
**The aging episodic memory
and factors which influence it:
An electrophysiological investigation**

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Index of Publication

Parts of this thesis are included in an article that has been published to a journal. Single passages and figures included in this article are taken over from the published form, which is not marked explicitly in the text. Throughout this thesis I will consistently use the term “we” instead of “I” to facilitate the process of writing and reading.

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Abbreviations

°	<i>degree</i>
”	<i>inch</i>
η_p^2	<i>partial eta squared</i>
ANOVA	<i>analysis of variance</i>
ANCOVA	<i>analysis of covariance</i>
BIC	<i>binding of items and contexts</i>
Br	<i>response bias</i>
CLS	<i>complementary learning systems</i>
CST	<i>counting span task</i>
CRUNCH	<i>compensation-related utilization of neural circuits hypothesis</i>
db	<i>decibel</i>
DC	<i>direct current</i>
DLPFC	<i>dorsolateral prefrontal cortex</i>
DPC	<i>dorsal part of the posterior parietal cortex</i>
DS	<i>digit symbol</i>
DTI	<i>diffusion tensor imaging</i>
EC	<i>entorhinal cortex</i>
EEG	<i>electroencephalography</i>
e.g.	<i>for example</i>
EOG	<i>electrooculogram</i>
ERPs	<i>event-related potentials</i>
et al.	<i>et alii</i>
FL	<i>frontal lobe</i>
fMRI	<i>functional magnetic resonance imaging</i>
HAROLD	<i>hemispheric asymmetry reductions in old adults</i>
HC	<i>hippocampus</i>
Hz	<i>hertz</i>
i.e.	<i>id est</i>
ISDRTs	<i>intraindividual standard deviations of reaction times</i>
k Ω	<i>kilo ohm</i>
LOP	<i>levels of processing</i>
LTM	<i>long-term memory</i>
M	<i>mean</i>
MMSE	<i>mini mental state examination</i>

mPFC	<i>medial prefrontal cortex</i>
MRI	<i>magnetic resonance imaging</i>
MTL	<i>medial temporal lobe</i>
MTLC	<i>medial temporal lobe cortex</i>
ms	<i>Milliseconds</i>
MWT	<i>multiple-choice-knowledge-test</i>
OA	<i>old adults</i>
OC	<i>occipital cortex</i>
PASA	<i>posterior-to-anterior shift in aging</i>
PDP	<i>process dissociation procedure</i>
PET	<i>positron emission tomography</i>
PFC	<i>prefrontal cortex</i>
PhC	<i>parahippocampal cortex</i>
PPC	<i>posterior parietal cortex</i>
Pr	<i>performance score</i>
PrC	<i>perirhinal cortex</i>
R-K	<i>remember-know</i>
ROC	<i>receiver operating characteristic</i>
RTs	<i>reaction times</i>
SD	<i>standard deviation</i>
SEM	<i>standard error of the mean</i>
VLPFC	<i>ventrolateral prefrontal cortex</i>
VPC	<i>ventral part of the posterior parietal cortex</i>
YA	<i>young adults</i>

Abstract

A core mechanism of age-related losses in episodic memory is deficient self-initiated processing. This provokes difficulties in old adults to internally create associations between information units and to initiate and execute appropriate encoding and retrieval processes. By this, aging disrupts particularly recollection-based remembering whereas familiarity is thought to remain rather intact. Age-related impairments are supposed to diminish when old adults can rely more on externally provided support or when memory can be guided by schematic information (environmental support). The aim of this thesis is to successively investigate how experimental settings with low demand on self-initiated processing that provide environmental support modulate episodic memory performance in elderly. Event-related potentials (ERPs) were additionally derived to investigate the impact of aging on familiarity and recollection under such conditions.

Experiment 1 investigated age-differences in item recognition by using colored object stimuli for which detailed and vivid memoranda can be formed and by manipulating response speed at test to foster familiarity-based processing. When response time was limited, performance was similar across age groups whereas older adults' recognition performance was impaired when response time was unlimited. In both deadline conditions an early frontal old/new effect, the ERP correlate of familiarity, was obtained for young and old participants whilst the late parietal old/new effect, the ERP correlate of recollection, was reliably found only for young adults. The combined behavioral and ERP data support the view that recollection is attenuated in old age and that age-related differences are negligible when memory relies predominantly on familiarity.

Experiment 2 tested the ability of older adults to form associative memories for object stimuli. Unitization - a process by which different components of an association are processed in such a way that they become integrated into a single unit - is supposed to facilitate the establishment of an associative memory representation and to increase familiarity-based processing at retrieval. We used pictures of arbitrary objects that were positioned, relative to each other, in either spatially plausible or implausible locations (e.g., a drill oriented towards or away from a donut), to create pairings that differed in their level of unitizability. By this age-related associative memory differences were expected to be smaller for unitizable than non-unitizable stimuli. Consistently, for spatially plausible pairings an early old/new effect was present in both age groups whereas for spatially implausible pairings it was only present in young adults. As in Experiment 1, the late parietal old/new effect was observable in both conditions for young but not old adults. However, despite a plausibility benefit in both age groups, age-related performance differences were actually increased for plausible compared to implausible pairings.

These findings suggest that even though associative memory is attenuated in older adults, they can still use knowledge about spatial object relations to form memory representations that support associative retrieval, but to a lesser extent than young adults.

Further, within Experiment 2, a larger N400 effect occurred for implausible compared to plausible pairings at test, suggesting that semantic processing of a plausible object-to-object arrangement is facilitated. Thus, Experiment 3 directly tested whether the facilitated processing of plausible pairings is produced by bottom-up semantic priming when the components of a pairing are presented consecutively. We observed no attenuated N400 effect suggesting that knowledge about location-based object relations is not sufficient to integrate these object pairings meaningfully.

The findings of this thesis allow new insights into the mechanisms of the age-related episodic memory decline and contextual influences that modulate age-related differences and might provide useful implications for future assessments of episodic memory changes in old age.

I AGING AND EPISODIC MEMORY CHANGES

We experience a considerable growth of the older population due to rising life expectancy and the extent of the aging population is even likely to ascend in future. Older adults' main concerns do not only regard effects of physical aging but also the experience of age-related memory loss. This entails increasing need in understanding age-related cognitive changes and developing procedures to remain mentally healthy and fit. The symptom of memory impairment is not simply restricted to dementing diseases but can even be observed in healthy old individuals (Ofen & Shing, 2013). Most older adults report that their ability to learn new information or to remember past experiences has become worse with age (Stokes, 1992). However, there is ample evidence showing that age-related memory changes are not uniform and that memory loss is not an inevitable consequence of aging. On the one hand inter-individual differences in the extent of cognitive changes in old age are large and on the other hand aging does not affect all forms of cognitive processes equally, causing deterioration in some memory aspects whereas others remain (relatively) spared (see Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012, for a review). One major aim in cognitive neuroscience of aging is to determine which memory processes are predominantly affected by aging and which remain preserved across lifespan and to identify the neural bases of cognitive decline and stability. A resultant endeavor further is to examine whether age-related memory differences can be alleviated by providing cognitive support. Past research has shown that particularly executive functions and episodic memory are susceptible to the effects of aging (Nyberg et al., 2012). Within the present thesis, the effects of aging on episodic memory processes and implications of cognitive support on older adults' memory performance are investigated. These broad issues are specified in detail in the subsequent sections of this thesis. To begin with, episodic memory functions as part of the declarative long-term memory are described.

1.1 Declarative memory across the lifespan

Long-term memory (LTM) is traditionally thought to comprise declarative and non-declarative forms of memory. Declarative memory constitutes explicit memory and refers to the ability to consciously remember facts and previously experienced events (Schacter & Tulving, 1994). Conversely, non-declarative memory constitutes implicit memory and refers to unconscious memory abilities that are processed on an automatic rather than controlled level, including priming, conditioning and skill and habit learning (Schacter & Tulving, 1994). These

two forms of long-term memory can be distinguished on the basis of brain structures: the declarative memory is assumed to depend on structures and connections within the medial temporal lobe (MTL) system, including the hippocampus (HC) and surrounding parahippocampal regions, while the non-declarative memory is assumed to be independent from the MTL (Henke, 2010; Squire & Zola, 1996). Support for this distinction comes from studies with amnesic patients suffering from MTL damage that show impaired memory performance on tests that assess explicit memory but perform normal on tasks assessing implicit memory functions (Squire & Zola, 1996; Squire, 1992).

Declarative memory can be further sub-divided into episodic and semantic memory that constitute different types of information stored in LTM: episodic memory includes memory for episodes and events as well as information about their temporal and spatial relations whereas semantic memory includes concepts and facts, such as general world knowledge (Schacter & Tulving, 1994; Tulving, 1972). Declarative memory can be tested with tasks that require explicit memory about facts (e.g., “Paris is the capital of France”) or about an item’s recent encounter (e.g., “I have seen this particular item during study”) and by this test semantic and episodic memory, respectively. Episodic memory is often tested with recall or recognition tasks. In these tasks, participants learn a series of stimuli and are later requested to recall the stimulus list or to decide for each stimulus whether it has occurred during the study episode or not, respectively. In traditional episodic memory tasks, when the to-be-remembered episodic information constitutes a well-known item that can be integrated meaningfully via links to concepts stored in semantic memory, these memory systems can be interrelated (Tulving, 1972). Further, semantic memory might initially develop through accumulated encoding of episodic information and might become free from episodic detail by extracting regularities from similar episodes over time (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Ofen & Shing, 2013; Van Kesteren, Ruiters, Fernández, & Henson, 2012).

Following the assumption that semantic memory is not associated with a particular time and place but rather organized in a distributed network of concept nodes (that contain e.g., name and feature information and that are connected to each other by means of commonality, Yee, Chrysikou, & Thompson-Schill, 2013), semantic memory is also often tested implicitly with priming paradigms. Priming refers to the improved performance (response speed, accuracy) through context or prior experience and bears on the assumption that when an information node within the network is activated (e.g., by a prime), it invokes connected concepts allowing facilitated processing of related information (Collins & Loftus, 1975; McNamara & Altabirra, 1988; McNamara, 2005, see section 1.3.7 for a more detailed discussion of implicit semantic memory).

However, besides the assumed episodic-semantic interrelation, there is also evidence that the episodic and semantic system can be dissociable, i.e. Vargha-Khadem and colleagues (1997) observed that early hippocampal lesions in young children impaired memory for autobiographical episodes but spared the acquisition and maintenance of semantic knowledge (Vargha-Khadem et al., 1997). This suggests that different brain structures are involved in processing episodic and semantic information, with the latter one being partially independent from the hippocampus (HC), and that both types, despite their interrelation, represent diverse forms of declarative memory that can be differentially impaired.

