was to determine whether neural responses differed between recollection and familiarity as indexed by objective reports of contextual details retrieved due to concerns about 6-year-old children's understanding of subjective judgments (cf. Ghetti et al., 2011).

Methods

Participants

Children

Twenty 6-year-old children (12 males and eight females, mean age = 6.52, SD = .28 years, range 6.03-6.95) contributed complete behavioral and electrophysiological data. An additional 18 children were excluded from analysis due to (a) incomplete behavioral performance (n = 1), (b) poor behavioral performance (< 55% accuracy for the contextual detail, n = 2), (c) equipment malfunction (n = 4), (d) poor overall EEG quality (n = 4), and (e) too few ERP trials per condition due to movement-related artifact or performance on the memory paradigm (n = 7). There were no age or sex differences between the final sample and participants excluded from analysis. Participants were recruited from a database maintained by the University Infant and Child Studies Consortium, and children received a small toy and a certificate for participation in the study. Parents provided informed consent for their children.

Adults

Twenty adults (10 males and 10 females, mean age = 20.91, SD = 2.43 years, range 18.48-26.95) contributed complete behavioral and electrophysiological data. An additional 16 adults were excluded from analysis due to (a) equipment malfunction (n = 2), (b) poor overall EEG quality (n = 4), (c) too few ERP trials per condition due to performance on the memory paradigm (n = 9), and (d) a diagnosis of an attention disorder that was not disclosed prior to data collection (n = 1). There were no age or sex differences between the final sample and participants excluded from analysis. Participants were recruited from the University community and either received course credit for participation or volunteered their time. All adults provided informed consent.

Stimuli

A total of 191 images of animals and common objects were selected from a colored version of the Snodgrass and Vanderwart line drawings (Rossion & Pourtois, 2004) and from external sources. Stimuli from external sources were comparable in image coloration and visual complexity. Eleven stimuli were used during the practice phase to ensure that participants understood how to perform the encoding tasks. Participants saw 120 stimuli during the encoding phase (60 per study block), and the remaining 60 stimuli were presented as new items during the retrieval phase. In order to account for the possibility of stimulus characteristics influencing memory performance, four sets of 45 stimuli were compiled to represent the following categories: big/living, big/nonliving, small/living, and small/nonliving. Fifteen stimuli from each category were randomly selected to create three sets of 60 objects. The sets of objects viewed during encoding and retrieval were counterbalanced across participants. Within each block, items were presented in a random order.

Procedure

All procedures were approved by the Institutional Review Board prior to the start of the study. Modeled after the study by Duarte and colleagues (2004), participants completed two encoding tasks while ERPs were recorded.

Participants were fitted with a Lycra stretch cap appropriate for their head circumference to collect EEG. All participants were seated comfortably approximately 90 cm from a computer screen in a dimly lit room. Participants performed both animacy and size judgment tasks during encoding. An instruction and practice phase was administered to ensure that all

participants understood the animacy and size judgment tasks. During instruction, participants were given descriptions in age-appropriate language and specific examples of items from each category. During practice, participants were asked to make animacy and size judgments; feedback was provided to ensure that participants understood the tasks prior to data collection. Also during the practice phase, the participants were instructed to respond verbally only after the presentation of the fixation cross to reduce movement artifacts during the recording epoch. The experimenter, who sat next to the participant throughout the entire study, recorded the participants' verbal responses via button press. Participants did not report their own responses in order to minimize ocular and movement artifact associated with the button press common in ERP studies with children (DeBoer, Scott & Nelson, 2007).

Participants were informed that their memory for the objects would be measured. ERPs and behavioral responses were collected during the two encoding blocks and behavioral responses were collected during the retrieval block. The order of the encoding blocks (animacy or size) was randomly selected for each participant by the presentation software. A fixation cross was displayed for an inter-trial interval of 500 ms. The stimuli were presented on a neutral white screen for 1500 ms. A fixation cross followed each stimulus and remained on the screen until the participants made their size or animacy judgment. Participants had a 1-minute break between encoding blocks. Participants performed two encoding blocks rather than complete the semantic judgments on an intermixed trial-by-trial basis to diminish executive functioning demands.

