

**Age Differences in Familiarity and Recollection:  
ERP Evidence for the Development of Recognition Memory  
in Childhood**

by

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Age Differences in Familiarity and Recollection:

ERP Evidence for the Development of  
Recognition Memory in Childhood

Dissertation

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***Memory is the food of mental growth.***

Nelson Cowan, *The Development of Memory in Childhood* (1997)



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Czernochoowski, D., Mecklinger, A., Johansson, M., & Brinkmann, M. (in press, Cognitive, Affective and Behavioral Neuroscience). Age-related differences in familiarity and recollection: ERP evidence from a recognition memory study in children and young adults.<sup>2</sup>

Czernochoowski, D., Mecklinger, A., Johansson, M., & Brinkmann, M. (in preparation). Why does this picture look familiar? An event-related potential study of continuous recognition memory in children and young adults.<sup>3</sup>

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<sup>1</sup> Experiments 1 and 2A

<sup>2</sup> Experiment 2B

<sup>3</sup> Experiment 3

# 1 Introduction

Depending on the task at hand, children's memory performance can vary enormously. On the one hand, young children acquire a variety of new skills and new knowledge every day. The seemingly effortless acquisition of language is just one example for how a young brain is able to collect and store new information. On the other hand, children's memories sometimes can be inaccurate and unreliable, for instance when important pieces of information are missing in a story about the other day's activities, but other details that never actually happened suddenly appear in that story.

One central question arising in such situations is what is unique about children's memories. Is there a qualitative difference between memory functions in adults and children? Alternatively, an increase in memory accuracy with age could reflect a more gradual development that could better be described in terms of increasing efficiency based on ongoing cognitive development rather than by assuming different processes.

One way to find out more about qualitative differences is to look for specific profiles of memory strengths and weaknesses across age groups. Children are prone to errors especially when the sources of information need to be retrieved along with the item itself. In this respect, they resemble the elderly. But do different profiles for item and source memory provide substantial evidence for different underlying processes in

adults and children, especially in the light of related memory problems in old age? Since adults sometimes use frontal brain structures that are not functionally mature in children during memory retrieval, is there evidence for an underlying neuronal substrate that is responsible for the discrepancy in performance between children of various ages and adults?

One way to find out more about qualitative differences in memory processing in children and adults is to look for dissociations in adults' memory processes. For instance, seeing a familiar face without being able to tell under which circumstances it was previously encountered is a well-known example of familiarity-based recognition memory (cf. Mandler, 1980). In other situations, the contextual details such as the person's name are easily accessible along with the face. Until now it remains unclear at which age during childhood this acontextual form of explicit memory develops and how it is related to contextual memory, i.e. the ability to recollect many specific details, thereby placing memories into the context of the study episode. The mechanisms underlying these two types of memory, familiarity and recollection, and their development during childhood are the focus of the present investigation. In three experiments, children and adults were examined during episodic memory retrieval using evidence from event-related potentials in order to compare behavioral performance as well as the underlying brain mechanisms.

In the following chapter, models of long-term memory are briefly resumed with a particular focus on dual process models of recognition memory and its neural correlates that give rise to distinct event related potential (ERP) components. In Chapter 3, real-life consequences of memory structures that have been disrupted very early are illustrated in three cases with selective hippocampal lesions acquired during or shortly after birth. These cases challenge traditional concepts of memory systems and raise new questions about memory development. Also, the importance of top-down control guided by the frontal lobes for successful memory retrieval is stressed by reviewing evidence from frontal lobe patients and healthy controls performing tasks of various specificity. Finally, the time frame of delayed maturation of the frontal lobes and other memory-related brain structures is briefly resumed.

In Chapter 3, children's memory performance is described in more detail. The methods predominantly used in developmental research as well as first findings with respect to recognition memory are pointed out. Particular focus is placed on the few

recognition studies with children that have used event-related potentials to provide additional information about memory development.

The method of recording electrophysiological brain activity and the advantages of examining event-related potentials are described in Chapter 4. At the end of this chapter, the four Experiments conducted in the present context and their main objectives are summarized.

In Experiment 1, an auditory novelty oddball paradigm was used to differentiate between unspecific maturational differences across age groups and to distinguish them from waveforms more specifically related with memory processes (Chapter 5).

Memory performance in an inclusion paradigm was examined in Chapter 6 (Experiment 2 A). In order to detect developmental changes occurring in middle childhood on the one hand and in adolescence on the other hand, 6-8 year old and 10-12 year old children were compared with young adults (20-29 years). The three age groups were required to recognize pictures of every-day objects and animals after studying either words or photos of the items.