Past research has shown that episodic and semantic memory are differentially susceptible to the effects of aging, with episodic memory being particularly impaired by aging whereas semantic memory remains relatively preserved in old age (Brickman & Stern, 2009). It is suggested, that as a consequence of declining episodic memory, older adults rely more on semantic information during memory retrieval (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Ofen & Shing, 2013). Accordingly, Levine and colleagues (2002), who tested younger and older adults' memory for events from different life periods in an autobiographical interview, observed that younger adults recalled many specific and vivid episodic details, whereas older adults' responses were biased towards semantic facts unconnected to time and place information. It has been shown that age-related episodic memory impairments persist when differences on background factors between young and old adults – such as education and fluid intelligence – were controlled (Nyberg, Bäckman, Erngrund, Olofsson, & Nilsson, 1996). Further, age differences even persist when investigated longitudinally rather than cross-sectionally. Cross-sectional data can overestimate age differences due to cohort effects and thus usually show a linear decline of episodic memory performance whereas longitudinal data, which are less influenced by cohort effects, indicate stable performance until about 60 to 65 years of age, which is then followed by accelerating decline (Nilsson, 2003; Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012).

Ofen and Shing (2013) proposed that accentuated reliance on semantic memory contents with age may be a consequence of reduced encoding and retrieval of specific episodic information (Levine et al., 2002; Ofen & Shing, 2013). Measuring cerebral blood flow during an encoding phase, Grady and colleagues (1995) observed that, relative to young adults, old adults showed no significant encoding activation in cortical and hippocampal areas indicating inadequate encoding of new information. It is further suggested that subtle changes within the hippocampal network produce a shift away from pattern separation towards completion, which results in generalization (Wilson, Gallagher, Eichenbaum, & Tanila, 2006). Pattern separation refers to processes that ensure the formation of separated memory traces to reduce interference

and pattern completion refers to processes of re-activating stored memory representation from a (partial) retrieval cue (Yassa & Stark, 2011). As a result of this shift already stored information is favored at the cost of processing new information. Pattern separation is useful in order to store sufficiently distinctive memory traces that do not interfere with already-stored information. Decreased efficiency in pattern separation during aging may decisively contribute to degraded episodic memory (Wilson et al., 2006). Further, Parkin and Walter (1992) suggested that episodic memory impairments in elderly might also arise at retrieval from problems to initiate adequate mental operations in order to evoke episodic information. Reduced detailedness of memory representations due to weak encoding in combination with impaired retrieval processes may provoke an adaptive shift in older adults to rely predominantly on well-developed semantic memories (Ofen & Shing, 2013).

Importantly, age effects on episodic memory have strong implications on older adult's everyday life, as episodic memory functioning is involved in remembering names, faces and contains personal memories about occasions in daily life. When memory about critical events from the past fades, elderly become concerned and sometimes experience a confinement of their daily life. This just highlights the importance of understanding the age-associated decline of episodic memory. The following sections will portray in more detail the impact of aging on episodic memory and physical changes of the brain that are likely to cause this decline. Further, potential moderating effects will be introduced and mechanism to aid older adults' episodic memory will be highlighted.

1.2 Effects of aging on episodic memory

Episodic memory refers to memoranda of past events and their contexts and can be investigated with different tasks such as tests of item recognition, associative recognition (e.g., contextual "source" memory) or recall. Studies investigating the aging episodic memory with different tasks have reported mixed results with regard to episodic memory performance in old compared to young adults. For instance, Craik and McDowd (1987) led participants study a list of phrases containing a target word (e.g., "a body of water – pond") and compared performance of young and older adults in a cued recall and recognition task. In the cued recall task, participants were given a cue (e.g., "a body of water") and they had to recall the target information ("pond"). In the recognition task, participants were presented with lists of single words containing target and distractor words and they had to indicate whether it was presented during study or not. Craik and McDowd (1987) reported age-related performance differences, that is impaired performance in old compared to young adults, to be larger in the recall compared

to the recognition task. Further, in source memory paradigms, where participants are required to retrieve source information (i.e., context) associated with an item, age differences are larger for source than item memory (Spencer & Raz, 1995). Bastin and Van der Linden (2003) tested age-related recognition differences in a yes-no recognition and a forced-choice recognition task. In the former recognition paradigm, stimuli are sequentially presented to participants and they have to indicate whether they recognize the current item from the study phase (old) or not (new). In the latter recognition paradigm, stimuli are presented concurrently and participants are required to choose the target item that is presented among one or more distractor items. It was observed that age effects were larger in the yes-no compared to the forced-choice condition.

Thus, the heterogeneity of findings on different tasks assessing age differences in episodic memory suggests that age-associated impairments can be attributed to the specific task demands rather than to episodic memory per se (Craik, 1994).

1.2.1 Deficient self-initiated processing in older adults

Consistent with previous work is the assumption that age differences vary with task demands on automatic and controlled operations (Hasher & Zacks, 1979). The term automatic and controlled refers to encoding as well as retrieval processes. Automatic processes occur without intention, whereas controlled operations are effortful and initiated intentionally. Automatic and controlled operations constitute the respective ends of a processing continuum and the contribution of encoding/retrieval processes to memory performance can fall somewhere onto this continuum (Hasher & Zacks, 1979; Unsworth, 2009). It has been suggested that older adults are at a disadvantage relative to their younger counterparts when effortful and controlled processing is required (Craik & Byrd, 1982; Craik & McDowd, 1987). In a variant of the automatic/controlled position, Craik, Routh, and Broadbent (1983) suggested that processing resources in older adults are diminished and, as a consequence, they are less likely to self-initiate effortful encoding and retrieval processes. At encoding, self-initiated processing requires the integration, elaboration and organization of to-be-remembered material. At retrieval, self-initiated processing requires the initiation of memory searches, the elaboration of memoranda and the monitoring of retrieved information in order to recapitulate details of the event (Craik, 1994; Simons & Spiers, 2003). By this account, memory tasks can vary in demands on memory control operations and the age-related decline is particularly pronounced in tasks that require self-initiated processing (see Figure 1).

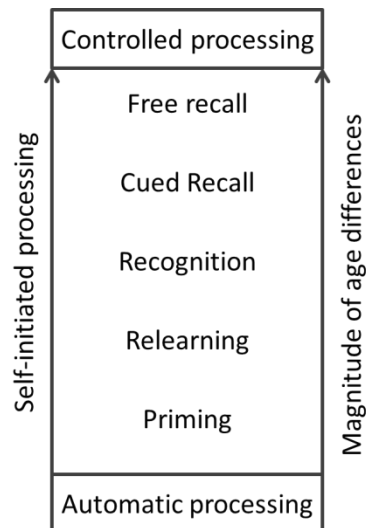


Figure 1 - Rank-ordered requirement of self-initiated processing to memory tasks and the hypothesized magnitude of age differences in these tasks (adopted from Salthouse, 2001).

For instance, more self-initiated processing is required on episodic memory tasks of recall than on recognition. In recall, when no (free recall) or few cues are provided (cued recall) one must initiate appropriate mental operations in order to reconstruct the original event. In contrast, in a recognition task, where information is represented to participants, retrieval processes are largely driven by the provided information and do not necessitate such effortful strategic and memory search processes (Craik & McDowd, 1987). To conclude, older adults are especially impaired in tasks requiring a large amount of self-initiated processing.

1.2.2 Associative memory deficit in older adults

Episodic memory does not only require self-initiated effortful processing but also mechanism that operate upon connecting multiple components to a bound representation (Unsworth, 2009). Binding different details of an event into a cohesive memory representation and retrieving bound unit information of previous experience and associated details are core functions of episodic memory. Binding mechanism can operate upon feature combinations of a given item (item + feature), contextual information of an item (item + context), an event occurring in conjunction with other items (item + item) and/or multiple contextual elements (context + context). Binding mechanisms can thus refer to processes that strengthen associations within a memory trace (within-item binding, intra-item associations) or across memory traces (relational binding, inter-item associations), the former of which represent intra-item associations and the latter inter-item associations (Zimmer, Mecklinger, & Lindenberger, 2006).

The ability to bind multiple information into cohesive representations is assumed to be largely susceptible to the effects of aging (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000). According to the associative memory deficit hypothesis, impaired memory performance in older adults is caused in part by their difficulty in creating and retrieving associations between multiple stimuli (Bender, Naveh-Benjamin, & Raz, 2010; Naveh-Benjamin, Brav, & Levy, 2007; Naveh-Benjamin, 2000) or stimulus characteristics (Naveh-Benjamin, 2000). This assumption receives approval by the consistent finding of studies reporting that elderly show disproportionately worse performance in recognition of associations in comparison to single item recognition (Chalfonte & Johnson, 1996; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003).

For instance, Naveh-Benjamin (2000) tested older adults' memory for single items (item memory) and for associations (associative memory) in a series of studies using arbitrary word pairs, word + nonword pairs and words written in different fonts. In the item recognition task, participants had to distinguish between old and new items (words, nonwords or fonts) whereas in the associative recognition task, participants were presented with old pairs (original pairing from the study phase) and recombined pairs (composed of components taken from different pair combinations) and had to indicate whether the current pair had appeared as such at study. Recombined pairs are usually used in studies of associative memory in order to prevent that participants can classify pairings as intact on the basis of pure item recognition. To distinguish between intact and recombined pairs one must retrieve the specific association between items in order to respond correctly (Quamme, Yonelinas, & Norman, 2007). Naveh-Benjamin (2000) showed that age deficits were consistently larger for recognition of associations than for single item information. The age-related associative memory deficit has been demonstrated for diverse sorts of associations (see Old & Naveh-Benjamin, 2008, for a meta-analysis), i.e. object picture pairs (Naveh-Benjamin et al., 2003), object and location (Chalfonte & Johnson, 1996), face pairs (Bastin & Van der Linden, 2006), face and location (Bastin & Van der Linden, 2006), face and temporal order (Bastin & Van der Linden, 2005), faces and names (Naveh-Benjamin, Guez, Kilb, & Reedy, 2004).

In his study from 2000, Naveh-Benjamin also manipulated whether encoding of associations was either intentionally (participants expected a test on the pair associations) or incidentally (participants expected an item recognition test). The age-related associative deficit was more pronounced after intentional than incidental encoding (see also Chalfonte & Johnson, 1996; Naveh-Benjamin et al., 2009). It was suggested that elderly were less able to build associations and that they were additionally disadvantaged under intentional encoding instructions due to deficient self-initiated processing, because young adults especially engaged in associative strategies in this condition. Indeed, when participants were asked for the kind of

strategy they had used during the experiment, young participants reported the use of integrative strategies (i.e., connecting the items via sentences) whereas older participants did not use any strategy or just rehearsed the pair at study (Naveh-Benjamin, 2000). “A failure to spontaneously implement efficient associative strategies seems to be one determinant of the older adults’ decline in associative memory” (Bastin et al., 2013, p. 275). To investigate the potential role of deficient processing resources on the age-related associative memory deficit the memory performance of older adults was compared to that of young adults who performed the encoding task under divided attention (Naveh-Benjamin, Guez, & Shulman, 2004). The results showed a specific deficit for associations in old adults and disruptive effects of divided attention on both, item and associative memory, in young adults. Hence, it was suggested that the age-related associative memory impairment is not solely caused by reduced processing resources (Naveh-Benjamin, Guez, & Shulman, 2004).