Following encoding, a 3- to 5-minute break was provided. Then, participants were presented with 120 stimuli previously presented during the encoding phase (i.e. old) and an additional 60 stimuli (i.e. new). A 500 ms fixation cross was presented prior to each stimulus. Stimuli were individually presented in a random order on a neutral white background and remained on the screen until participants provided their verbal responses. Participants were asked whether the object was 'old' or 'new', and, if 'old', whether the semantic judgment they previously made was regarding animacy or size. As in the encoding phase, responses were recorded by the experimenter via button press. This assessment allowed for the examination of memory for the item and its associated contextual detail, as assessed by memory of the encoding task completed (i.e. to index recollection and familiarity).

Based on the participants' responses, stimuli were sorted into the following categories: remembered and missed. Remembered responses were subsequently sepa-

rated further into subsets of 'recollected' and 'familiar' items. Recollected items were those that the participants correctly identified as old and remembered the correct task judgment, a measure of memory for the contextual detail associated with the image. Familiar items were those that the participants correctly identified as old but misidentified the task judgment. This procedure is consistent with other studies evaluating memory performance on objective judgments regarding which task was performed at encoding (Duarte et al., 2004; Friedman & Trott, 2000; Ghetti et al., 2010; Guo et al., 2006; Ofen et al., 2007). This procedure differed from that of Duarte and colleagues (2004) in which recollection and familiarity were assessed based on subjective remember/know judgments (Tulving, 1985). Missed items were later identified as 'new' although they were viewed during the encoding phase. Correctly rejected items were new items accurately identified as new. Missed items and false alarms, new items identified as old, reflect the inverse of later remembered and correctly rejected items, respectively, and are not reported in behavioral analyses. Since ERPs were only collected during encoding, false alarms and correct rejections were only examined in behavioral analyses to assess the accuracy of memory performance.

Behavioral data were assessed to examine age-related differences in the identification of previously encountered items, rejection of novel items, and memory for which task was performed at encoding. The context recollection score was calculated based on the number of items for which participants correctly identified the task performed at encoding in relation to the number of items remembered.

ERP recording

ERPs were collected during the encoding phase of the study to index electrical brain activity related to the encoding of each object. EEG was continuously recorded with a sampling rate of 512 Hz (BioSemi Active 2) from 64 active Ag-AgCl scalp electrodes and two vertical and two horizontal electrooculogram (EOG) channels.

EEG data were re-referenced offline to an average reference configuration using Brain Electrical Source Analysis (BESA) software (MEGIS Software GmbH, Gräfelfing, Germany). Consistent with previous ERP studies in children and adults, trials containing ocular artifacts were corrected (Cycowicz *et al.*, 2003; Marshall *et al.*, 2002) applying the Ille, Berg and Scherg (2002 algorithm. Data were high and low pass filtered at 0.1 Hz and 80 Hz, respectively. Trials were hand-edited to remove movement-related artifact. Trials were 1500 ms in duration, including 100 ms baseline period, which occurred prior to stimulus onset. Consistent with

previous research and current methodological recommendations, a minimum of 10 trials was required for each condition (DeBoer, Scott & Nelson, 2005, 2007). Missing data from individual channels were interpolated for a maximum of 10% of bad channels (i.e. six per participant; see DeBoer et al., 2005). ERPs were averaged based on behavioral performance as described above for later remembered and missed items. As with behavioral data, remembered items were also separated into recollected and familiar items for secondary analysis. For adults, the mean trial numbers (range) were 80 (58-106) for remembered, 20 (10-29) for missed, 61 for recollected (38-84), and 20 (11-32) for familiar. For children, the mean trial numbers (range) were 66 (34–95) for remembered, 19 (10–41) for missed, 46 (22–72) for recollected, and 20 (11-36) for familiar. Time windows for analysis were selected based on previous studies (e.g. Duarte et al., 2004) and visual inspection. Mean amplitudes in adults were assessed for 250-400 ms, 400-600 ms, and 600-800 ms epochs. In the child sample mean amplitudes were assessed for 250-400 ms, 500-700 ms, and 700-900 ms epochs.

Analyses

PASW Statistics 17.0 was used for all statistical analyses (SPSS Inc., Chicago, IL, USA). Behavioral analyses examined effects of age group (children, adults) on response accuracy at encoding and retrieval. Using a component independent analysis approach, ERPs for each time window included an omnibus ANOVA with Age Group (children, adults) as the between-subjects factor and the following within-subjects factors: 2 Condition (remembered, missed) × 4 Coronal Plane (frontopolar, frontal, central, parietal) × 3 Sagittal Plane (left, midline, right) at the following leads: Fp1, Fpz, Fp2, F3, Fz, F4, C3, Cz, C4, P3, Pz, P4. Secondary analyses to explore whether neural activity differed as a function of the memory processes engaged (i.e. recollection and familiarity) were conducted using a 3 Condition (recollected, familiar, missed) factor. When appropriate, the Greenhouse-Geisser correction for nonsphericity was applied. Only condition main effects and interactions with condition are reported.