In an exclusion paradigm, the same participants were required to indicate whether a given item had been presented in a target context (i.e. word or photo) in the previous study phase or not (Experiment 2 B). This paradigm was chosen because both subprocesses of recognition memory (i.e. familiarity and recollection) will lead to different responses, since familiarity is not sufficient to solve this task. Only recollection of target items along with their context will lead to correct responses. The results of this source memory task are summarized and discussed in Chapter 7.

In Experiment 3, the source of an information was defined by the temporal order of presentation. Older children and adults were required to indicate repetitions in a continuous recognition paradigm, either in a series of new or in the context of previously repeated items. (Chapter 8).

Finally, in Chapter 9 the results of the present experiments are discussed in a more general framework. Four key issues are selected and discussed in more detail, while open questions and conclusions are highlighted.

A German summary of the theoretical background and the experiments conducted for this thesis and the discussion is given in Chapter 10.



## 2 Recognition memory and its neuronal correlates

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In this chapter, models of memory systems in general and dual process models of recognition memory in particular are described (Section 2.1). The distinction between familiarity and recollection originally established on the basis of behavioral data and introspective observations is confirmed by a number of recent studies using various neurophysiological methods with a focus on event-related potentials (Section 2.2). Patients with selective lesions can provide a new methodological insight into the functional significance of precisely defined anatomical structures. In Section 2.3, the clinical observations and extensive neuropsychological testing of Jon, a patient with selective bilateral hippocampal lesions, are described as well as the considerable debate about hippocampal functioning in healthy participants that resulted from this case study. Section 2.4 deals with the contributions of the frontal lobes to memory processes, with a particular focus on memory retrieval. Chapter 2 concludes with a description of the delayed maturation of the prefrontal cortex (PFC) during childhood.

## **2.1 Dual process models of recognition memory**

A number of models have tried to explain the complex findings obtained while studying recognition memory in healthy individuals and amnesic patients. Most models agree on the distinction between explicit memory that can be consciously accessed and implicit memory guiding future behavior although no conscious memory trace is accessible (e.g. Squire & Zola, 1996, 1998). Implicit memory as measured by indirect tasks such as word stem completion or lexical decisions is usually unimpaired in amnesic patients (cf. Yonelinas, 2002).

Explicit memory has further been subdivided into episodic and semantic modules. In the Squire model, declarative (i.e. explicit) memory is described as consisting of two parallel subsystems that are responsible for either personal events (episodic) or general facts (semantic). Both are considered to depend on the same medial temporal lobe structures on the basis of examination of amnesic patients who were impaired in both memory for episodes and for general facts (Squire & Zola, 1998).

Memory abilities can be assessed using various retrieval tasks. In (cued) recall the task is to retrieve previously studied items with or without the help of specific retrieval cues. In recognition memory tasks, previously studied items are presented again at test along with new items. Participants are asked to indicate whether the items have been shown before or not. Dual process models assume that two qualitatively distinct processes are involved in recognition memory: a relatively fast process that is accompanied by a context-free feeling of familiarity and a slower, more controlled process that reinstates certain details of the study episode to be remembered (recollection). An extensive review of experimental manipulations that allow to differentiate between those two processes is given by Yonelinas (2002). Similar to this distinction, Tulving introduced an experimental technique to dissociate the subjective awareness during recognition (Tulving, 1985). It is possible to distinguish between items for which participants are able to become consciously aware of some aspects of the previous presentation ('remember', i.e. they will be aware of when and where they have previously met a person before) and those that give rise to a feeling of familiarity in the absence of remembering, so-called 'knowing' (i.e. a person is familiar, but participants cannot think of where they have met before).

Episodes that have been personally experienced typically contain many details connected with the original event, whereas semantic knowledge is usually not connected with a detailed reinstatement of the context in which the fact was encountered for the first time. Although the distinction between episodic and semantic memories and the subprocesses of recognition memory, namely recollection and familiarity, come from different theoretical backgrounds and are based on different assumptions, there is growing evidence that semantic memory and familiarity-based recognition on the one hand and episodic memory and recollection on the other hand bear functional similarities and are mediated by at least partly the same neural systems (Vargha-Khadem et al., 1997; Varha-Khadem, Gadian, & Mishkin, 2001; Vargha-Khadem, Salmond, Watkins, Friston, Gadian, & Mishkin, 2003). With respect to the development of these memory systems, the model developed by Tulving and Markowitsch (1998) states that episodic memory develops considerably later than semantic memory, since children acquire semantic knowledge before they remember episodes like adults do (Tulving & Markowitsch, 1998). This in turn leads to the hypothesis that young children predominantly rely on familiarity and only gradually increase their use of recollection.