1.2.3 Two-component framework of episodic memory across the life-span

Shing and colleagues (2008, 2010) subsumed abovementioned findings on age-related impairments in self-initiated processing and associative memory within a two-component framework of episodic memory across the life-span suggesting that episodic memory task performance in elderly is driven by deficient associative and strategic processes. Associative processes contain binding mechanism that are engaged relatively automatic (i.e. when the presented information is sufficient to generate associations) whereas strategic processes refer to strategies to organize and elaborate memoranda that can be self-initiated or activated by instruction (Shing et al., 2010; Unsworth, 2009). Thus, when associative processing is not sufficient, participants need to engage in strategic processing (Unsworth, 2009).

Shing and colleagues (2008) tested (german) participants from different age groups across the lifespan in an associative recognition task. The involvement of the associative component was manipulated by the type of to-be-associated word pair that was either of low (German-German word pair) or high (German-Malay word pair) associative demand. The strategic demand varied with the type of encoding instruction that was provided and that emphasized either an item encoding, pair encoding or an elaborative-strategy encoding. The results show that older adults did benefit less from strategy instruction than younger adults suggesting an inefficient use of the provided strategy and their recognition performance was especially low in the high-associative demand condition, suggesting an additional associative deficit (Shing et al., 2008).

To summarize, converging evidence from behavioral studies indicates an age-related episodic memory impairment with a particular decline in memory for associations (Naveh-Benjamin et al., 2003; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). This associative deficit has been related to deficient associative binding mechanism that integrate separate information into a coherent memory representation and to reduced self-initiation of controlled strategic processes which further degrades the associative memory in older adults (Cohn, Emmrich and Moscovitch, 2008; Shing et al. 2010).

In the following section, episodic memory functioning will be discussed on the basis of dissociable sub-components and the “dual-process perspective” of episodic memory (Mandler, 1980; Yonelinas, 2002) and age-associated changes will be examined.

1.3 The aging episodic memory from a dual-process perspective: familiarity and recollection

Episodic memory has been extensively investigated with recognition memory experiments that require the ability to make judgments about an item’s previous occurrence. According to the dual-process perspective, recognition of past events can be based on two dissociable components, the retrieval of item-related information (familiarity) and retrieval accompanied by specific details or context (recollection) (Mandler, 1980; Yonelinas, 2002). Familiarity is often characterized as a strength-based process that reflects a gradual change in recognition confidence and that is considered to operate more automatic. In contrast, recollection is described as a threshold process that allows the retrieval of qualitative information from a prior study event and that is considered to be more effortful and strategic than familiarity (Yonelinas, 2002). Thus, recollection requires the self-initiation of strategies and building of memory associations during encoding/retrieval (Naveh-Benjamin, 2000; Shing et al., 2010; Yonelinas, 2002). It is generally assumed that familiarity is more rapidly available than recollection, though both processes can operate independently but also in parallel (Yonelinas, Aly, Wang, & Koen, 2010). Importantly, whereas both processes can account for recognition of item information, recognition of associated information depends primarily on recollection (Yonelinas et al., 2010).

1.3.1 Behavioral assessment of familiarity and recollection

Past research has shown that familiarity and recollection are functionally distinct processes (Ranganath et al., 2004; Squire, Wixted, & Clark, 2007; Yonelinas, 2002) and in order to

dissociate them, several techniques have been used that can be divided into process-estimation and task-dissociation methods.

Process-estimation methods

Process-estimation methods allow the derivation of the relative contribution of familiarity and recollection to recognition memory and specific estimation methods have been developed, such as receiver operating characteristics (Yonelinas, 2002), the remember-know procedure (Gardiner & Richardson-Klavehn, 2000) or the process-dissociation procedure (Jacoby, 1991).

For instance, receiver operating characteristics (ROCs) are functions that plot the cumulative probability of hits (i.e., correct “old” classification of old items) versus false alarms (i.e., incorrect “old” classification of new items), computed from different levels of recognition confidence ratings, that depict a curve. Following the assumption that recollection is predicated on a threshold process that occurs for high confidence judgements while familiarity is predicated on a signal-detection process varying gradually with confidence, the plotted curves differ in their distribution: recollection is indexed by the asymmetry of the curve and familiarity by the degree of curvilinearity (Yonelinas, 1997). ROC curves provide graphical information about the portion of the underlying sub-processes and allow the derivation of estimates for familiarity and recollection (Squire, Wixted, & Clark, 2007; Yonelinas, Kroll, Dobbins, Lazzara, & Knight, 1998).

In remember-know (R-K) paradigms, recognition requires a judgment of whether an item is recognized on the basis of remembering specific details of the study episode associated with the item (recollection) or on the basis of knowing that the item has occurred previously without explicit memory about associated detail information (familiarity) (Yonelinas, 2002). Since the remember/know judgement relies on participants’ subjective experience, it is important to clearly instruct participants on the definition of these two response options.

Another method to separate familiarity and recollection is the process-dissociation procedure (PDP) (Jacoby, 1991). Items are studied in different contexts (i.e., being presented in different color or in different modality) and have to be recognized in different test conditions. In the inclusion test participants are instructed to categorize all items irrespective of study context according to whether they have been studied or not. In the exclusion test, participants are instructed to select those items that have been studied in one particular context and reject items studied in the other context. Because correct recognition in the former task can be based on both processes whilst correct recognition in the latter task must rely on recollection, parameters for

familiarity and recollection can be derived by contrasting inclusion and exclusion performance (Yonelinas, 2002).

Task-dissociation methods

Task-dissociation methods, such as comparison of recall/recognition performance, item/associative recognition or response deadline procedure, intend to isolate one of the two processes by task demands (Yonelinas, 2002).

While item recognition can be based on a feeling of familiarity or on recollection of additional information, tests of recall and associative recognition require recollection. In recall tests where no or partial retrieval cues are provided (free versus cued recall, respectively) and in associative recognition tests, where participants are required to distinguish between old and recombined pairs, one must self-initiate controlled memory operations and retrieve qualitative information associated with an item (Quamme, Yonelinas, & Norman, 2007). Thus, tests of recall and associative recognition reflect recollection-based memory whereas item recognition reflects the contribution of both processes.

A task-dissociation between familiarity and recollection can further be based on the different temporal dynamics of both processes. Since familiarity is characterized as completed rapidly, whereas recollection requires more time, limiting the time to respond (i.e., when participants must respond within 700 ms) at recognition should attenuate the contribution of recollection while leaving familiarity largely unaffected (Boldini, Russo, & Avons, 2004). This task-dissociation method is called response deadline procedure and compares performance of a speeded response condition with a non-speeded version of the task (Yonelinas, 2002).

However, task-dissociation methods do not derive direct estimates of familiarity and recollection. Hence, inferences can be made only indirectly. For instance, when aging effects associative memory more than item memory, then it effects recollection more than familiarity.

1.3.2 Age-associated effects on behavioral estimates of familiarity and recollection

As mentioned in section 1.2.2, recognition of single items is less affected by aging than is associative recognition, probably due to deficient recollection (Benjamin & Craik, 2001; McIntyre & Craik, 1987; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). Using more direct behavioral measures of familiarity and recollection, for instance when recognition memory for

pictures is tested with the ROC procedure, estimates of recollection were lower in old compared to young adults whilst familiarity estimates were comparable across groups (Howard, Bessette-Symons, Zhang, & Hoyer, 2006). These studies suggest that normal aging impairs recollection but leaves familiarity rather intact (for a review see Persson & Nyberg, 2008; Yonelinas, 2002).

However, there are also studies suggesting an increased contribution of familiarity to episodic recognition in older adults in light of degraded recollection. Using the R-K paradigm, it has been shown that elderly exhibit a decline in recognition based on remembering and an increase in recognition based on knowing (Parkin & Walter, 1992; Perfect, Williams, & Anderton-Brown, 1995). Similar results have been observed by Bastin and Van der Linden (2003), who compared young and older adults' performance in a forced-choice recognition test using face stimuli. Participants were required to base their decision on whether they remembered or knew this item to be old. Older adults made fewer correct 'remember' responses, but disproportionately more correct 'know' responses than young adults, suggesting reduced recollection-based recognition together with an overreliance on familiarity. In a forced-choice task, when participants can choose between two stimuli, recognition based on familiarity is assumed to be facilitated. This is because participants can respond to that item that is more familiar without evaluating the response against an internal recognition criterion (Westermann & Payne, 2003, see also section 3.4 for a discussion of facilitated familiarity-based recognition in forced-choice tasks). Thus, over-reliance on familiarity in older adults might occur in tasks that facilitate familiarity-based recognition. Over-reliance on familiarity has also been related to the elevated false alarms rates in older adults (Light, Patterson, Chung, & Healy, 2004). For instance, Light, Chung, Pendergrass, and Van Ocker (2006) tested participants' recognition of words that were presented once or several times at study and that were later tested as old or plurality-reversed words (e.g., *cats* instead of *cat*) with a speeded or non-speeded response deadline. All these manipulations, study repetition plurality-reversal, and a speeded response deadline, were assumed to enhance the familiarity-based false alarm rate in young and older adults. Older adults made more false alarms to plurality-reversed words at test compared to young adults, especially when these words had been repeated at study and were tested under speeded responding (Light et al., 2006). To conclude, these studies suggest that familiarity remains intact in older adults and that an age-related over-reliance on familiarity can be observed in tasks that support familiarity-based retrieval.

However, along the finding of intact familiarity, a recent meta-analysis by Koen and Yonelinas (2014a) also reported age-related decreases in familiarity. In that study familiarity estimates derived from ROC and PDP were found to be intact with age while the familiarity estimate derived from the R-K procedure was found to be reduced in old compared to young

adults. It was suggested that young and older adults probably differ in interpreting instructions for 'remember' and 'know', i.e. when older adults base their 'remember' response on a strong familiarity signal, this would reduce their estimate of familiarity. On the basis of this meta-analysis, a recent study by Koen and Yonelinas (2014b) again investigated whether age-related differences in familiarity varied with the type of the estimation method. Rather than comparing performance between young and old adults on each task, they observed covariations between process estimates and chronological age in a group of midlife and older adults (ranging from 40 to 81 years) and found negative correlations with age in estimates of recollection, but not familiarity, across all three methods (ROC, R-K, PDP).

