The Development of Episodic Memory

Evidence from Event-Related Potentials
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Introduction

Remembering past experiences is an essential part of human cognition. The ability to encode new events as well as to mentally travel back in time to re-experience past events and the spatial and temporal context in which they occurred is a central aspect of daily cognitive functioning. Not all mnemonic processes show the same developmental pattern, however: while young children's performance on perceptual implicit memory tasks resembles that of young adults (see Schneider and Pressley, 1997, for a review), episodic memory shows remarkable changes during childhood and adolescence, allowing young children, who typically perform poorly on tests of episodic memory, to improve dramatically as they grow. In the current review, we will highlight distinctions between mnemonic processes in terms of their developmental patterns. Before reviewing event-related potential (ERP) studies of episodic memory development, we will briefly discuss two features that are central to the understanding of childhood episodic memory and its maturation.

The first of these concerns the differential developmental trajectories of familiarity and recollection throughout childhood and adolescence Dual-process perspectives of recognition hold that familiarity and recollection are two distinct processes that can contribute to episodic recognition judgments (Yonelinas, 2002; see also Chapter 9). Familiarity, a fast-acting process by which the strength of memory representations is assessed without retrieval of contextual details of a prior episode, appears to mature during early childhood (Ghetti and Angelini, 2008; Mecklinger, Brunnemann, and Kipp, 2011), whereas recollection, the retrieval of detailed information from a prior study episode including its spatial and temporal context, continues developing throughout adolescence (Brainerd and Reyna, 2004; Ghetti and Angelini, 2008; Sprondel, Kipp, and Mecklinger, 2011).

A second theme of central relevance in research on memory development relates to improvements in cognitive control processes that contribute to episodic memory performance (see Chapters 7 and 15). For example, children perform disproportionately

worse in episodic memory tasks that require the specification of contextual information of a study episode, such as the color in which a picture was seen or the voice in which a word was spoken (Lindsay, Johnson, and Kwon, 1991). Children of early school age also encounter problems in reality monitoring tasks, in which they have to discriminate between memories of imagined and actually performed actions (Foley and Johnson, 1985). The low reliability of children in eyewitness testimony is also thought to be a reflection of their poor memory for the sources of events (Bruck and Ceci, 1999). An influential account of these difficulties is provided by the source monitoring framework, which emphasizes the role of operations involved in identifying and examining the source of remembered events, such as the time of day an event occurred or the location where an object was left (Johnson, Hashtroudi, and Lindsay, 1993; for more discussion, see Chapter 8). According to this framework, children encounter source memory difficulties because source information is not automatically reinstantiated but critically depends on cognitive control processes and purposeful retrieval strategies which are still unavailable to younger children.

Event-Related Potential Measures of Episodic Memory

In this chapter, we review event-related potential (ERP) studies that provide important insights into the development of episodic memory in general, with a particular focus on the two themes of interest here. ERPs can reliably be recorded in a variety of explicit memory tasks, and the processes involved in encoding information into and retrieving it from episodic memory have been related to various ERP differences between experimental conditions (for reviews see Friedman and Johnson, 2000; Rugg and Curran, 2007; see also Chapter 5). An important feature of the ERP technique is its excellent temporal resolution (in the millisecond domain) by which functionally relevant brain activity can be monitored. ERPs thus allow processes of interest to be examined online, at the speed at which they unfold (Friedman, 2012), a possibility that is not available to some other neuroimaging measures such as fMRI. The ERP technique is also ideally suited for use with children, as it is easy to apply and ensures that the child finds him- or herself in a relatively comfortable laboratory environment.

ERP components are characterized by their amplitude (the magnitude by which two experimental conditions differ), their latency, and their scalp distribution (Rugg and Coles, 1995). The distortion of electrical signals by biological tissues (e.g., scalp, skull) means that the ERP technique is not well-designed for identifying functionally relevant brain regions. The use of high-density electroencephalography (EEG) recordings together with source localization techniques, however, makes the estimation of the neural generators of ERP components increasingly plausible (Luck, 2004). The ease of data collection, alongside its high temporal resolution, makes the ERP technique a valuable tool for examining developmental changes in episodic memory processes across different age groups (Friedman, 2012). Nonetheless, surprisingly few developmental ERP studies have examined commonalities and differences in encoding and retrieval-related processes across age groups to date. In this review we will focus on ERP measures of retrieval-related processes (see Friedman, 2012, for developmental aspects of encoding and memory formation).