Results

Behavioral memory performance

At encoding, children and adults were highly accurate at both the animacy and size tasks (see Table 1), although adults were overall more accurate than children, F(1, 28)

= 6.24, p = .02. During retrieval (see Table 1), both children and adults performed above chance when recognizing previously encountered items. Children and adults later remembered a similar proportion of previously viewed items, t(38) = -.86, p = .40. However, adults more accurately recollected the task performed at encoding, t(38) = -2.33, p = .03. This finding is consistent with studies showing that recollection follows a more protracted developmental trajectory than item recognition (Ghetti & Angelini, 2008; Ghetti et al., 2010). Children were more likely than adults to reject novel items, t(38) = 2.78, p = .03.

Event-related potential effects

Significant effects are summarized first and followed by supporting statistical analyses. ERPs recorded at encoding differed in amplitude as a function of subsequent memory performance in both children and adults (see Figure 1). As illustrated, the temporal and topographical qualities of the subsequent memory effects differed between children and adults. Adults demonstrated a subsequent memory effect 400-600 ms poststimulus onset whereas the effect in children did not occur until 700-900 ms. Although a subsequent memory effect was present in both children and adults at the frontopolar leads, the direction of the effect was reversed. Further, the topographical distribution of the subsequent memory effects differed for children and adults. Secondary analyses aimed at assessing whether recollection and familiarity were dissociable at encoding found little evidence in support of this hypothesis (see Figure 2).

Subsequent recognition effects

Early-latency time window (children and adults, 250-400 ms). There was no significant main effect of or interaction with Condition in the early time window.

 Table 1
 Mean percent accuracy (and standard error) during
 encoding and retrieval phases

Measure	Children (n = 20) M		Adults $(n = 20)$ M	SE
		SE		
Encoding overall	92.38	2.39	98.4	.28
Animacy task	93.90	3.29	99.35	.23
Size task	90.85	2.57	97.45	.51
Retrieval				
Later remembered	77.55	11.03	79.95	5.96
Correctly rejected	95.58	5.93	91.92	4.09
Context recollected	71.05	1.64	75.8	1.22

Context recollection was calculated only for items later remembered.

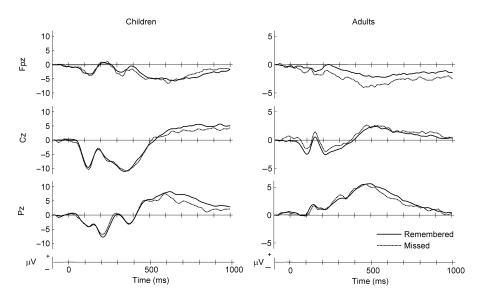


Figure 1 Grand average waveforms illustrating subsequent memory effects in children and adults at Fpz, Cz, and Pz.

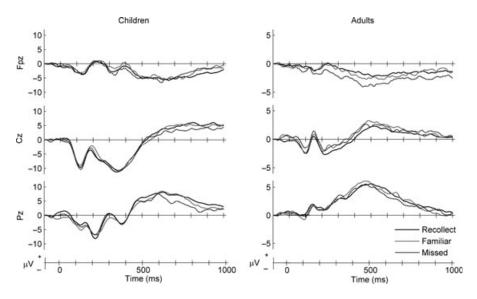


Figure 2 Grand average waveforms illustrating ERPs elicited to items subsequently classified as remembered, familiar, and missed in children and adults at Fpz, Cz, and Pz.

Mid-latency time window (children, 500–700 ms; adults, 400–600 ms). For the mid-latency time window there was a main effect of Condition, F(1, 38) = 4.57, p = .04, which was qualified by an Age Group × Condition × Coronal Plane interaction, F(3, 114) = 3.24, p = .04. Follow-up analyses revealed that, in the child sample, there was no significant main effect of or interaction with Condition. In the adult sample, there was a significant main effect of Condition, F(1, 19) = 10.49, p < .01. The mean amplitude of the later remembered items ($M = .51 \pm .16 \,\mu\text{V}$) was more

positive than the mean amplitude of the missed items $(M = .14 \pm .17 \mu V)$.