Furthermore, using neuropsychological measures that are associated with functions of the frontal lobe (FL, e.g., working memory tasks) and MTL (e.g., long-term memory tasks), Davidson and Glisky (2002) characterized older adults according to whether they were high or low performing on the FL and MTL measures and investigated their episodic memory with the PDP. Relative to young adults, recollection was impaired in old adults of low MTL and of low FL function, whereas familiarity was only impaired in those old adults with low MTL function. This indicates that familiarity and recollection are supported by different brain structures and that individual difference in FL and MTL integrity in old adults may account for differences in performance (Davidson & Glisky, 2002; Prull, Dawes, McLeish, Rosenberg, & Light, 2006).

Taken together, behavioral findings of age effects on familiarity and recollection reveal that recollection is generally more impaired by aging than familiarity. This is in line with the assumption that effortful and strategic memory operations such as recollective retrieval of associative information are more vulnerable to aging than more automatic memory operations such as overall familiarity of item recognition (Hasher & Zacks, 1979; Unsworth, 2009; Naveh-Benjamin, 2000; Yonelinas, 2002). The extent to which episodic memory is affected in old adults may depend largely on individual differences in the integrity of underlying brain structures (Davidson & Glisky, 2002; Prull et al., 2006). The functional dissociation between familiarity and recollection is related to the involvement of different brain regions that support this distinction. Before age-related changes of brain regions involved in familiarity and recollection processing are discussed in more detail, the function of these regions within the episodic memory network will be described.

1.3.3 The neural network of episodic memory

The medial temporal lobe

Studies investigating the neural substrates of episodic memory jointly regard the MTL to be involved in memory encoding and retrieval and thus consider it as one critical structure for recognition memory (Aggleton & Brown, 1999; Brown & Aggleton, 2001; Diana, Yonelinas, & Ranganath, 2007; Graham, Barense, & Lee, 2010; Ranganath, 2010; Wang, Ranganath, & Yonelinas, 2014). Specifically, it is suggested that different sub-regions within the MTL are associated with processing different types of information (Aggleton & Brown, 1999; Diana et al., 2007; Preston & Eichenbaum, 2013; Ranganath, 2010). Importantly, a critical distinction is made between the HC and the surrounding MTL cortex (MTLC). The MTLC includes the entorhinal cortex (EC) and the perirhinal cortex (PrC), which constitute the anterior part of the parahippocampal gyrus and are also referred to as rhinal cortex, and the parahippocampal cortex (PhC) that is the posterior portion of the parahippocampal gyrus. According to the Binding of Items and Contexts (BIC) model (Diana et al., 2007), the PrC receives input from the “*what*”-stream of cortical association areas and is critically involved in encoding of item information, while the PhC receives input from the “*where*”-stream of cortical areas and thus encodes context information (Diana et al., 2007). Input of these two regions converges within HC that in turn binds together the incoming information to coherent representation that allow the formation of specific episodic memory traces. At retrieval, reactivation of specific item memory traces within PrC supports familiarity, whereas recollection is related to reactivation of contextual representations and item-context representations within PhC and HC (see Figure 2).

The neuro-computational principles underlying PrC-mediated familiarity and HC-driven recollection have been described with regard to generalization (i.e., underlying pattern completion) and discrimination (i.e., underlying pattern separation). According to the complementary learning system (CLS) theory (Norman & O’Reilly, 2003), the MTLC, including the PrC, is suggested to encode overlapping representations that capture generalities by using a pattern generalizing algorithm, thereby enabling familiarity (Mayes, Montaldi, & Migo, 2007). Through a sharpening process, item representations become sharper over time and familiar items activate a smaller number of MTLC neurons (Norman & O’Reilly, 2003). Thus familiarity-related responses in MTLC are associated with deactivations (LaRocque et al., 2013; Mayes et al., 2007; Norman & O’Reilly, 2003). In contrast the HC supports the rapid formation of arbitrary item-context bindings using a pattern separation algorithm that generates highly interconnected and flexible but non-overlapping memory representations. By this the HC is able to reinstate the original activation pattern via pattern completion that enables recollection. Recollection-related

responses in HC are thus associated with activations (Diana et al., 2007; Norman & O'Reilly, 2003).

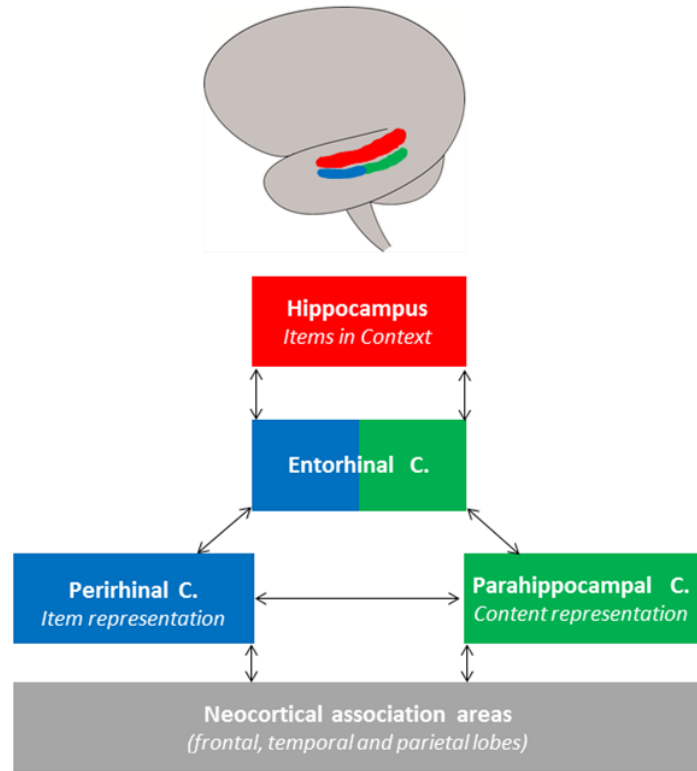


Figure 2 - Schematic representation of the functional organization of sub-regions of the MTL according to the BIC model, with the PrC, PhC and HC involved in processing item information, context information and binding, respectively (adapted from Ranganath, 2010).

Support that different MTL sub-regions are involved in processing different types of information comes from a large amount of imaging and patient studies (Addante, Ranganath, Olichney, & Yonelinas, 2012; Aminoff, Gronau, & Bar, 2007; Bowles et al., 2007; Ranganath et al., 2004; Staresina, Cooper, & Henson, 2013; Staresina & Davachi, 2008; Wang et al., 2014). In line with a signal-detection/threshold theory of familiarity and recollection (Yonelinas, 2002), familiarity-related activity has been found to linearly decrease as a function of perceived oldness (as indicated by confidence judgements) in rhinal cortex, whereas recollection-related activity has been found to nonlinearly increase for the extremes of the oldness scale in the HC (Daselaar, Fleck, & Cabeza, 2006b; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006a; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000). Further, patients suffering MTL damage restricted to the HC show profound impairments in tasks that require the contribution of recollection (e.g., recall and associative recognition), but perform relatively normal in item

recognition tasks (Giovanello, Verfaellie, & Keane, 2003; Holdstock, Mayes, Gong, Roberts, & Kapur, 2005; Yonelinas et al., 2002). In contrast, a patient with MTL damage that encompassed the rhinal cortex (EC and PrC) but spared the HC and PhC, showed intact recollection but reduced familiarity-based memory (estimated with R-K, ROC and response deadline procedure) (Bowles et al., 2007). Furthermore, in functional magnetic resonance imaging studies (fMRI), it has been shown that recognition of object-color associations compared to item recognition is accompanied by greater activations of the HC and PhC (Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001).

The prefrontal cortex

An important role in episodic memory has also been assigned to the PFC (Anderson, Guild, Cyr, Roberts, & Clare, 2012; Cruse & Wilding, 2009; Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Davidson & Glicks, 2002; Hawco, Berlim, & Lepage, 2013; Preston & Eichenbaum, 2013; Simons & Spiers, 2003; Van Kesteren et al., 2012) whereby the medial PFC (mPFC) supports binding of new information with pre-existing neocortical networks of knowledge (schemata) as a function of its congruency (Van Kesteren et al., 2012) and lateral and anterior PFC regions are related to memory control operations that support elaborative encoding and strategic retrieval of information (Simons & Spiers, 2003).

According to the framework proposed by Van Kesteren and colleagues (2012), mPFC – MTL interactions are modulated by the congruency of new information with existing schemata in the neocortex. When the mPFC detects such congruency, MTL binding mechanisms are inhibited because the current information can be related to existing schema knowledge and direct connections between new and existing information is strengthened. In cases when new information is incongruent with existing schemata, MTL-mediated binding mechanism will support the formation of new memory representations (Van Kesteren et al., 2012). Evidence for this account comes from studies reporting reduced mPFC-MTL coupling, along with greater mPFC synchronization during encoding of information that fits prior knowledge (i.e., when the final part of a movie fits with its initial part) (Van Kesteren, Fernández, Norris, & Hermans, 2010) and increased mPFC activity during retrieval of schema-congruent information (i.e., when word-fabric associations are consistent with existing schemata) (Van Kesteren, Rijpkema, Ruiter, & Fernández, 2010).

However, when information is incongruent with an existing schema (i.e., when information is arbitrary as in many associative recognition paradigms), sub-regions of the lateral

PFC are suggested to be involved in top-down mediated control operations (Brod, Lindenberger, Werkle-Bergner, & Shing, 2015; Brod, Werkle-Bergner, & Shing, 2013). According to the framework proposed by Simons and Spiers (2003), the ventrolateral PFC (VLPFC) is involved in elaboration of MTL representations and in implementing elaborative strategies that bind together different episodes, while the dorsolateral PFC (DLPFC) ensures the formation of distinct memory representations at encoding (Davis, Love, & Maddox, 2012; Lu, Wang, Chen, & Xue, 2015; Simons & Spiers, 2003). At retrieval, VLPFC is assumed to be involved in controlled processes that elaborate and maintain retrieval cues (Badre & Wagner, 2007; Simons & Spiers, 2003), whereby DLPFC is involved in monitoring and evaluation of retrieved information (Murray & Ranganath, 2007; Ranganath, 2010; Simons & Spiers, 2003). Additionally, the anterior PFC is recruited when retrieval operations are particularly complex. Evidence for the involvement of the lateral PFC in episodic memory comes from studies showing that VLPFC and DLPFC are differentially activated across semantic encoding (VLPFC) and source retrieval (VLPFC and DLPFC), consistent with their hypothesized role in (semantic) cue specification and relational binding/retrieval monitoring, respectively (Dobbins, Foley, Schacter, & Wagner, 2002). Further it has been shown that damage to the lateral PFC causes larger deficits in retrieval of context information than in item recognition (Janowsky, Shimamura, & Squire, 1989; Shimamura, Janowsky, & Squire, 1990; Swick, Senkfor, & Van Petten, 2006). Even though the lateral PFC is assumed to be critically for familiarity too (Duarte, Ranganath, & Knight, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006), the differential effects of PFC lesions on episodic memory indicate that effortful processing, such as recollection, might rely more on lateral PFC regions than instances of familiarity-based recognition (Montaldi et al., 2006; Simons & Spiers, 2003; Swick et al., 2006).