The Development of Episodic Recognition

To date the majority of developmental memory studies have focused on age differences in recall and recognition and have found large age-related differences in both tasks. Interpretations derived from these studies are limited, however, because comparisons between recall and recognition tasks are not process-pure, making it difficult to make specific claims about which processes are responsible for age-related changes (Ghetti and Angelini, 2008). Multiple processes are thought to contribute even to seemingly simple recognition judgments (Herron and Rugg, 2003). The dual-process view states that two distinct processes contribute to recognition memory. The first, familiarity, is a process which assesses the strength of a memory representation without the retrieval of contextual details of prior study episodes, and as such is sufficient for making adequate recognition memory judgments. A second process, however, recollection, is necessary to retrieve the context in which an event was situated. Several studies suggest that the development of recollection extends from early childhood to adolescence, whereas familiarity matures early and becomes stable during childhood (Billingsley, Smith, and McAndrews, 2002; Ghetti and Angelini, 2008; Ofen et al., 2007). Data of this kind come from the remember/know (R/K) procedure (Tulving, 1985) in which participants have to evaluate their memory experience and indicate whether they recollect qualitative details from a study episode (R response) or merely have a feeling of familiarity for the test item (K response). In one study of this kind, Billingsley, Smith, and McAndrews (2002) reported that the proportion of R responses from early school age to adulthood increased while there were no differences in K responses across age groups. The procedures employed for measuring familiarity and recollection in studies with adults are not necessarily suited for use with children, however. The R/K procedure may not be appropriate in developmental or clinical studies because of its susceptibility to inter-individual variability. For example, children of early school age have been shown to be unable to distinguish between mental states such as knowing, believing, or remembering (Perner and Ruffman, 1995). Any age-related differences in familiarity and recollection as revealed by the R/K procedure may thus reflect differences in the ability to assess mental states rather than different developmental trajectories of the two processes.

An increasing number of studies indicate that familiarity and recollection can be mapped onto qualitatively different ERP old/new effects. Familiarity appears to be well reflected by more positive-going waveforms for studied than non-studied items, with a maximum difference between 300 and 500 ms at frontocentral recording sites, an effect that has been termed the mid-frontal old/new effect (for reviews see Mecklinger and Jäger, 2009; Rugg and Curran, 2007; but see Paller, Voss, and Boehm, 2007 for an alternative view of the mid-frontal old/new effect). Recollection is associated with a later-occurring effect, specifically with more positive-going ERP waveforms for old than new items between 400 and 800 ms. This effect is termed left parietal old/new effect, because it reaches its maximal amplitude at left parietal recording sites (for reviews see Friedman and Johnson, 2000; Mecklinger, 2000; Rugg and Curran, 2007). In view of the two distinct ERP effects strongly related to familiarity and recollection, and the fact that ERP measures do not presuppose the ability to distinguish between mental states, ERP measures provide a valuable tool for investigating similarities and differences between recognition memory subprocesses across age groups.

The Development of Recollection

As will be briefly reviewed here, developmental recognition memory studies have shown that the ERP correlate of recollection, the left parietal old/new effect, can reliably be recorded at early school age. The few studies comparing ERP correlates of recollection in children and adults used item recognition tasks with pictorial materials. Using pictures of real-world objects as both study items and retrieval cues, Cycowicz, Friedmann, and Duff (2003) found highly similar parietal old/new effects in 10-yearold children, adolescents, and young adults. Similarly, Czernochowski et al. (2005) used line drawings of real-world objects as retrieval cues for studied words or realworld photographs. Parietal old/new effects comparable to those of adult participants were found in children as young as 6-8 years. Although these effects might suggest that recollection, as reflected by the parietal old/new effect, is relatively mature at early school age, it could be argued that, rather than reflecting recollective processing, these effects are an indication of children's greater reliance on verbatim memory traces and perceptual matching between study and test materials. To test this possibility we directly contrasted the parietal old/new effects for test blocks in which lowmatching (words) or high-matching (photographs) study materials were defined as targets in the aforementioned study. No differences were found in the parietal old/ new effects for high-matching and low-matching study items, suggesting that a perceptual matching account is unlikely.

Evidence of age invariance of the ERP correlate of recollection in children, adolescents, and young adults has also been reported in other episodic recognition tasks. Sprondel, Kipp, and Mecklinger (2011) employed a continuous recognition memory task in which new (un-repeated) and old (repeated) items were presented continuously and old/new judgments were required for each item. The old/new effects for children (7–8 years), adolescents (13–14 years), and adults are illustrated in Figure 16.1.

Consistent with previous studies, highly similar parietal old/new effects were found in all three age groups. The primary difference across age was a larger and delayed effect in the group of children, for whom the effect occurred 100–200 ms later. In a repeated testing paradigm designed to explore ERP indices of recognition memory across the lifespan, Friedman et al. (2010) tested participants on the same (pictorial) materials over four cycles. Highly similar parietal old/new effects and repetition effects were found in children (9–10 years), adolescents (13–14 years), and young adults.

Despite the broad similarities in the ERP correlates of recollection from 6–8 years to young adulthood, several ways in which this ERP effect differs with age do need to be addressed. First, in most studies the parietal old/new effect is broader, topographically less accentuated, and larger in amplitude in children than in adults. Changes in ERP components of that kind are frequently found in developmental ERP studies (see Segalowitz, Santesso, and Jetha, 2010, for a review) and may reflect functional differences across age groups. For example, children may require an increase in effortful attention towards a retrieval cue, and this may necessitate the contribution of a greater number of brain regions to the old/new effect. The larger magnitude of the parietal old/new effect in younger populations (an example is shown in Figure 16.1) and/or its more widespread topographical distribution could also reflect neurophysiological differences between developing and adult brains, however, such as