Late-latency time window (children, 700–900 ms; adults, 600–800 ms). For the late-latency window there was a significant Age Group × Condition × Coronal Plane interaction, F(3, 114) = 4.46, p < .01. In the adult sample, there was no significant main effect or interaction with Condition. For the child sample, there was a significant Condition × Coronal Plane interaction, F(3, 57) = 4.57, p < .01. Follow-up analy-

ses revealed a significant main effect of Condition at the frontopolar leads, F(1, 19) = 5.05, p = .04. The mean amplitude of the later remembered items $(M = -3.33 \pm 1.05 \,\mu\text{V})$ was more negative in amplitude than the mean of the missed $(M = -1.76 \pm 1.31 \,\mu\text{V})$. Condition effects were not significant at frontal, central, or parietal leads.

Subsequent recollection effects

Secondary analyses revealed that despite children's and adults' high levels of recollection performance, there were few differences in ERP responses to subsequently recollected and familiar items (see Figure 2). There was no significant main effect nor an interaction with Condition in the early or mid-latency time windows. In the late-latency time window (children, 700–900 ms: adults, 600-800 ms) there was an Age Group \times Condition × Coronal Plane interaction, (228) = 2.89, p = .01. There were no significant effects in adults. For children there was a significant Condition \times Coronal Plane interaction, F(6, 114) = 86.73, p = .02, such that differences across conditions were maximal at the frontopolar leads. However, as can be seen in Figure 2, this effect is similar to the subsequent memory effect, meaning that the ERP response was similar for recollected and familiar items but these responses differed from subsequently forgotten items. Follow-up analyses revealed no main effect of Condition at the frontopolar, frontal, central, or parietal leads.

Topographical analysis

To examine whether different neural generators were engaged by children and adults during encoding,

topographical analyses were performed. Based on the temporal differences reported above, mean amplitudes from the 400-600 ms window were used for adults and mean amplitudes from the 700-900 ms window were used for children. The scalp topographies of the mean amplitudes for children and adults are shown in Figure 3. Since differences in overall amplitude across groups and conditions can confound topographical analyses, data were normalized for each group and condition using the McCarthy and Wood (1985) method. Then, data were analyzed using a 2 Age Group (children, adults) × 2 Condition (remembered, missed) × 4 Coronal Plane (frontopolar, frontal, central, parietal) × 3 Sagittal Plane (left, midline, right) ANOVA at the following leads: Fp1, Fpz, Fp2, F3, Fz, F4, C3, Cz, C4, P3, Pz.

Differences in scalp distributions during encoding between children and adults were suggested by significant Age Group \times Coronal Plane, F(3, 114) = 8.45, p < .01, and Condition × Coronal Plane, F(3, 114)= 6.46, p < .01, interactions as well as a marginal Age Group × Condition × Coronal Plane interaction, F(3, 114) = 2.43, p = .08. Although the three-way interaction did not reach the conventional level of statistical significance, this effect aids in the explanation of the secondary interactions and in the description of agerelated differences in encoding processes. Follow-up analyses revealed group differences at the frontal, F(1, 38)= 10.42, p < .01, central leads, F(1, 38) = 5.42, p = .03, and parietal leads, F(1, 38) = 24.01, p < .01. At the central leads, this effect was qualified by an Age Group × Condition interaction F(1, 38) = 5.42, p = .03. The difference between children and adults was present for items that were later remembered, F(1, 38) = 7.33, p < .0, but not items that were later missed, F(1, 38)= .03, p = .87.

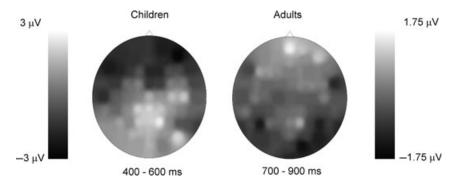


Figure 3 Voltage maps illustrating the subsequent memory effects (later remembered minus missed) in children and adults. Data are displayed for the 400-600 ms time window for children and in the 700-900 ms window for adults. Different scales are used for children and adults to account for age-related amplitude differences.

Discussion

The primary goal of the current study was to examine differences in encoding processes in children and adults using ERPs. We assessed whether subsequent memory effects were present in children and if these effects differed from those in adults. An exploratory aim was to determine whether ERPs at encoding could differentiate the processes of recollection and familiarity in either children or adults using an objective task. Six-year-old children and adults performed a task that assessed memory for individual items and a contextual detail (i.e. task performed at encoding). ERPs were collected during the encoding phase. Subsequent memory effects were detected in both children's and adults' ERP responses. Interestingly, these effects differed between age groups in that (1) they occurred at a later time point in children, (2) they were in the opposite direction, and (3) they were elicited by different patterns of neural activity. The current study did not detect differences in the processes of recollection and familiarity at encoding in either children or adults.