The posterior parietal cortex

The posterior parietal cortex (PPC) depicts another important structure in episodic memory that has been suggested to be involved in retrieval via attentional processes that can enhance cognitive processing (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). The assumption is that the PPC increases attention on relevant stimuli and enhances their salience and probability to be retrieved via PFC. The dorsal part of the PPC (DPC) operates in a top-down manner and allocates attentional resources to memory representations when memory is weak and the confidence about memories is low. The ventral part of the PPC (VPC) operates in a bottom-up manner by automatically mediating the attentional capture of strong and detailed memory outputs of the MTL (Cabeza et al., 2008). An fMRI study investigating activations of confidence

during recognition memory found the DPC to be greater activated for low- than high-confidence recognition, whereas the VPC showed the opposite pattern, suggesting different roles of these regions for familiarity- and recollection-based recognition (Kim & Cabeza, 2007). Further support for the differential involvement of PPC sub-regions in familiarity- and recollection-related processing comes from studies showing greater PPC activation for correctly classified old than new items (so-called old/new effects) in various episodic memory paradigms (see Cabeza et al., 2008, and Wagner, Shannon, Kahn, & Buckner, 2005, for a review). Moreover, these old/new effects have also been investigated with electrophysiological measures of brain activity using event-related potential (ERPs), and specifically the ERP component associated with recollection, that is typically observed over posterior scalp recordings (see 1.3.6 for a thorough discussion of ERP old/new effects), is likely to be generated by neurons of (or in the vicinity of) the ventral PPC (Vilberg & Rugg, 2008).

1.3.4 Structural changes of the aging brain

A large body of cross-sectional and longitudinal data have shown that aging is associated with structural changes of brain regions involved in episodic memory processing (Burzynska et al., 2012; Nyberg et al., 2012; Raz et al., 1997, 2005; Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010; Raz, Rodrigue, Head, Kennedy, & Acker, 2004). It is suggested that structural changes are accompanied by changes in behavioral performance and that better memory performance can generally be observed in those elderly that undergo less structural brain changes (Burzynska et al., 2012; Nyberg et al., 2012).

Importantly, age-related changes to brain structure particularly pertain to regions critically involved in recollection (Raz et al., 2010; Schiltz et al., 2006). Volumetric changes of the aging brain have been investigated with magnetic resonance imaging (MRI) and accelerated shrinkage has been mostly reported for prefrontal white and grey matter and for the HC (Raz et al., 1997, 2004, 2005, 2010; Schiltz et al., 2006), whilst smaller changes were observed in regions such as the superior parietal cortex (Raz et al., 2005, 2004) and relative stability within the entorhinal cortex (Raz et al., 2005, 2010). Volumetric decline within PFC has been shown to proceed linearly across the lifespan, whilst the senescent trajectory for HC volume is nonlinear with accelerated decline at advanced age. The individual variability in the atrophy rate across brain regions is significantly large and at least one modifier for this variability has been potentially reported in hypertension. It is suggested that hypertension in older adults accelerates the pace of the hippocampal volume loss (Raz et al., 2005, 2010; Raz, Rodrigue, & Haacke, 2007).

Schiltz et al. (2006) investigated age-related changes of brain volume and brain integrity. Brain volume and regional brain integrity was assessed with combined MRI volumetry and diffusion tensor imaging (DTI), that tracks the diffusion process of molecules in brain tissue and allows an evaluation of the integrity of the brain. Young and old individuals performed a source-memory recognition task for faces presented in front of different backgrounds while electrophysiological correlates of recognition memory were recorded and additionally performed neuropsychological tests. In elderly but not young adults, hippocampal DTI correlated with an electrophysiological correlate of recollection (the late parietal old/new effect, see 1.3.6). Additionally, hippocampal volume was correlated with performance on a neuropsychological test of declarative learning and recall. In a similar vein, it was shown that decreased functional activity and structural volume of the HC, measured within a period of five years, was associated with declining episodic memory performance (Persson et al., 2012). These studies suggest a relation between brain volume and integrity and aspects of cognition in old age (Charlton, Schiavone, Barrick, Morris, & Markus, 2010; Rosano et al., 2012).

1.3.5 Functional changes of the aging brain

In line with age-related structural changes, fMRI and positron emission tomography (PET) studies report age-related functional brain changes for encoding- and retrieval-related activity in episodic memory tasks.

One common pattern of age differences in brain activity is that elderly compared to young adults display decreased activity in occipital cortex (OC) and MTL together with increased activity in PFC regions during episodic retrieval (Cabeza et al., 2004; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008) even when performance between young and old adults was matched (Davis et al., 2008). This pattern is known as the posterior-to-anterior shift in aging (PASA). Since reduced OC activity was shown to be correlated with increased activation in PFC, it was suggested that top-down modulated cognitive processes may compensate for increased neural “noise” due to deficient sensory processing (Davis et al., 2008). The sensory deficit is assumed to have a global impact on cognitive mechanism (Lindenberger, Scherer, & Baltes, 2001) given that PASA has been observed across different tasks (perception, attention, working memory, episodic retrieval) (Dennis & Cabeza, 2008).

Increased PFC activation in elderly during episodic memory tasks has been reported in the context of a more bilateral PFC activation while young adults typically show asymmetric PFC activation (Cabeza et al., 2004). This pattern is known as HAROLD (hemispheric asymmetry

reduction in old adults) and is characterized by age-related activation decreases in the hemisphere that is preferentially activated in young adults and/or increased activation in the contralateral hemisphere (Cabeza et al., 2004, 2002; Dennis & Cabeza, 2008). The HAROLD pattern has been discussed with regard to compensation and dedifferentiation (Cabeza et al., 2004; Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, 2008; Reuter-Lorenz et al., 2000; Spaniol & Grady, 2012) in light of various cognitive aging theories, including theories of a sensory, a resource, an inhibition, and a recollection deficit (Dennis & Cabeza, 2008).

Since increased PFC activity has been reported to co-vary with better performance in elderly (Cabeza et al., 2002; Rosen et al., 2002), it was suggested that these activation increases reflect the successful compensation of age-related neural changes in brain function. Cabeza et al. (2002) observed that older adults with low mnemonic function (on neuropsychological measures) recruited similar (right-)lateralized PFC regions as young adults at source memory retrieval, whilst high old individuals additionally recruited contralateral PFC regions. This suggests compensational mechanisms in the latter group of elderly, probably to counteract hippocampal binding deficits (Park & Reuter-Lorenz, 2009).

However, some researches have reported increased PFC activity to occur independent of performance. For instance, McDonough, Wong, and Gallo (2013) led participants study words and pictures in separate study blocks that were later tested in criterial recollection tests (word and picture test). Despite older adults' performance was poorer in the word test and similar to young adults in the pictures test, they observed increased right PFC activity in old adults at word and at picture retrieval that did not co-vary with performance. Right PFC activity has been associated with retrieval monitoring and verification processes (Cabeza et al., 1997; Cabeza, Locantore, & Anderson, 2003). The elevated right PFC activity in elderly was thus interpreted as prefrontal dysfunction or dedifferentiation during retrieval monitoring, such as inefficient or non-selective recruitment in an attempt to perform the task at hand.

It has further been suggested that these differential effects of aging might in part stem from differences in task difficulty (according to the compensation-related utilization of neural circuits hypothesis, CRUNCH, Grady, 2012). It was proposed that at lower levels of task demands older adults over-recruit PFC regions in order to compensate for insufficient processing resources whereas these compensatory mechanism are less effective in difficult tasks (Grady, 2012; Spaniol & Grady, 2012). Consistently, during item and source memory retrieval younger adults showed increased PFC activity during a difficult version (one rather than multiple study presentation) of these tasks, whereas PFC activation in older adults was increased during the easy and the difficult version of the task (Spaniol & Grady, 2012).

In contrast to the observed age-related activity changes within PFC, findings with regard to retrieval-related MTL activity in aging are less complex. The prevailing outcome is a reduction in HC activity coupled with an increase in frontal regions at episodic retrieval in old compared to young adults. This supports the notion that elevated activations of frontal regions in elderly might be compensatory for reduced MTL function (Cabeza et al., 2004; Daselaar et al., 2006a; Daselaar et al., 2003; Dulas & Duarte, 2011; Grady, McIntosh, & Craik, 2005; Park & Reuter-Lorenz, 2009). During encoding, reduced activity within MTL has been linked to age-related difficulties in elaborative encoding (Daselaar et al., 2003). Most interestingly, during item recognition (in a R-K paradigm), decreased HC activity has also been reported to happen along increased activity within the rhinal cortex (Cabeza et al., 2004; Daselaar et al., 2006b), even though performance was matched between age groups (Daselaar et al. 2006a). Since rhinal activity was correlated with the number of know responses (Cabeza et al., 2004) and linearly modulated by perceived oldness, whereas the HC was modulated in a nonlinear fashion by perceived oldness (as indicated by confidence judgements, Daselaar, et al. 2006a), this finding was interpreted as a preferred reliance on rhinal-mediated familiarity in older adults in order to compensate for reduced hippocampal-mediated recollection (Daselaar et al. 2006a).

In the study by Daselaar et al. (2006a), age-related activity changes within PPC have also been reported: in line with the assumption that dorsal and ventral PPC regions are differentially engaged in familiarity and recollection, respectively (Cabeza et al., 2008), familiarity-related activation in parieto-occipital regions was similar between age groups whilst recollection-related activation in parieto-temporo cortex was attenuated in old adults (Cabeza et al., 2008; Hutchinson, Uncapher, & Wagner, 2009). These brain activation patterns in MTL and PPC during episodic retrieval complement behavioural findings about larger age-related deficits for recollection than familiarity.

Recently, Fandakova, Lindenberger, and Shing (2015) recorded age-related activation patterns during successful detection of recombined pairs in an associative recognition task. They reported that those older adults, that showed similar activation patterns in PFC and PPC as young adults (high maintenance) also showed the better memory performance compared to older adults with activation patterns largely deviating from that of the young adults (low maintenance, which was particularly reflected in an underactivation of fronto-parietal regions). Additionally, high maintenance old adults showed stronger functional connectivity between PFC and MTL regions than low maintenance old adults. This finding is in line with the assumption that brain maintenance, that is preserving a youthful brain, might be “the key to successful memory aging” (Nyberg et al., 2012).