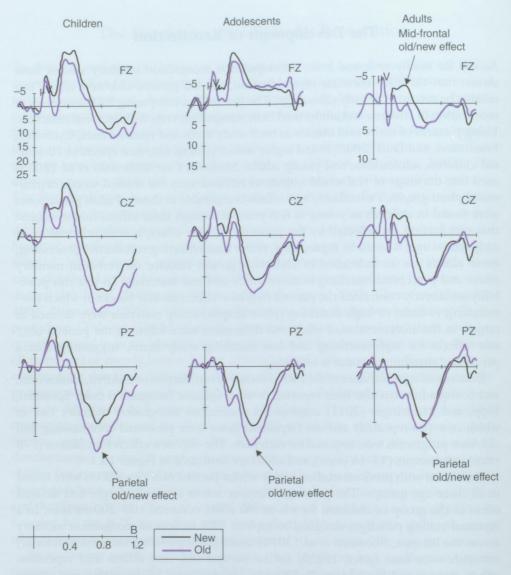


Figure 16.1 Grand average ERP waveforms at the mid-frontal (FZ), central (CZ), and parietal (PZ) recording sites for correctly classified old (blue line) and new items (black line) in children, adolescents, and adults in the continuous recognition task employed by Sprondel, Kipp, and Mecklinger (2011). The vertical lines mark stimulus onset.

less well-refined cognitive networks, or the smaller distance between neural generators and recording sites that results from children's smaller head sizes (Picton and Taylor, 2007).

Second, irrespective of topographical differences, the parietal old/new effect, similar to other ERP effects, is often delayed in children. Delayed ERP components are accompanied by increased response latencies in most cases, and the most important determinant of the latency of information processing is thought to be the myelination of neural pathways, which starts prenatally and continues into young adulthood

(Picton and Taylor, 2007). Incomplete myelination during early childhood is likely to be a candidate factor in the delayed manifestation of the parietal old/new effect in these studies.

Interestingly, although recollection-based processes (as reflected in the parietal old/new effect) at 6–8 years of age have repeatedly been shown to be similar to those of adults, a consistent finding in developmental memory research is that recognition memory performance in item memory tasks continuously improves throughout childhood and adolescence. One interpretation of this pattern is that, rather than being a direct consequence of recollection per se, developmental improvements in recognition memory performance depend upon changes in the cognitive control of retrieval processes and strategies (Friedman, 2012; Siegler, 1998).

The Development of Familiarity

While developmental ERP studies suggest that recollection-based processing is relatively mature at early school age, the picture is less consistent with respect to the development of familiarity. The few behavioral studies that have investigated the development of recognition memory from a dual-process perspective suggest that familiarity matures early and becomes stable during childhood (although the problems surrounding the study of mental experiences in children nonetheless apply here; Billingsley, Smith, and McAndrews, 2002; Ghetti and Angelini, 2008). Conversely, ERP studies reveal an inconsistent pattern of results. In the studies introduced above (Czernochowski et al., 2005; Sprondel, Kipp, and Mecklinger, 2011) the mid-frontal old/new effect, the putative ERP correlate of familiarity, was virtually absent in the young and older child groups, but was present for adults (see also Figure 16.1). Likewise, the mid-frontal old/new effect was obtained for adolescents, young adults, and old adults in the repetition study by Friedman et al. (2010) but was absent for the child group. Two studies have in fact reported old/new differences between 300 and 500 ms at frontal recording sites which differ in polarity from the pattern typically observed (i.e., more positive-going ERPs for new than for old items) (Czernochowski, Mecklinger, and Johansson, 2009; Hepworth, Rovet, and Taylor, 2001). One interpretation of this finding is that children may allocate more attention to new items in some situations, and that this is reflected in an attenuated frontally distributed negativity (the so-called Nc; Czernochowski, Mecklinger, and Johansson, 2009).

In a recent study (Mecklinger, Brunnemann, and Kipp, 2011) we set out to explore whether the ERP correlate of familiarity can be reliably recorded in children of early school age using a more sensitive paradigm designed to capitalize on a widely established operational definition of familiarity. We focused on the different temporal dynamics of familiarity and recollection and tested recognition memory with a response deadline procedure in which recognition decisions have to be given very quickly. Following demonstrations that the use of familiarity is fostered and recollection is diminished under speeded response conditions (Boldini, Russo, and Avons, 2004; Light *et al.*, 2004), we predicted the ERP correlate of familiarity would be present and the correlate of recollection diminished in this condition. Children aged 8–9 years and young adults were tested in a speeded and non-speeded version of a recognition memory test with colored line drawings as stimulus materials.

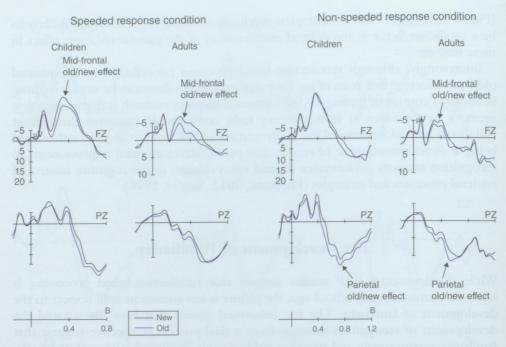


Figure 16.2 Grand average ERP waveforms at the mid frontal (FZ) and parietal (PZ) recording sites for correctly classified old (blue line) and new items (black line) in children and adults in the speeded and non-speeded response condition in the study by Mecklinger, Brunnemann, and Kipp (2011). To take into account the delayed response latencies of children, different response deadlines were used for adults (750 ms) and children (1050 ms) in the speeded condition. The vertical lines mark stimulus onset. This is a modified version of a figure presented by Mecklinger, Brunnemann, and Kipp (2011).