ERPs at encoding are related to memory performance at retrieval

To our knowledge, this is the first study to report a subsequent memory effect using ERPs in children. Agerelated differences were present in the timing, direction, and topographical distribution of encoding processes in children compared to adults. These effects are important because of the prolonged development of encoding processes that influence children's memory capabilities (see Bauer et al., 2006; Carroll et al., 1985; Ghetti & Angelini, 2008; Ghetti et al., 2011; Menon et al., 2005; Ofen et al., 2007).

For adults, subsequently remembered items elicited a more positive response than missed items 400–600 ms post-stimulus onset. A main effect of condition was present that was visually maximal over the frontopolar leads. This finding is similar to the most consistently reported subsequent memory effect in the current literature that occurs 400–900 ms post-stimulus onset and is widespread across frontal, central, and parietal leads (Friedman & Johnson, 2000; Friedman et al., 1996; Johnson, 1995; Smith, 1993; Wagner et al., 1999). In contrast to the finding with adults, the subsequent memory effect present in children emerged later, not diverging until 700-900 ms, was specifically focused on the frontopolar leads, and was larger in amplitude to subsequently missed items.

The temporal difference between ERP findings in children and adults converges with behavioral studies showing increased efficiency in encoding (Ghetti & Angelini, 2008; Morgan & Hayne, 2006). For example, the duration of exposure necessary to encode items decreases with age (Ghetti & Angelini, 2008; Morgan & Hayne, 2006). One hypothesis is that the length of time necessary to categorize stimuli during the encoding task may be directly related to the timing of subsequent memory effects. One way to test this in future studies would be to allow participants to use a button press during encoding to address whether reaction times are related to the timing of the subsequent memory effect. This was not done in the present study to minimize motion artifacts during ERP recording.

A directional difference in the effects was also observed; specifically, an inversion of polarity was present between age groups. For adults, the mean amplitude to later remembered items was more positive than missed items whereas for children the missed items elicited a more positive-going waveform than later remembered items. Differences in polarity have been reported in developmental studies of memory, face processing, and auditory processing across different age groups (Bauer et al., 2006; Carver, Dawson, Panagiotides, Meltzoff, McPartland, Gray & Munson, 2003; Maurer, Bucher, Brem & Brandeis, 2003) and stimulus conditions (de Haan & Nelson, 1997). Researchers have argued that task difficulty influences effect polarity based on behavioral differences across age groups (Bauer et al., 2006; Maurer et al., 2003) and task demands (de Haan & Nelson, 1997). Inversion of polarity across development may reflect qualitatively distinct neural processes, cortex immaturity, or the change in how processes with opposed polarities contribute to the observed surface polarity (deHaan & Nelson, 1997; Maurer et al., 2003). Future research is needed to determine which, if any, of these underlie the observed difference in these subsequent memory effects.

Finally, differences in the spatial distribution of the subsequent memory effects were present between children and adults. This finding suggests that children and adults may recruit functionally distinct systems during encoding, which is consistent with recent fMRI studies showing differential recruitment of the prefrontal cortex and medial temporal lobes during encoding with age (Ghetti et al., 2010; Menon et al., 2005; Ofen et al., 2007). Further, this finding extends current studies using ERPs that show differences in topography of frontal brain activity at retrieval between children and adults (Cycowicz et al., 2003; Czernochowski et al., 2005; Mecklinger et al., 2010; Sprondel et al., 2011) and highlights the importance of encoding processes as an important source of developmental change in need of continued investigation. One caveat regarding our conclusions about age-related differences in the direction, timing, and topography of subsequent memory effects is that they are all based on ERP amplitude. Given that this is the first report of a subsequent memory ERP effect in children, future studies should continue to investigate subsequent memory effects using ERP and fMRI methodologies to provide support for our conclusions.

In addition to the suggestions above, future research should determine whether there are age-related differences in the recruitment of pre-existing knowledge and/ or strategic encoding processes (Ghetti et al., 2010; Wagner et al., 1999). Further, future studies should assess whether ERP differences are present between encoding conditions (e.g. deep/shallow, level of participation, and stimulus modality) as these have been shown in behavioral studies to influence children's subsequent memory performance (Baker-Ward, Hess & Flannagan, 1990; Carroll et al., 1985; Ghetti & Angelini, 2008; Passolunghi, Brandimonte & Cornoldi, 1995). Finally, manipulations such as stimulus type (i.e. pictures/words), the task performed at encoding (i.e. intentional/incidental), and the type of detail recollected (i.e. objective vs. subjective information) that influence the subsequent memory effect in adults should be assessed to determine age-related differences (Wagner et al., 1999).