Taken together, these findings suggest that structural and functional brain changes pertain particularly to those regions associated with recollective processing. In line with behavioural results of age effects on familiarity and recollection, the neural age-related activation pattern within MTL and PPC complements these findings by showing a preferred recruitment of regions associated with familiarity. However, these findings further suggest a large heterogeneity in age-related structural and functional brain changes associated with episodic memory function, as some older adults show little changes whereas changes in other older adults are more excessive due to compensational or deficient processing.

1.3.6 Electrophysiological estimates of familiarity and recollection

Extending abovementioned findings that familiarity and recollection rely on different brain structures, they can also be ascribed to electrophysiological indicators. Event-related potentials (ERPs) show a more positive-going waveform for correctly judged old (hits) compared to new items (correct rejections) in response to stimuli in a recognition paradigm (see Figure 3). Familiarity and recollection are associated with different ERP old/new effects that exhibit distinct temporal and topographical distributions (Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007). Familiarity is associated with an early (approximately 300-500 milliseconds) frontally distributed old/new effect, which is often termed the early mid-frontal old/new effect. The late parietal old/new effect, which is associated with recollection, can reliably be observed at posterior electrodes in a later time window between 500 and 700 ms and is maximal over left-parietal scalp regions. Although the term mid-frontal and left-parietal old/new effect is often used in the literature, these ERP components will be referred to as *early frontal old/new effect* and *late parietal old/new effect* throughout the course of this thesis.

In the following - though highly selective - overview, ERP evidence will be presented that shows that familiarity is a fast-acting, more automatic process that is not accompanied by the retrieval of associative information, while recollection is a more effortful and strategic process, that requires more time and that is associated with the retrieval of associative information.

In line with behavioral findings, ERP old/new effects are differentially sensitive to experimental manipulations that affect familiarity and recollection (for a review see Rugg & Curran, 2007). For instance, the late parietal old/new effect was shown to be sensitive to levels of processing (LOP) manipulations and larger for deeply studied words (i.e., when words are incorporated into sentences at encoding) compared to shallowly studied words (i.e., when participants make an alphabetical order decision about the first and last letter of the word),

whereas the early frontal old/new effect was insensitive to encoding depth (Rugg et al., 1998, see Figure 3). This is in line with the assumption that recollection is a more elaborate process than familiarity (Rugg et al., 1998a).

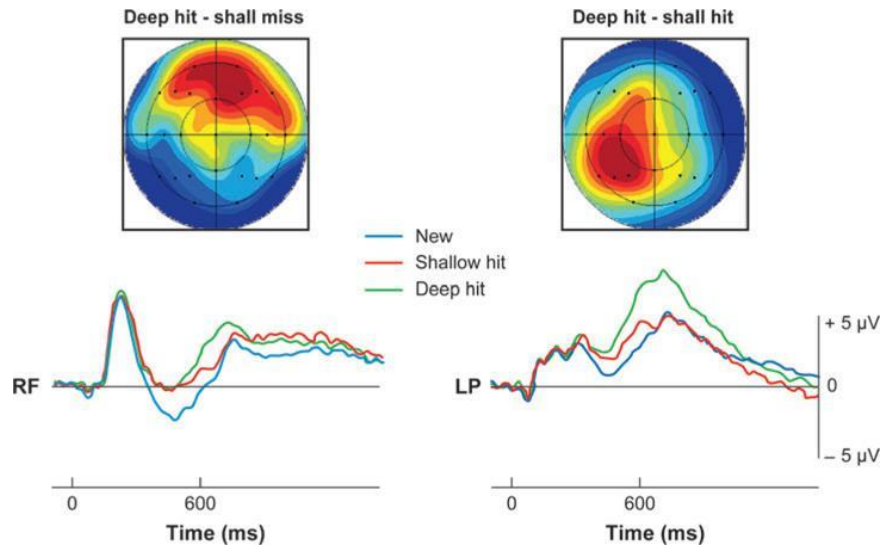


Figure 3 - ERPs from Rugg, Herron, and Morcom (2002) illustrate the waveform and topography of the early frontal old/new effect (left panel) and the late parietal old/new effect (right panel) associated with familiarity and recollection, respectively. Negativity is plotted downwards. In this study, familiarity was evident for items encoded deeply and shallowly, while recollection was substantially stronger for deeply encoded items (taken from Eichenbaum, Yonelinas, & Ranganath, 2007).

Further, Curran (2004) demonstrated that the late parietal old/new effect was reduced at test when items were encoded under divided attention whereas the early frontal old/new effect was not, suggesting that familiarity is a more automatic process than recollection. It has also been demonstrated that manipulating the similarity between new and studied items at test (i.e., by plurality changes of studied items, such as *car* and *cars*) enhances familiarity-driven false alarms rates. Consequently a mid-frontal old/new effect was elicited for studied items (*car*) and similar lures (*cars*), whereas the late parietal old/new effect differentiated between studied items and similar lures and appeared only for correctly recognized old items (Curran, 2000).

Using a modified R-K procedure, in which ‘know’ judgements were segregated according to their recognition confidence (varying on a four-point scale from confident new to confident old), the early frontal old/new effect was shown to vary monotonically with confidence strength but was insensitive to whether an item was ‘remembered’. In contrast, the late parietal old/new effect displayed a larger positivity for ‘remembered’ compared to high confident old items, but was insensitive to familiarity strength (Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010).

This is in line with the assumption of a continuous familiarity and a threshold-like recollection process, the latter of which is related to high confidence recognition and retrieval of associative information.

Additionally, following the assumption that familiarity is related to item recognition and that recollection is related to correct associative recognition and recall, the early frontal old/new effect was reported absent while the late parietal old/new effect was observed to be evident in an associative recognition and a recall task (Donaldson & Rugg, 1999). In line with the view that the HC is particularly involved in creating and retrieving associations and by this critically involved in recollection-based recognition decisions, an ERP study with a patient suffering hippocampal damage shows that the late parietal old/new effect is more affected than the early frontal old/new effect by this lesion (Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001).

Finally, investigating familiarity and recollection based on their different temporal dynamics, Mecklinger, Brunnemann, and Kipp (2011) observed that recollection was attenuated for speeded compared to non-speeded recognition decisions in young adults, whereas familiarity was unaffected by such a response deadline manipulation. This complements behavioral findings and suggests that familiarity is a fast-acting process and can contribute to recognition decisions under speeded responding while recollection requires more time.

Taken together, these ERP findings support the view that the early frontal and late parietal old/new effect can be associated with familiarity- and recollection-based memory recognition.

1.3.7 Dissociating familiarity from conceptual fluency

However, the close link between the early frontal old/new effect and familiarity has been called into question by findings showing that the early ERP component was modified by the meaningfulness of stimuli (Voss & Paller, 2007, 2009). In one of these studies, participants learned a series of abstract, novel shapes (squiggles) while evaluating their meaningfulness on a rating scale and were later tested with the R-K procedure. The early frontal old/new effect varied with the perceived meaningfulness of the stimuli, despite familiarity was held constant (comparable number of know responses for squiggles of high and low meaning) (Voss & Paller, 2007). In another study, participants studied kaleidoscope images that lacked any meaning and in a later recognition test, no early frontal old/new effect was observed (Voss & Paller, 2009). It was thus suggested that the early frontal old/new effect is related to facilitated semantic processing rather than familiarity (Paller, Voss, & Boehm, 2007). Specifically, the early frontal

old/new effect is considered merely a modulation of the N400 component, which is associated with early conceptual and semantic processing (Kutas & Federmeier, 2011; Kutas & Hillyard, 1984). A close relationship of the early frontal old/new effect and the N400 is also suggested by an alternative naming of the ERP correlate of familiarity, namely “frontal N400-like negative component” (FN400) (Curran, 1999).

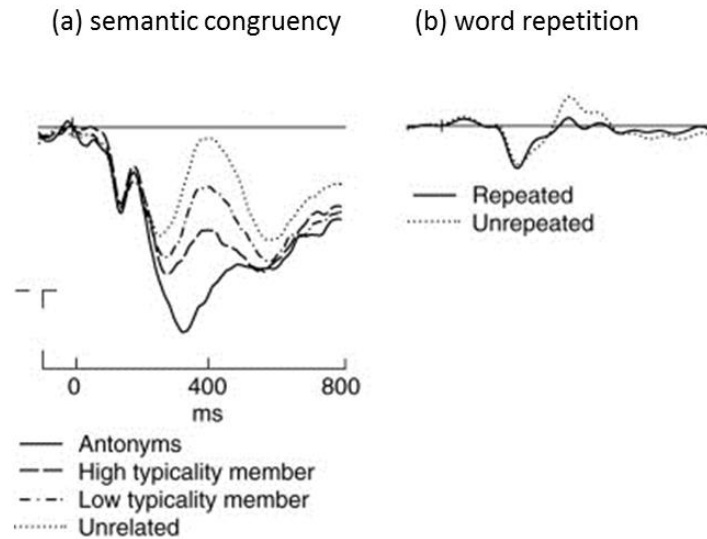


Figure 4 - Depicted are modulations of the N400 (a) by semantic congruency to antonyms (e.g. the opposite of black... WHITE), to category members of high typicality (e.g., A type of bird... ROBIN) and of low typicality (e.g., A type of bird... TURKEY) and to semantically unrelated items (e.g., the opposite of black... CARROT) and (b) by word repetition. Negativity is plotted upwards (adopted from Kutas & Federmeier, 2000).

The N400 displays a negative deflection peaking around 400 ms that is typically right-lateralized and accentuated at centro-parietal electrodes (see Figure 4). Kutas and Hillyard (1980) observed variations of the N400 in response to sentence endings that were either semantically congruous or incongruous. The N400 was found to be more negative for incongruous terminal words and less negative when the sentence ended appropriately (i.e., the sentence *he spread the warm bread with ___* ended with *socks* or *butter*, respectively). It has further been shown that the N400 varies systematically with participants' expectations about the terminal word, suggesting that the N400 reflects semantic priming and is attenuated when semantic integration of a word into its context is facilitated (Kutas & Hillyard, 1984). However, the N400 has not only been observed in the context of language processing, but with all kinds of meaningful stimuli including words, pictures, faces and sounds. As the N400 occurs automatically even without explicit task demands, it is typically investigated in implicit tests of priming (see also section 1.1 and chapter VII). For instance, when individuals respond to a series of stimuli, quicker response times can be observed when the preceding item (prime, i.e., *doctor*) is related to the currently presented item (target, i.e., *nurse*) (Kutas & Federmeier, 2011).