As illustrated in Figure 16.2, consistent with our prediction, children and adults showed the mid-frontal old/new effect and an attenuated parietal old/new effect in the speeded condition. By showing that the ERP correlate for familiarity can be reliably recorded in children under speeded response conditions, these results show the importance of taking account of the differential temporal dynamics of familiarity and recollection when endeavoring to measure the ERP correlate of familiarity and its developmental characteristics. These findings also support models of memory development that assume familiarity matures relatively early and does not show much developmental change after 8–9 years of age (Brainerd and Reyna, 2004; Ghetti and Angelini, 2008; Shing et al., 2010).

In the non-speeded condition, however, age differences were obtained: both groups showed a parietal old/new effect, whereas the mid-frontal effect was observed only for adults. The absence of an ERP correlate of familiarity in the group of children resembles earlier findings from item memory tasks and raises the question why this effect cannot reliably be found in standard episodic recognition tasks in which recognition judgments are given without time pressure. It is conceivable that in such situations children, owing to the immaturity of cognitive control processes, tend to rely more on recollection and are less flexible in using multiple memory signals for episodic recognition. In line with this notion is the finding that the absence of the ERP correlate of familiarity in children in some studies is accompanied by a more

conservative decision criterion than in adults (Czernochowski et al., 2004; Friedmann et al., 2010). This difference might indicate that children judged items as old only when the amount of contextual information available was sufficiently high to inform that judgment. It should also be noted that most of the developmental ERP studies were not explicitly designed to explore ERP correlates of familiarity and recollection (Cycowicz, Friedmann, and Duff, 2003; Czernochowski et al., 2005) and may not have been sensitive enough to dissociate both subprocesses electrophysiologically in children. Likewise, the use of relatively high-frequency words (van Strien et al., 2009) might have ensured that pre-experimental familiarity was at a level that meant that familiarity increments as a function of repetition within the experiment would no longer be diagnostic for episodic recognition in children.

The Impact of Infant Febrile Seizures on the Development of Recognition Memory

Motivated by the fact that it is possible to record the ERP correlates of familiarity and recollection in children at early school age, in a next step we explored whether these electrophysiological measures of memory can also be used to assess abnormal forms of recognition memory development (Kipp et al., 2010). To this end, we investigated children who suffered from febrile seizures during infancy. Infant febrile seizures (IFS) are convulsions triggered by a fever that occurs most often in otherwise healthy children between the ages of 6 months and 5 years (Sadleir and Scheffer, 2008). IFS incidents are associated with hippocampal pathology, and a potential consequence of IFS on episodic memory development might then be disruption of memory processes that depend on the integrity of the hippocampus, such as recollection. We tested this by exploring recognition memory in a group of 17 seven- to nine-year-old children, who suffered from IFS between seven months and three years of age, and an agematched control group. Familiarity and recollection estimates were derived from ERP measures (the mid-frontal and parietal old/new effect). An additional volumetric analysis of the hippocampus was conducted in both groups. The principal findings were as follows. No group differences were found for absolute or normalized hippocampal volumes, but the absolute hippocampal volume (collapsed across groups) correlated positively with recognition memory performance (hit rates), which was high and did not differ between groups. There were no behavioral differences in task performance between the patient and the control group. However, pronounced group differences were obtained in the ERP correlates of familiarity and recollection. Consistent with other ERP studies with children in this age range, we observed a large parietal old/new effect for the control group but no ERP correlate of familiarity (Figure 16.3). For the IFS group, the parietal old/new effect was absent, but a significant ERP correlate of familiarity was obtained.

To the extent that the early frontal and parietal old/new effects in children reflect familiarity and recollection in the same way as in adults, these results suggest that familiarity is preserved and recollection is impaired in school-age children who suffered from IFS. The highly similar recognition performance across groups despite differences in the ERP indices of familiarity and recollection may reflect the compensation of degraded recollection in IFS children by familiarity. These results

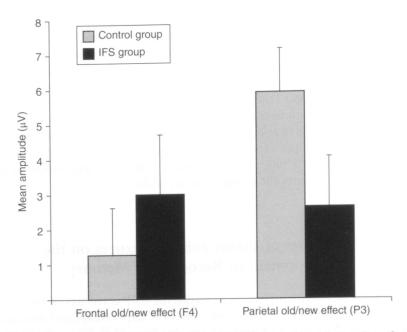


Figure 16.3 ERP old/new amplitude differences (in microvolt) and error bars for the IFS and the control group at a frontal (F4) and a parietal (P3) recording site where the mid-frontal and late parietal effects were largest. The frontal old/new effect was significant for the IFS group but not for the control group, whereas the parietal old/new effect reached significance for the control group but not for the IFS group. This is a modified version of a figure presented by Kipp *et al.* (2010).

not only challenge the commonly held view that IFS does not have consequences for episodic memory development during childhood, they also suggest that even in the absence of structural changes in the hippocampus (as revealed by hippocampal volumetry) IFS can lead to subtle changes in the medial temporal lobe (MTL) memory network, which remain undetected by behavioral measures but can be disclosed by means of ERP measures of episodic recognition.