ERPs were not related to contextual details objectively retrieved

An exploratory goal of the study was to assess whether ERP amplitude differed as a function of contextual information retrieved. The current study did not detect differences in ERPs associated with recollection and familiarity, the processes that are hypothesized to underlie recognition memory (Yonelinas, 2002), in either children or adults. Although many explanations could account for why subsequent recollection effects were not found in the current study, two explanations seem most plausible. Subsequent memory effects may only be present when using subjective rather than objective methods. A meta-analysis of fMRI studies suggests that objective and subjective memory assessments recruit partially overlapping yet dissociable neural circuits (Spaniol, Davidson, Kim, Han, Moscovitch & Grady, 2009). To date, some ERP studies using the remember/ know paradigm or similar methods have reported differences between recollection and familiarity at encoding (Duarte et al., 2004; Mangels et al., 2001; Yovel & Paller, 2004; cf. Smith, 1993). Fewer studies have been conducted that use objective measures of recollection, but overall they have been less successful in elucidating recollection effects at encoding (Duarte et al., 2004; Friedman & Trott, 2000; Guo et al., 2006).

Friedman and Trott (2000), who employed a withinsubjects design assessing recollection at encoding using both objective and subjective measures, were only able to distinguish between recollection and familiarity at encoding using their subjective measure. Alternatively, it is equally likely that subsequent recollection effects may not have been discernible in the current study because familiarity could have supported accurate task judgments. Participants completed one encoding block (e.g. animacy) prior to completing the second encoding block (e.g. size). Therefore, when deciding at retrieval which encoding task was performed, participants could rely on temporal information to make the task judgment because recent items would be more familiar than distal items (Yonelinas, 2002). In contrast, if semantic judgments were made on a trial-by-trial basis, recency would not support task recollection. Since the current study included both children and adults, we opted to limit executive function demands associated with switching tasks by having participants perform a blocked task.

Future studies will need to be performed to further investigate the neural activity underlying the processes of recollection and familiarity at encoding. For example, researchers could examine whether increasing the signal to noise ratio for the recollection condition by using a more difficult objective measure (e.g. increasing the possible number of contexts or the number of to-be-remembered contextual details) allows for the differentiation of recollection and familiarity at encoding. Researchers could also employ methods used by Ghetti and colleagues (2011) to assess recollection subjectively during examination of age-related differences in subsequent recollection.

Behavioral memory performance

Children performed comparably to adults when identifying previously viewed items. This is consistent with studies showing similar levels of item recognition between older children and adults (Ghetti et al., 2010). Also consistent with previous studies, 6-year-old children were less accurate than adults at remembering a contextual detail associated with the items (Cycowicz et al., 2001; Cycowicz et al., 2003 Ghetti & Angelini, 2008; Ghetti et al., 2010; Ghetti et al., 2011; Ofen et al., 2007). However, children correctly rejected novel items more than adults. This pattern of results may have emerged for a number of reasons. Adults and children may have differed in their use of encoding strategies since participants were aware that their memory for items would be assessed. Research has shown that adults are more likely to utilize semantic information when making memory judgments, whereas children are more likely to utilize perceptual information (Ghetti et al., 2011). If adults in the current study used semantic information to encode items, they may have been more likely to falsely endorse having seen a new item that was semantically related to encoded items (e.g. falsely identify seeing a blue jay after having seen a seagull). Alternatively, children and adults may have differed in whether they were more likely to respond 'old' or 'new'. For example, children may have made more 'new' judgments to complete the task faster or adults may have been more concerned than children with accurately identifying previously viewed items and adopted a more liberal response threshold. Importantly, rates of correct rejection did not predict acceptance of previously encountered items in either children or adults, showing that neither group displayed an overall propensity to accept or reject items. As stated above, future research should examine differences in strategy use on subsequent memory effects during development.

Summary

The current study supports the utilization of ERPs in the assessment of encoding processes developmentally. Results suggest that neural responses recorded during encoding in children and adults differ in terms of timing, direction, and topography. Further investigation of these differences will allow additional insight into how developments in encoding processes contribute to age-related changes in memory performance.

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