## ***2.2 Neuronal correlates of familiarity- and recollection-based recognition***

Strong evidence for two qualitatively different subprocesses of recognition memory comes from the search for the underlying neural substrate(s). Aggleton and Brown (1999, see also Brown & Aggleton, 2001) were able to demonstrate that familiarity and recollection are mediated by different neuronal circuitries and accomplished by different binding mechanisms. The explicit retrieval of specific details of a study episode depends on inter-item binding mechanisms mediated by the hippocampus, whereas the perirhinal cortex has been associated with the assessment of familiarity. For instance, single cell recordings from the anterior inferior temporal cortex of monkeys, including the perirhinal cortex, during the repeated presentation of novel or familiar items (i.e. items the animals have been familiarized with prior to the experiment) have demonstrated that some neurons respond to the first presentation

of an item, but less so to repeated presentations (Brown & Aggleton, 2001; see also Wan, Aggleton, & Brown, 1999; Xiang & Brown, 1998). Since this pattern holds for familiar as well as novel items, these neurons appear to be specialized to detect relative recency. Other neurons respond to novel stimuli even when presented repeatedly, but respond less to familiar stimuli irrespective of whether they are presented for the first or for the second time, thereby signalling relative familiarity. Novelty is detected by a third type of neurons that responds less to repeated presentation of novel items, at the same time the duration of the response is shorter for familiar stimuli. These three types of neurons are found mainly in the perirhinal cortex and are the only neural substrate known so far that can provide a signal for the relative familiarity, relative recency or novelty of an item.

In an event-related fMRI study, Eldridge et al. (2000) provided evidence for a selective involvement of the hippocampus during recollection-based recognition: activity in the hippocampus only increased when memory retrieval was accompanied by recollection and not during familiarity-based memory (Eldridge, Knowlton, Fumanski, Bookheimer, & Engel, 2000; but see Fan, Snodgrass & Bilder, 2003; for more extensive reviews, see e.g. Brown & Aggleton, 2001; Simons & Spiers, 2003).

### **Evidence from event-related potentials**

Studies recording ERPs in the test phase of recognition memory tasks have found a robust ERP difference between correctly judged old and new items: this ERP old/new effect starts around 300 ms after item presentation and takes the form of more positive waveforms for correctly recognized old compared to new items that lasts for several hundred milliseconds (cf. Mecklinger, 2004). An increasing number of recent ERP studies suggest that the topographical distribution and the time course of the old/new effect allow to disentangle both subprocesses involved in recognition memory. Typically, an early midfrontal old/new effect between 300 and 500 ms can be dissociated from a later effect with a more parietal topography between 400 and 600 ms (cf. Curran, 2000; Mecklinger, 2000). These dissociations have been demonstrated in a variety of ERP studies (Curran, 2000; Curran & Cleary, 2003; Friedman & Johnson, 2000). The parietal effect has been demonstrated to vary according to the amount of information retrieved from episodic memory (Wilding, 2000) and hence been taken as a correlate of recollection (e.g. Wilding & Rugg 1996). In contrast, the early midfrontal component has been associated with the

global assessment of the similarity between study and test items that is accompanied by a subjective feeling of familiarity (e.g. Curran, 2000; Nessler, Mecklinger, & Penney, 2001). Although the proposed functional significance of the early mid-frontal component has not remained unchallenged (e.g. Yovel & Paller, 2004), many studies conclude that the early midfrontal component is independent of recollection since it does not vary along with the amount of information retrieved in source tasks (Wilding, 2000). Recent studies suggest that in addition to the midfrontal effect between 300 and 500 ms reflecting an amodal matching between study and test items, there is an even earlier onsetting fronto-polar old/new effect which is modality specific (Curran & Dien, 2003). The midfrontal old/new effect has furthermore been dissociated from ERP correlates of implicit memory processes (Nessler, Mecklinger, & Penney, 2005; Rugg et al., 1998).