Retrieval Control Processes

The engagement of memory strategies requires mentally effortful, goal-directed processes that are adapted to enhance memory performance (Bjorklund and Douglas, 2002; for more discussion of strategy use and memory training, see Chapters 15 and 21). Strategies can be used to support the encoding of information into long-term episodic memory, to improve rehearsal but also to retrieve information from memory. Retrieval strategies improve remarkably from early childhood to adolescence (Schneider and Pressley, 1997), and developmental memory studies suggest that children at early school age require more explicit retrieval cues to reinstantiate memory representations than older children. In one illustrative study, children learned pictures together with cue cards that helped to classify the pictures into categories during learning (Kobasigawa, 1974). Later they were asked to remember the pictures under

three different retrieval conditions. Memory performance of the 6- to 7-year-old children was remarkably low under free recall conditions in which no explicit retrieval cues were given but improved to the level of 11- to 12-year-olds when cue cards were available and the children were informed how many pictures had been learned with each cue. Younger children thus appear to learn as much information as their older peers but require specific and explicit cues for successful remembering (Bjorklund and Douglas, 2002).

A classic approach used to investigate the control processes which support the engagement of retrieval strategies involves source memory tasks. In laboratory studies of source memory, participants have to discriminate between items studied in a particular context (e.g., words presented in a male voice or pictures studied on the left side of the screen) from items presented in another context (e.g., words spoken by a female voice or pictures on the right side of the screen) and new, unstudied items. In these tasks, being able to correctly identify the source is enhanced by the engagement of a variety of retrieval strategies. For example, cue specification processes are processes applied to retrieval cues in order to facilitate the access and recovery of task-relevant aspects of a memory trace (Mecklinger, 2010; Rugg and Wilding, 2000). Post-retrieval monitoring refers to the evaluation and verification of retrieved memory contents and is necessary for determining whether retrieved memory content meets the current task demands. It is generally assumed that lateral regions of the prefrontal cortex (PFC) are involved in this range of strategic retrieval operations (Mecklinger, 2010; Simons and Spiers, 2003) and that the generally poor ability of children to specify contextual information associated with an event (Cycowicz, Friedmann, and Duff, 2003; Czernochowski et al., 2005; Drummey and Newcombe, 2002) results from the delayed maturation of the PFC (see below).

In a recent study we investigated ERP correlates of strategic retrieval in a source memory task from a developmental perspective (Sprondel, Kipp, and Mecklinger, 2011). On the basis of prior studies showing that early adolescence is a critical period for the maturation of strategic retrieval processes, this study included a group of 13to 14-year-old adolescents as well as 7- to 8-year-old children. We used a continuous recognition memory task in which participants had to indicate by button press whether or not each item was previously presented within an experimental run. Within-run repetitions were denoted as targets. Critically, participants also completed a second run, in which repetition items from the first run were included (denoted as non-targets) alongside within-run repetitions (targets). These cross-run non-target repetitions had to be classified as new. Successful memory performance in the second run thus required discriminating between targets and non-targets on a temporal dimension. As children should have difficulties in temporal source memory, we expected target/non-target discrimination (operationalized as false alarms to non-targets) to be disproportionally lower than item memory performance (as revealed by false alarms to new items).

In line with this prediction, overall task performance in children was generally lower than in adults, and false alarms to non-targets in children were disproportionally more likely to occur than those to new items. Adolescents' item memory performance was slightly lower than for adults but no difference in source memory was found for the latter two groups. Our ERP analyses focused on the age comparison of the old/new effects for non-targets.

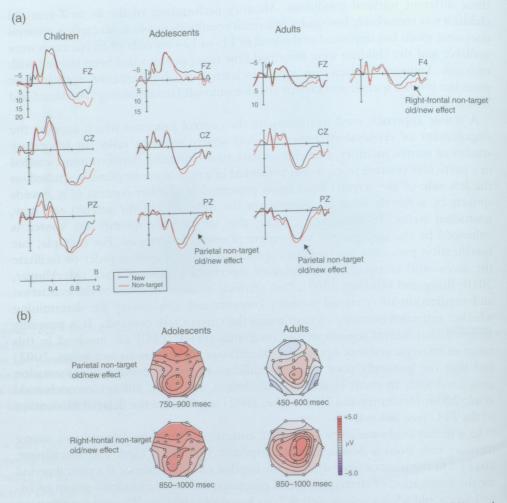


Figure 16.4 (a) Grand average ERP waveforms at the mid-frontal (FZ), central (CZ), and parietal (PZ) recording sites for correctly classified non-targets (red line) and new items (black line) in children, adolescents, and adults in the study by Sprondel, Kipp, and Mecklinger (2011). For adults the ERP waveforms are additionally shown at a right frontal recording site (F4). (b) Scalp distributions of the parietal non-target old/new effects and the right frontal old/new effect for adolescents and adults.