Voss & Paller (2007) claim that this type of fluency-related implicit memory can contribute to explicit recognition decisions and thus contaminate what is usually referred to as familiarity-based memory. The early frontal old/new effect in recognition memory paradigms might thus simply arise from an attenuation of the N400 due to item repetition (from study to test) reflecting facilitated access to semantic meaning, also termed as conceptual fluency. Concordantly, Voss, Schendan and Paller (2010) reported that the magnitude of the behavioral conceptual fluency effect was positively correlated with the size of the FN400 for high meaning squiggles, suggesting that conceptual priming is associated with the early frontal old/new effect (Paller et al., 2007).

There are numerous findings challenging the assumption that the early frontal old/new effect reflects merely conceptual priming. For instance, the early frontal old/new effect was shown to be sensitive to perceptual changes in stimuli from study to test, despite conceptual information remained unchanged (Groh-Bordin, Zimmer, & Mecklinger, 2005). Further in the same study, the early frontal old/new effect was only elicited under explicit retrieval conditions and not in an implicit task (Groh-Bordin et al., 2005; for the full argument see also Mecklinger, Frings, & Rosburg, 2012). A more direct argument disputing the position that the early frontal old/new effect comprises an index of implicit conceptual fluency rather than explicit familiarity comes from a recent ERP study. In that study a semantic priming paradigm was employed that served as implicit encoding phase for an unexpected recognition memory test. Results show different scalp distribution for the N400 and the early frontal old/new effect, suggesting that these two processes are functionally dissociable and that the ERP correlate of familiarity does not merely index automatic conceptual processing (Bridger, Bader, Kriukova, Unger, & Mecklinger, 2012).

Despite the functional distinction between familiarity and conceptual priming, several studies suggest a close relationship between behavioral estimates of familiarity and conceptual priming by observing the PrC to be critically involved in familiarity-based recognition (Daselaar et al., 2006b; Diana et al., 2007; Yonelinas, Aly, Wang, & Koen, 2010) and conceptual priming (Voss, Hauner, & Paller, 2009; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010). Accordingly, Wang and Yonelinas (2012) examined behavioral estimates of familiarity (using ROC and R-K procedure) and conceptual implicit priming (using a free association task) in a within-participant design and found familiarity and conceptual priming to be correlated. A correlation between conceptual priming and recollection was not observed, which is in line with the assumption that recollection reflects the explicit and effortful retrieval of detailed information associated with an event rather than occurring relatively automatic (Mecklinger, 2000, 2010; Yonelinas, 2002). Importantly, Wang and Yonelinas (2012) also reported that the familiarity

measure accounted (only) for approximately half of the variance in conceptual implicit memory, suggesting (only) a partial overlap between these two processes.

Further, it has been shown that meaningful semantic elaboration of items during encoding does enhance their later recognition based on familiarity relative to non-semantic encoding (Gallo, Meadow, Johnson, & Foster, 2008; Greve, Van Rossum, & Donaldson, 2007; Toth, 1996). For instance, Meyer, Mecklinger, and Friederici (2007) reported that the negativity of the N400 elicited by incongruous sentences in a sentence comprehension task was negatively correlated with the size of the early frontal old/new effect elicited by old words in a subsequent surprise recognition task. It was suggested that the expectancy violation by incongruous sentences led to higher semantic elaboration at study that benefited familiarity-based recognition at test. Additionally it was shown that manipulations of conceptual fluency at test, when studied words are preceded by a predictive compared to a non-predictive sentence stem at recognition, attenuated the N400 and increased the rate of correct and incorrect 'old' responses (Wolk et al., 2004). It was proposed that facilitated conceptual processing at test was (erroneously) attributed to a prior study experience and by this enhanced familiarity and the likelihood to judge an item as old. But since ERPs based on participants 'old' and 'new' responses were not influenced by the fluency manipulation, it is unclear whether conceptual fluency really contributed to familiarity-based responding (in the subsequent sections support for the assumption that conceptual fluency can contribute to familiarity-based responding will be provided).

Taken together, these results suggest that familiarity and semantic processing seem to involve similar operations and brain regions (Meyer et al., 2007), suggesting that they are closely related and can interact under certain conditions. Important however is the finding that ERPs can clearly dissociate between familiarity and semantic processing, justifying the relation of the early frontal old/new effect to familiarity in episodic memory recognition.

1.3.8 Absolute and relative familiarity

To further complicate the matter of the concept of familiarity, it has been suggested that familiarity is multiply-determined and that it can arise as an *absolute* or *relative* familiarity signal. Absolute familiarity refers to the pre-experimental baseline familiarity of an item, and relative familiarity to the increment in familiarity beyond that baseline after the item has been presented in the study phase (Bridger, Bader, & Mecklinger, 2014; Coane, Balota, Dolan, & Jacoby, 2011; Mandler, 1980). It was proposed that absolute familiarity is highly diagnostic for the recent encounter of an item in situations in which all stimuli are pre-experimentally unknown and

experienced the first time throughout the study phase of an experiment, while relative familiarity might be more diagnostic to identify the recent encounter of already known items (Bridger et al., 2014; Mandler, 1980). Since most ERP studies of recognition memory usually use pre-experimentally familiar stimuli (such as meaningful words) and (as discussed in the previous section) typically report the early frontal old/new effect, this ERP effect can be taken as index of *relative* familiarity.

Another ERP signal with a similar time course, but with a more posterior distribution, by contrast, may index absolute familiarity. Support for this idea comes, for example, from a recent study by Bridger et al. (2014) that directly investigated the ERP correlates of absolute and relative familiarity in a recognition experiment using high frequency (e.g., *part, free, speak*) and low frequency (e.g., *sickle, sloppy, to milk*) words as stimuli. Because participants have much lower levels of prior exposure to low frequency words, they are expected to have lower absolute familiarity than high frequency words and consequently receive a greater boost in (relative) familiarity when re-encountered throughout the experiment. In line with the hypothesized dissociation of the frontal and parietal early effects, Bridger et al. (2014) observed an early posterior ERP difference between high and low frequency new words (with high > low, reflecting absolute familiarity) and larger early frontal old/new effects for low than high frequency words. These findings provide evidence for the view that the early frontal old/new effect indexes relative familiarity while the early parietal effect indexes absolute familiarity. Notably, from an ERP contrast of new items, such as the contrast between high and low frequency new words in Bridger et al. (2014), one cannot unequivocally infer that this attenuated negativity for high frequency words reflects explicitly available processing. Rather, the difference may be due to a relatively automatic conceptual fluency signal. Support for this view comes from studies that showed that low frequency words elicit a greater N400 than high frequency words, consistent with the notion that high frequency words are more accessible than low frequency words (Rugg, 1990; Van Petten & Kutas, 1990). The N400 has a similar spatial distribution than the early parietal effect described in this section and may therefore reflect the same cognitive process. It is difficult to distinguish between an absolute familiarity or conceptually-driven familiarity interpretation of the early parietal ERP effect, but at least these interpretations do not contradict each other (Bader, Mecklinger, Hoppstädter, & Meyer, 2010; Wiegand, Bader, & Mecklinger, 2010), as it has been shown that perceived conceptual fluency at test can be attributed to the study phase and contribute to familiarity-based responding (Whittlesea & Williams, 2000). Consequently, Bridger et al. (2014) observed the false alarm rate to be increased for high frequency compared to low frequency words, suggesting explicit processing, as the

stronger signal of high frequency new words has been attributed to a prior encounter during study.

Moreover, in another recognition study an early parietal old/new effect was associated with absolute familiarity. In this study, pre-experimentally unfamiliar faces were used as stimuli that were completely free from contextual information (no hair, clothes, background) (MacKenzie & Donaldson, 2007). Participants had to learn face-name pairings during study and at test make old/new recognition judgements to faces and in cases when these were old, to indicate whether they retrieved the name or any other specifics. An early old/new effect associated with familiarity-based recognition decisions (face recognition in the absence of recollection of contextual information) was maximal at posterior recording sites. Since unknown faces should exhibit very low levels of absolute familiarity, it was suggested that this posterior early old/new effect reflects absolute familiarity (MacKenzie & Donaldson, 2007). Importantly, in this study, faces were conceptually processed during encoding (e.g., “does the face fit the name?”) (MacKenzie & Donaldson, 2007), suggesting that subsequent conceptual fluency was probably boosted through this kind of encoding and might have contributed to familiarity-based responding at test. By this, the absolute familiarity signal discussed in this section, reflected in the early parietal old/new effect, may be relevant for recognition decisions when an item is perceived as conceptually fluent. The perceived conceptual fluency signal is attributed to the recent encounter with the stimulus in the study phase, and can hence be used to guide decisions about an item’s prior occurrence (see also Whittlesea & Williams, 2000).

In sum and in line with assumptions from the previous sections, the early frontal old/new effect can be regarded as a reliable index of relative familiarity in recognition memory paradigms that use pre-experimentally familiar stimuli. Further, when stimuli are pre-experimentally unfamiliar, absolute or conceptually-driven familiarity might be diagnostic for distinguishing studied items from unstudied lures, as indexed by an early parietal old/new effect.

Hence, the early frontal and late parietal old/new effect that are observed in standard recognition paradigms using pre-experimentally familiar material can be regarded as reliably reflecting familiarity- and recollection-based episodic memory retrieval. In light of this, age-related differences in these ERP components will be discussed in the following section. Importantly, the subsequent sections of the current chapter refer to findings on the early frontal old/new effect while reference to the early parietal old/new effect, that is usually not observed in standard recognition paradigms when stimulus material is highly familiar, won’t be made until chapter II.

1.3.9 Age-related changes in the ERP correlates of episodic memory

An increasing number of studies examining age-related differences in episodic memory use ERP measures and these studies to some extent support the aforementioned view that aging primarily impacts recollection (see Figure 5).