For instance, participants in the experiment by Curran and Cleary (2003) studied pictures and were explicitly instructed to memorize each picture's left/right orientation. During the test phase, old pictures were presented along with new pictures and similar old pictures that were left/right mirror reversals. The task was to respond 'old' only to stimuli that were repeated in the previous orientation and to reject both similar and new pictures. Since both studied and similar pictures should elicit a feeling of familiarity, these were compared with new stimuli. In a similar line of argumentation, new items were compared with those conditions that required recollection for correct responses, namely correctly accepted old or correctly rejected similar stimuli. According to the predictions, an early (300-500 msec) midfrontal effect was associated with familiarity-based false alarms to similar pictures, whereas recollection-based memories were associated with a 400-800 ms parietal effect only for those participants showing good discrimination between old pictures and their mirror images (Curran & Cleary, 2003).

A third old/new effect that is often observed during recognition memory retrieval is pronounced at right frontal recordings. It is maximal at around the time the participants are responding and sustains in time for several hundred milliseconds. This old/new effect was first reported in a source memory study by Wilding and Rugg (1996), in which it was termed the right frontal old/new effect. While it has originally been considered as an electrophysiological correlate of successful retrieval (e.g. Wilding & Rugg, 1997), it has more recently also been found in situations in which memory retrieval was not successful (e.g. Trott, Friedman, Ritter, Fabiani, &

Snodgrass, 1999). Hence the effect is less likely to reflect retrieval success per se, but rather processes contingent upon retrieval, also termed post-retrieval monitoring and evaluation (cf. Friedman & Johnson, 2000).

Finally, in a number of recognition memory studies, a negative going old/new effect, the late posterior negativity (LPN), has been reported over posterior regions with about the same temporal characteristics as the right frontal effect. On the basis of an extensive literature review, Johansson and Mecklinger (2003) suggest that the LPN is related to forming and maintaining a bound representation of the recognized item and task-relevant contextual attributes pertaining to the study episode.

### ***2.3 Neuropsychological findings***

Unlike the well-controlled lesion studies with animals, for a variety of reasons brain damage that occurs in human patients is quite often distributed broadly over several brain structures. Rare cases of selective lesions offer the opportunity to examine the functional consequences of the loss of specific brain tissue for cognitive functions. Vargha-Khadem and colleagues (1997) reported three cases with early bilateral hypoxic lesions that were selective to the hippocampus. Although these patients were unable to retrieve episodic information, they were able to acquire semantic knowledge after their injury unlike most adult amnesics. Considerable debate is still ongoing whether the relative sparing of semantic memory is due to a) the selectivity of the insult to only the hippocampus sparing the subhippocampal cortices, b) the partial sparing of the hippocampus itself or c) some functional reorganisation occurring after this very early injury (Vargha-Khadem et al., 1997, 2001; Squire & Zola, 1998).

The most pressing problems that parents reported in the patients' everyday life involve extreme difficulties in spatial navigation, orientation in time and date as well as an inability to remember the days' activities. Neuropsychological testing confirmed these parental observations: in all tests of delayed recall, performance levels were significantly impaired and close to floor levels (Vargha-Khadem et al., 1997).

To elucidate the exact nature of this memory impairment, extensive testing of one of these patients, Jon, aged 23 at the time, and two age-matched controls was

performed (Baddeley, Vargha-Khadem, & Mishkin, 2001). Careful comparison of recognition and recall tasks that were matched for difficulty confirmed the earlier observations that recall performance was considerably impaired. On the other hand, performance in recognition tasks was within the normal range. Recall performance of a TV news show improved drastically when the material was presented repeatedly (4 vs. 1 presentations), suggesting that under certain possibly quite restricted conditions recollection might not critically depend on the hippocampus. However, the attempt to ask about the subjective experience during memory retrieval ('remember-know' judgments) failed because it was not possible to explain the meaning of 'remember' to Jon (Baddeley et al., 2001). In an ERP study with Jon, parts of these findings were confirmed by the ERP components. While the early (300-500 ms) midfrontal effect was found for previously studied compared to new words, Jon lacked the parietal ERP effect associated with recollection that was reliably elicited in healthy controls between 500-700 ms (Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001). These findings confirm the notion that recollection critically depends on the hippocampus, but that familiarity and semantic knowledge do not involve contextual information and therefore are not critically dependent on inter-item bindings mediated by the hippocampus (Baddeley et al., 2001; Düzel et al., 2001; Vargha-Khadem et al., 1997, 2001).