As is apparent in Figure 16.4a, non-target old/new effects were absent in children but present for adults. Critically, a non-target effect was also observed for adolescents, albeit later and with a wider topographic distribution than in adults (Figure 16.4b). A further age-related finding was that an additional late old/new effect for non-targets showed a right frontal distribution for adults, was topographically more widespread in adolescents, and was virtually absent in children. According to the prevailing view, this right-frontal old/new effect reflects processes engaged to monitor and evaluate the products of retrieval (Rugg and Wilding, 2000). In line with this post-retrieval monitoring account is the fact that the effect has often been observed in paradigms that require a considerable degree of retrieval control (Hayama, Johnson, and Rugg, 2008). The observation that

children failed to show this effect at all, and that adolescents did not display the typical right-frontal distribution of this late effect, therefore likely indicates that adults engaged in this kind of post-retrieval processing to a larger extent than adolescents.

Two main conclusions can be drawn from these results. First, the combination of elevated false alarm rates for non-targets and absent non-target old/new effect suggests that children of early school age were less efficient at retrieving the temporal context in which an item occurred and at using this information for adequate source memory performance. One way to solve the source memory task in this experiment is to recollect contextual information for both targets and non-targets and to reject an item as new when it does not meet the correct task demands. Children appeared to be less able to engage in this kind of recall-to-reject strategy. Second, despite comparable source memory performance for adolescents and adults, the non-target retrieval effect was delayed and topographically less focused at parietal recordings in adolescents. In addition, ERP evidence for late post-retrieval monitoring processes was found for adults but not for adolescents and children. The missing right frontal accentuation in adolescents may be a reflection of the immaturity and ongoing refinement of the neural systems supporting strategic retrieval processes during adolescence. Our results resemble those found in another ERP source memory task in which a late positivity to targets showed a clear right frontal focus in adults but was topographically more widespread in adolescence, although only marginally significant group differences in source memory performance were obtained (de Chastelaine, Friedman, and Cycowicz, 2007).

A limitation of the source memory task described above is that the examination of ERP correlates of non-target retrieval is complicated by several factors. The continuous character of the task required the simultaneous encoding of new items and retrieval of old items. Due to these interleaved encoding and retrieval demands, there were no explicit retrieval instructions. This may have induced variability across age groups with respect to the retrieval strategy adopted to perform the task. Using a similar continuous recognition memory paradigm, for example, Czernochowski, Mecklinger, and Johansson (2009) found that children allocated more attention to the encoding of novel (unrepeated) items than to the retrieval of source information associated with repeated items, and, as such, bypassed the engagement of more demanding retrieval strategies. Also, the different repetition lags for targets and non-targets may have made non-target retrieval contingent upon the general ability to retrieve an item's temporal context, thus increasing variability within and across age groups. To overcome these limitations and to explore in more detail the circumstances that determine non-target retrieval in source memory tasks and their developmental characteristics, we employed a variant of a memory exclusion task in which source-specifying features were not repeated at test and the task-relevant source feature was held constant within a test block (Sprondel, Kipp, and Mecklinger, 2012). As the previous study indicated that adolescence is a critical phase for the maturation of strategic retrieval processes, we compared the ERP correlates of target and non-target retrieval in 13- to 14-year-old adolescents and young adults.

Previous studies indicate that in tasks of this kind, the likelihood of non-target retrieval depends on the ease of target discrimination. Several studies report reliable non-target left parietal old/new effects when target discrimination was difficult but less so when target discrimination was easy (Herron and Rugg, 2003; Rosburg, Mecklinger, and Johansson, 2011). This observation implies that whenever target-specifying aspects of memory representations are difficult to reinstantiate, selective target retrieval is

insufficient for adequate task performance and the recollection of both non-target and target information can boost memory performance. With these considerations in mind, we examined target and non-target retrieval in two conditions in which target/non-target discrimination was either easy or difficult. Participants learned list of words presented in one of two colors. At test they had to respond "old" for words presented in the target color and "new" to words presented in the other color and to new (unstudied) words. The color of target and non-target words was similar (red/pink) in the difficult condition and less similar in the easy source discrimination condition (green/pink). To further enhance the differential task demands, longer study and test lists were employed in the difficult condition. As expected, source memory performance was higher in the easy than in the difficult condition and was higher for adults than for adolescents. The ERP data depicting the target and non-target old/new effects for both age groups and difficulty conditions are illustrated in Figure 16.5. Adults showed reliable target old/new effects but no evidence of non-target retrieval in either condition, suggesting that

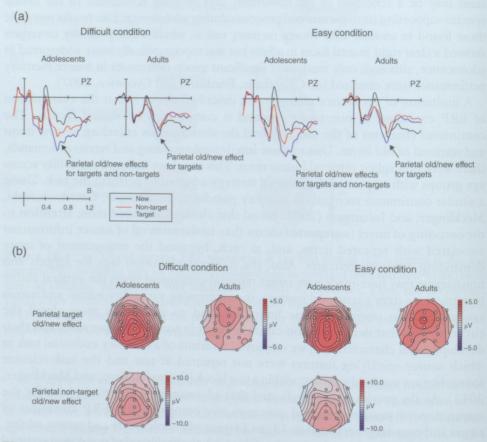


Figure 16.5 (a) Grand average ERP waveforms at the mid-parietal (PZ) recording sites for correctly classified targets (blue line), non-targets (red line), and new items (black line) in the easy and difficult source memory condition for adolescents and adults in the study of Sprondel, Kipp, and Mecklinger (2012). (b) Scalp distributions of the parietal target old/new effects (both age groups) and the non-target old/new effect (adolescents only). This is a modified version of a figure presented by Sprondel, Kipp, and Mecklinger (2012).

adults prioritized target over non-target retrieval irrespective of task difficulty. Conversely, adolescents showed reliable old/new effects for both targets and non-targets.

Notably, the absence of target-selective retrieval was not just a reflection of task difficulty, in the sense that the lower target discriminability boosted additional non-target retrieval for adolescents. Source memory performance for adults in the difficult condition and adolescents in the easy condition was virtually identical. Nevertheless there was a non-target retrieval effect for adolescents but not for adults in this difficulty-equated comparison. This striking finding indicates that rather than solely reflecting lower target discriminability, the absence of target-selective retrieval in adolescents is a reflection of immature strategic retrieval processes. This finding is important, because it implies that despite performance comparable to that of adults there are still immaturities in the adolescent brain which limit the flexible use of cognitive control to support episodic recognition (Luna, Padmanabhan, and O'Hearn, 2010).

Insights into the mechanisms that underlie the ERP difference between the target and non-target old/new effects come from an additional correlation analysis. We found that for adults only, the ERP target versus non-target difference amplitude correlated positively with working memory capacity as revealed by the operation span task (Turner and Engle, 1989) (Figure 16.6). In other words, the degree to which the ERP old/new effects were larger for targets than for non-targets increased as working memory capacity increased in adults but not in adolescents (see Elward and Wilding, 2010, for similar results). This finding suggests that the more resources available for cognitive control, as indexed by working memory capacity, the more likely it is that a target-selective retrieval strategy will be effectively implemented. The absence of this correlation in adolescents, whose working memory capacity scores did not differ from adults, provides further evidence for the immaturity of cognitive control during adolescence and indicates that 13- to 14-year-olds are not yet as efficient in allocating

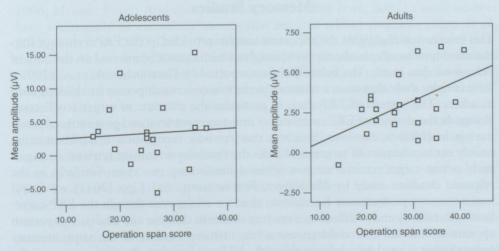


Figure 16.6 Scatterplots showing the correlation between the ERP target/non-target difference amplitudes at a left parietal recording site (P3) and working memory capacity in the easy condition for adolescents and adults in the study of Sprondel, Kipp, and Mecklinger (2012). The correlation was significant for adults (r=0.49, p<0.05) but not for adolescents (r=0.05). This is a modified version of a figure presented by Sprondel, Kipp, and Mecklinger (2012).

resources for cognitive control to prioritize target over non-target recollection. An alternative yet complementary account can be derived from the recent proposal that the parietal old/new reflects the active maintenance of recollected information (Vilberg and Rugg, 2009). By this account, adult participants with high working memory capacity are more likely to allocate cognitive resources to the active maintenance of recollected task-relevant (target) information. In any event, further studies are warranted to explore the extent to which processes involved in recollecting and maintaining episodic contents depend on the availability of working memory resources and how this relationship is modulated by the maturation of cognitive control processes.

Taken together, the poorer source relative to item memory performance of children can be related to immature cognitive control operations. While children do not show evidence for the strategic use of non-target retrieval to improve source memory performance, this ability seems to develop during adolescence. In this phase of memory development, ERP correlates of strategic retrieval can be observed although they are poorly refined compared to those recorded from the adult brain (de Chastelaine, Friedman, and Cycowicz, 2007; Sprondel, Kipp, and Mecklinger, 2011). In the current task, adolescents engaged in additional, perhaps compensatory, retrieval of non-targets. The absence of a correlation between working memory capacity and the magnitude of the ERP index of selective target recollection in adolescents points to a reduced efficiency in allocating resources for cognitive control to the retrieval and maintenance of episodic memory contents. These data add to the converging evidence that adolescence is characterized by limitations in several subcomponents of cognitive control, such as response inhibition or post-error processing (Velanova, Wheeler, and Luna, 2008).

Relationship to Other Neuroscientific Developmental Memory Studies

This brief review highlights the important insights provided by the ERP technique into the development of episodic memory, insights which cannot be inferred on the basis of behavioral data alone. The behavioral data reported by Czernochowski et al. (2005), for example, show that source memory performance is much poorer in children than in adults. The pattern of ERP data, in particular the correlate of target recollection alongside the absence of ERP correlates of non-target retrieval and post-retrieval monitoring in children, however, indicates that episodic recognition in children relies mainly on recollection of targets and lacks the flexibility to initiate retrieval strategies such as non-target retrieval or post-retrieval monitoring processes. Similarly, in the response deadline study by Mecklinger, Brunnemann, and Kipp (2011) we found lower memory performance for children than for adults even though the ERP correlates of familiarity and recollection were very similar in children and adults. This pattern appears to indicate that children use a less matured version of the same memory network that is used by adults in this task. ERP studies also allow inferences on the developmental trajectories of memory processes even in the absence of differences in memory performance across age groups. As reviewed above, despite the absence of performance differences between adults and adolescents, we observed changes in the topography of ERP correlates of non-target retrieval and post-retrieval monitoring which are in line with underdeveloped control processes during adolescence which

differ from those of adults (Sprondel, Kipp, and Mecklinger, 2011). Similarly, in a further study in which source memory performance was equated across the two age groups, we found that adolescent but not adult ERPs were characterized by a correlate of non-target retrieval, indicating that adolescents were not yet able to strategically prioritize target over non-target retrieval (Sprondel, Kipp, and Mecklinger, 2012).