Two explanations are conceivable for these results: either children with developmental amnesia are still able to perform recognition tasks because children in general predominantly rely on memory processes that do not depend on the hippocampus (i.e. familiarity and semantic knowledge). The alternative explanation attributes the sparing of semantic memory in developmental amnesia to functional reorganisation, i.e. plasticity in young brains. According to this argument, the age of injury should affect the severity of the memory impairments with earlier injuries having less devastating effects on memory processes. Vargha-Khadem and colleagues (2003) were able to demonstrate that 6 children who suffered an early hypoxic-ischemic injury (within the first three months of life) did not exhibit fewer long-term memory problems than a second group of patients injured between the ages of 6 and 14 years. Vargha-Khadem concludes if developmental amnesia is critically dependent on an early timing of injury, then this critical period extends at least from birth to puberty (Vargha-Khadem et al., 2003).

McClelland and colleagues (1995) differentiate between episodic (i.e. dependent on hippocampal activity) and semantic memories (i.e. not dependent on hippocampus, but rather neocortical structures) in terms of the rate of memory consolidation: while incorporation of newly formed memory representations into the neocortical system takes a long time, hippocampal incorporation rates are considerably shorter. When acquiring new semantic knowledge, this mechanism is able to reduce interference resulting from already existing semantic representations at the cost of a long learning period. Based on findings on retrograde amnesia and a connectionist model, they propose that the rate of neocortical learning might vary with age, since at a young age there is no need to reduce interference due to former experiences. The acquisition of new information could be faster during a time when semantic knowledge needs to be expanded rapidly, and then gradually slow down to enable the integration of new semantic information to the already existing knowledge base. The authors made the prediction that in younger amnesics a '...much more rapid acquisition of the shared structure of events and experiences ... than in older amnesic groups' should be seen (McClelland, Naughton, & O' Reilly, 1995, p.447). This prediction could explain why Jon and the other cases of developmental amnesia were able to acquire new semantic knowledge unlike older patients with similar hippocampal lesions. Guillery-Girard and colleagues (2004) recently demonstrated the acquisition of new semantic material in two young amnesic participants using repeated presentation of the material in a prospective study (Guillery-Girard, Martins, Parisot-Carbuccia, Eustache, 2004).

## ***2.4 Frontal lobe contributions to memory processes***

Frontal lobe structures have been implicated to play a crucial role in memory formation at encoding (Buckner, Kelley & Petersen, 1999) as well as retrieval (Düzel et al., 1999; Rugg & Wilding, 2000; Wagner, 2002). At encoding, the areas within the mediotemporal lobes (MTL) receive input from many cortical structures. The binding of these inputs to item-context conjunctions or even to existing memory representations has been connected to the hippocampus. A critical part of newly formed associations is the input the hippocampus receives from the PFC (Buckner et

al., 1999). Successful memory retrieval of these bound representations from long-term memory involves the search for specific item attributes that have been studied. Consistent with the notion that prefrontal control mechanisms are essential for effective memory retrieval, several clinical studies examining patients with frontal lobe pathology report specific problems during memory retrieval: Mayes and colleagues (2002) demonstrated that frontal lobe patients were able to perform at close to normal levels in an item recognition test, but were at floor levels when source information was asked for (cf. Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002; Simons & Spiers, 2003, Simons et al., 2002, Schneider, 2003). This deficit is sometimes called source amnesia (Simons et al., 2002). In a similar vein, elderly people have been demonstrated to suffer from less effective prefrontal control functioning and have more severe problems with source memory requirements than would be expected from their item memory performance (e.g. Friedman, 2000; Trott et al., 1999; Dywan, Segalowitz, & Webster, 1998).

Memory impairments in frontal lobe patients - and to a lesser degree also in the elderly - are prominent in tasks critically depending on recollection. Whereas item recognition can be based on both familiarity and recollection, details about the study episode are necessary in order to successfully decide in which context the item has been presented before. Source memory requires the reinstatement of item features and their context (i.e. recollection). Often the recollected details about an item are not those that are used as test probes. Therefore successful source memory involves the recollection of the relevant item features and the specific search for these relevant item attributes. In this respect, source memory tasks resemble recall tasks, which require the use of specific retrieval strategies in addition to recollection of the items (Simons et al., 2002).

### **Role of the PFC during retrieval**

A number of recent studies have stressed the important role of the prefrontal cortex (PFC) during explicit memory retrieval (e.g. Ranganath 2004; Dobbins, Simons, & Schacter, 2004; Wagner, 2002). It is generally assumed that control processes mediated by the prefrontal cortex are responsible for guiding the efficient search for relevant item attributes or item-context attribute conjunctions (e.g. Dobbins, Foley, Schacter & Wagner, 2002; Simons & Spiers, 2003). These control processes involve hierarchical top-down control and the selection and maintenance of task-relevant information. In this respect, the interaction between the PFC and the MTL is

particularly important during memory retrieval: while the ventrolateral PFC is responsible for the specification and elaboration of retrieval cues, the dorsolateral PFC is engaged during the comparison of the retrieved information and the particular retrieval criteria (cf. Simons & Spiers, 2003). In the dynamic filtering theory, Shimamura (2002) distinguishes between four hierarchically organized aspects of executive control mediated by the PFC: Selecting, Maintaining, Updating and Rerouting. Selection of relevant information and its maintenance in working memory are more basic abilities that are necessary for a variety of tasks. Updating or modulation of information (as measured for instance in the backward digit span) involves more complex operations. Rerouting refers to the ability to switch from one cognitive process to another and is assumed to be the most complex aspect of executive control (Shimamura, 2002).

Rugg and Wilding (2000) distinguish between several classes of retrieval processes: retrieval mode (a maintained state associated with intentional retrieval), retrieval orientation (dependent on the specific task at hand, e.g. recognition vs. source judgements), retrieval effort (processing resources that vary along with task difficulty) and retrieval success (processes elicited only by true memories, Rugg & Wilding, 2000). Düzel and colleagues (1999) compared ERPs and PET activation during episodic and semantic retrieval of old and new words denoting living and nonliving items. Episodic retrieval was accompanied by right prefrontal activation, whereas semantic retrieval was associated with left frontal and temporal lobe activity (Düzel et al., 1999). Combining the high temporal resolution of ERPs with the superior spatial resolution of PET allowed to trace the origin of the ERPs at frontal recording to activity within in the PFC.

Even episodic tasks can require various degrees of specificity with which information is searched for and retrieved from memory. The more specific the retrieval task, the more important are control processes for the successful retrieval of *relevant* information from episodic memory (Ranganath & Paller, 1999, 2000). Ranganath (2004) recently proposed a model of hemispheric asymmetries in prefrontal control as a function of specificity of the retrieved information (see also Nolde, Johnson & Raye, 1998). According to this account, the left PFC is responsible for the selection of specific information from the study episode, whereas the right PFC is concerned with the retrieval of more undifferentiated memory contents that requires close monitoring of item familiarity. This view is confirmed by an fMRI study by Dobbins

and colleagues (2004), in which item memory and judgments of frequency was directly compared. For judgments of frequency, it was predicted that the recollection of an item's previous occurrence will be largely ineffective since all items have previously occurred, hence, participants need to monitor the level of each item's familiarity. In fact, this monitoring was reflected by right prefrontal activity that was not influenced by relative difficulty or the presence or absence of an identical retrieval cue (Dobbins et al., 2004).

### **Delayed maturation of the PFC**

The fact that the frontal lobes are not only implicated in the control of memory functions, but also among the latest brain structures to mature in the course of development reveals their relevance for studying memory development. In a recent structural MRI study, delayed verbal memory functioning in children aged 7-16 years was predicted by frontal lobe gray matter volume *reduction*, and more so than by MTL gray matter volume or age (Sowell, Delis, Stiles, & Jernigan, 2001). Paus (2005) recently proposed that synaptic pruning, i.e. the elimination of unused synaptic connections, might not be the only reason for a reduction in grey matter. Alternatively, it might be closely related to the increase of cortical myelination occurring in adolescence, sometimes related to the onset of puberty. While it is currently impossible to distinguish between the effects of these two factors, both mechanisms eventually lead to more efficient synaptic transmissions (cf. Paus, 2005).

There is evidence that memory related brain structures within the medial temporal lobe also continue to develop during childhood and adolescence (i.e. 6-12 years). While most structures within the hippocampal formation are cytoarchitecturally mature prenatally, the dentate gyrus seems to have a more protracted development (Nelson, 1997). Although the hippocampal formation of newborn infants has the necessary synaptic connections for memory formation, a number of postnatal morphological changes suggest a significant modification of hippocampal circuits from birth until adulthood (Seress, 2001). The total temporal volume appears stable between 4 and 18 years, whereas hippocampal volume increases with age for females and amygdala volume increases with age for males. This process is probably related to the distribution of sex hormone receptors, namely predominantly androgen receptors in the amygdala and mainly estrogen receptors in the hippocampus (Casey, Giedd, & Thomas, 2000). Giedd and colleagues report increasing temporal lobe gray matter