These studies have shown that all the age groups examined here engaged recollection when discriminating old and new items, and that the immaturity of episodic remembering appears to result from the slower and protracted maturation of prefrontal-based control systems that allow the flexible use of retrieval strategies. Retrieval control processes which support the engagement of retrieval strategies can operate at multiple stages, and the studies reviewed here focused on those control process that support retrieval strategies during retrieval or at post-retrieval stages. The maturation of control processes that can support successful retrieval even at pre-retrieval stages, such as retrieval orientation, is currently under investigation (Sprondel, Kipp, and Mecklinger, 2013).

The subprocesses of retrieval control that allow the flexible use of what is retrieved from memory emerge in middle childhood to adolescence and are associated with robust patterns of activation in the PFC and posterior parietal cortex (Cabeza et al., 2008; Hutchinson, Uncapher and Wagner, 2010; Mecklinger, 2010; see also Chapter 7). One notable longitudinal structural neuroimaging study revealed that the volume of gray matter in the frontal and parietal lobes shows a pre-adolescence increase followed by a decline in the post-adolescence phase (Giedd et al., 1999). Additional studies are necessary to clarify how these structural changes in the frontal and parietal cortex are related to the delayed maturation of cognitive control.

Evidence for the view that the delayed maturation of the PFC determines poor source memory performance in children comes from recent neuroimaging studies. While the majority of these studies have focused on memory formation (Chiu et al., 2006; Menon, Boyett-Anderson, and Reiss, 2005; Ofen et al., 2007) a small number have additionally or exclusively investigated retrieval-related processes (Kipp et al., 2012; Ofen et al., 2007, 2012; Paz-Alonso et al., 2008). Using a false memory paradigm, Paz-Alonso et al. (2008) found less lateral PFC activation related to the retrieval of semantic features of studied words and no PFC activation related to post-retrieval monitoring in 8-year-olds as compared to older children and adults. In a seminal fMRI study by Ofen et al. (2007), activations in encoding-related brain structures were compared with age-related improvements in an un-scanned source memory task in children and adults ranging from 4 to 24 years. Participants viewed line drawings and made memory judgments regarding contextual features of the study episode. Source memory performance increased with age and correlated with activation in the lateral PFC (Brodmann area [BA] 9), one of the encoding-related brain structures identified before. No correlations with source memory were found in any other encoding-related brain region, and no reliable correlations between source memory and any brain activation pattern remained when the age factor was controlled for. In addition, the PFC regions critically involved in successful memory encoding and source retrieval were additionally characterized by negative correlations between gray matter and age. Together, these results speak for a strong association of childhood and adolescent memory development and both the structure and function of the PFC.

These data provide strong evidence for the view that it is the functional immaturity of lateral PFC regions that limits children's ability to discriminate between source-specifying

memory representations. This notion is in line with the view of the important role the PFC plays in the maturation of episodic memory processes. In addition, several MTL regions, including the hippocampus, have been shown to be critically associated with the formation and retrieval of episodic memories. These MTL regions reach maturity during the first year of life, even though the dentate gyrus within the hippocampal formation shows prolonged development (Richmond and Nelson, 2007). Consistent with this early maturation of memory-relevant MTL regions, the imaging studies reviewed here reveal few age differences in MTL activity related to memory encoding and retrieval (Chiu et al., 2006; Ofen et al., 2007, 2012), although Paz-Alonso et al. (2008) report less recruitment of the hippocampus during item-specific recollection in 8-year-olds. This finding suggests that a network comprising MTL and PFC regions is critically involved in memory retrieval and its strategic control. MTL regions in this network show little developmental change during childhood and adolescence, and this early maturity of the MTL system may also account for the small developmental changes in familiarity and recollection and their ERP correlates. Conversely, it is the late maturation of the PFC-based brain systems that underlies the delayed developmental trajectories of strategic retrieval processes.

Conclusions

This selective review of ERP studies on the development of episodic memory shows how the ERP technique provides important insight into the developmental trajectories of episodic retrieval and its modulation by controlled cognitive operations. The review has focused on two features which are, in our view, central for the understanding of episodic memory development: the maturation of episodic recognition memory and the development of retrieval control as revealed by source memory tasks. Investigation of the development of recognition memory reveals early maturation of recollection and familiarity and their ERP correlates at the age of 6-8 years but a limited and inflexible use of strategic retrieval at this phase of memory development. The reduced ability to specify contextual details of memory contents is likely to be a direct consequence of the immaturity of prefrontal-based systems for retrieval control. These systems show maturational changes during adolescence, a phase in which source memory performance begins approximating that of adults. These changes are assumed to be characterized by relatively poorly refined cortical networks and an inefficient allocation of resources for cognitive control to episodic remembering. From here, it is necessary to conduct more fine-grained investigations into the developmental trajectories of the cognitive control of episodic remembering during the critical adolescent phase, and to use combined ERP and brain imaging approaches to further characterize these developmental trajectories and their neural characteristics.

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