Mostly, ERP studies employing old/new recognition memory paradigms, source memory and R-K paradigms, have shown that the late parietal old/new effect, the ERP correlate of recollection, is diminished in older adults (Eppinger, Herbert, & Kray, 2010; Friedman, de Chastelaine, Nessler, & Malcolm, 2010; Nessler, Johnson, Bersick, & Friedman, 2008; Walhovd et al., 2006; Wegesin, Friedman, Varughese, & Stern, 2002). Moreover, in a recent study it was shown that the magnitude of the late parietal old/new effect was modulated by aging and executive-control functions, such that the ERP correlate of recollection was generally smaller in old adults, but especially diminished for elderly with low executive functioning (Angel, Fay, Bouazzaoui, & Isingrini, 2010a). This finding is in line with the assumption that recollection is dependent upon strategic retrieval. Congruently, several researchers have shown that the late parietal old/new effect in older adults varies with their cognitive performance (Friedman et al., 2010; Friedman, 2013; Wolk et al., 2009). For instance Duarte and colleagues (2006) conducted a source memory task, requiring participants to give remember/know/new decisions during recognition and additionally a source judgement for all items recognized as old. They reported that only high performing older subjects displayed the late parietal old/new effect (contrasting remembered and new items) even though their source memory accuracy was reduced compared to the younger adults, suggesting that older adults might recover less contextual information. Similarly, intact ERP correlates of recollection in high but not in low performing older adults were also observed by other researchers (Dockree, Brennan, O'Sullivan, Robertson, & O'Connell, 2015; Friedman et al., 2010). In addition to an age-related reduction in magnitude, some studies have also reported a delayed onset of the parietal old/new effect in older adults (Duarte, Ranganath, Trujillo, & Knight, 2006; Mark & Rugg, 1998; Wegesin et al., 2002). While these ERP studies support the view that aging is associated with impaired recollection, at least in old adults with low maintenance of cognitive functioning, the picture is less consistent with respect to age effects on the ERP correlate of familiarity.

Based on the majority of studies that employ behavioral estimates of familiarity and recollection and find preserved familiarity in older adults, one would expect the early frontal old/new effect, the ERP correlate of familiarity, to also be spared from aging. A few studies, however, have not detected the ERP correlate of familiarity in older adults (Guillaume et al., 2009; Swick et al., 2006) and this has been found to be the case even for high performing old

adults (Wolk et al., 2009) or when performance (Duarte et al., 2006) or strength of familiarity (Wang, de Chastelaine, Minton, & Rugg, 2012) was matched with groups of younger participants. These findings conflict with the aforementioned reports of behaviorally preserved familiarity in old age (see section 1.3.2) and indicate that the absence of the ERP correlate of familiarity in elderly cannot only be attributed to differences in task performance or memory strength across age groups. At the same time, however, the early frontal old/new effect has been observed in a selection of other ERP studies testing old/new recognition in older adults and in these studies was similar in amplitude to the corresponding effect in younger adults (Ally et al., 2008; Eppinger et al., 2010; Friedman et al., 2010; Morcom & Rugg, 2004). It is important to note that in the studies where the effect was found to be comparable across age groups, perceptually rich colored pictures of nameable objects were employed as test stimuli. In those studies where the early frontal old/new effect was not observed in elderly, stimuli consisted of greyscale portraits of famous people (Guillaume et al., 2009), greyscale photographs of meaningful objects (Duarte et al., 2006) or word stimuli (Wang, de Chastelaine, Minton, & Rugg, 2012; Wolk et al., 2009). One possibility is that the use of colored pictures as opposed to perceptually less rich stimuli, engenders higher levels of familiarity (Yonelinas, 2002). This view is supported by the fact that age-related memory impairments are generally smaller for nonverbal than for verbal materials (Ally et al., 2008; Craik & Schloerscheidt, 2011; Gallo et al., 2008; McDonough et al., 2013) and indicates the importance of material selection when studying the effects of healthy aging on episodic memory.

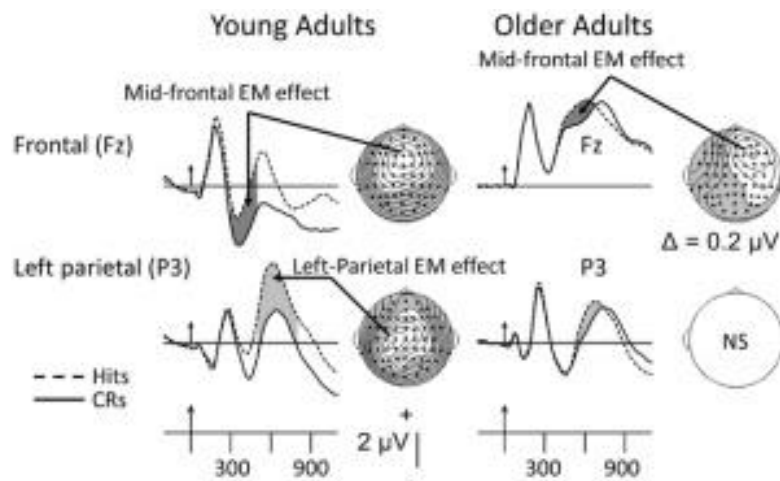


Figure 5 - Illustration of age-related differences in the early frontal and late parietal old/new effect, with negativity plotted downwards. While the early frontal old/new effect can be observed in older adults, the late parietal old/new effect is typically absent in elderly (taken from Friedman, 2013).

To summarize, aging is associated with impairments in episodic memory and a considerable number of studies have shown that recollection is disproportionately more attenuated in older adults than familiarity. The above-mentioned ERP findings provide an important complement to this view by showing an attenuated late parietal old/new effect, the ERP correlate of recollection, in older adults that is particularly reduced in low performing individuals. Conversely, there is some inconsistency in the presence of the ERP correlate of familiarity in older adults, with some studies reporting the early frontal old/new effect to be intact while other studies report this effect to be absent in elderly.

II THE CONTRIBUTION OF FAMILIARITY TO ASSOCIATIVE RECOGNITION

In simple item recognition tasks, one must distinguish previously learned (old) from unlearned (new) information, whereas in typical associative recognition tasks, containing item-item or item-context associations (both reflecting inter-item associations), individual stimuli are equally familiar and the retrieval of additional information about the relationship between items or item and context is necessary. For instance, to successfully retrieve inter-item associations such as word pairs, one must distinguish whether the configuration of an item pair has been encountered as such during study (old pairing) or whether the single components have occurred in different combinations during study (recombined pairing). “The critical distinction between item and associative recognition is that the prior occurrence of an individual item is diagnostic for item recognition but not for associative recognition” (Quamme et al., 2007, p. 192). Thus, item recognition can occur through the specific recollection of information about the prior study episode or simply through an items’ familiarity. In contrast, associative recognition depends largely on recollection of the particular stimulus pairing.

Evidence for this assumption comes from ERP studies that typically observe an early frontal and late parietal old/new effect during item recognition (Mecklinger, 2000; Rugg & Curran, 2007; Rugg & Yonelinas, 2003; Woodruff et al., 2006), whilst only the late parietal old/new effect has been observed during associative recognition (Donaldson & Rugg, 1999, see also Section 1.3.6). For instance, in an associative recognition task, Donaldson and Rugg (1998) observed a larger positivity for old compared to recombined items in a time window associated with recollection, but no ERP correlate of familiarity. This is congruent with the assumption that discriminating between old and recombined pairs relies primarily on recollection of associative information.

As outlined in section 1.2.2, associative memory does not only refer to inter-item associations, but also to intra-item associations. Yonelinas, Kroll, Dobbins, and Soltani (1999) tested participants’ associative memory for faces that were presented either in an upright or inverted orientation. By changing facial features (i.e., internal facial features, such as mouth, nose, eyes, or external facial features, such as hair, chin, shoulders) from study to test, old faces had to be discriminated from recombined faces (consisting of rearranged facial features from different old faces) at test. ROC was curvilinear for upright and linear for inverted faces, suggesting that participants used familiarity to discriminate old from recombined upright faces, but mainly recollection when faces were inverted. It was suggested that upright faces allow binding of intra-

item associations, whereas inversion of faces results in conjunction of separate features (inter-item associations) and that these different forms of associations differentially support familiarity- and recollection-based retrieval. Similarly, in an ERP study by Ecker, Zimmer, and Groh-Bordin (2007), participants learned item-context associations and were later tested on these pairings, while for parts of stimuli either the color of the object or the type of context had changed. Manipulation of color modulated the ERP correlate of familiarity and recollection, whereas a context change only modulated the late parietal old/new effect.

These results suggest that intra-item associations, such as color of an item or facial features that depict within-item binding, can be integrated meaningfully and perceived as a single entity, thus relying on familiarity. In turn, inter-item associations depict relational binding between separate items that require recollection-based retrieval (Mayes, Montaldi, & Migo, 2007, Yonelinas et al., 1999; Zimmer et al., 2006). This suggests that in some cases familiarity can contribute to the retrieval of associative information.

2.1 The unitization versus domain-dichotomy view

There are two broad assumptions about how familiarity can contribute to associative recognition, the unitization view and the domain-dichotomy (DD) view.

According to the unitization view, familiarity can mediate associative memory whenever the to-be-associated components of a pairing can be integrated meaningfully into a unified representation and perceived as a single entity. Unitization refers therefore to processing that transforms multiple items into a single coherent unit (Parks & Yonelinas, 2015). Intra-item associations do inherently represent unitized associations, since they consist of associations between features of one single unit. The occurrence of unitization is not restricted to intra-item associations and can theoretically emerge for all sorts of to-be-associated components, whether within-domain (e.g., word pairs, picture pairs) or between-domain (e.g., face-name pairs) associations (Yonelinas et al., 2010). In line with the view that unitized associations are treated as single items, it is suggested that the PrC also mediates familiarity for this type of associations while the HC supports recollection of inter-item associations (Diana et al., 2007). Quamme et al. (2007) investigated associative memory performance in patients with hippocampal lesions that have previously demonstrated severe recollection deficits but intact familiarity across different measurement methods. Patients encoded word pairs (e.g., *cloud-lawn*) either as compounds, because a definition for the word pair was provided (“a *cloud-lawn* is a yard used for sky-gazing”, Parks & Yonelinas, 2015, p. 882), or as loosely related items, since they were embedded in a

sentence frame (“the *cloud* could be seen from the *lawn*”, Parks & Yonelinas, 2015, p. 882). These patients showed enhanced performance for compounds compared to item-pairs from the sentence condition. This was taken as evidence that intact regions of the PrC could have supported familiarity for unitized associations. Since it is “impossible to know in any absolute sense whether an individual has treated a stimulus as a single item or as a set of associated features” (Yonelinas et al., 2010, p. 1186), unitization needs to be understood as a continuum, along which different levels of unitization can occur, rather than a dichotomy. Therefore, typical unitization paradigms contrast conditions that are differentially likely to support unitization (high versus low unitization encoding; Parks & Yonelinas, 2015; Yonelinas et al., 2010).

An alternative view, the domain-dichotomy (DD) theory (Mayes et al., 2007; see also Montaldi & Mayes, 2010, for the extended DD version, the Convergence, Recollection, and Familiarity theory, CRAFI) holds that not only unitized associations but also non-unitized associations can elicit familiarity at recognition, namely when multiple items “feel like [they] have appeared together in the past” (associative familiarity; Montaldi & Mayes, 2010, p. 1296), suggesting that a familiarity signal alone is not sufficient to make inferences about unitization. This view suggests that also non-unitized within-domain associations may elicit familiarity because they share many features and thus activate overlapping representations within PrC. Between-domain associations would not converge sufficiently within PrC, because they share only few features, and instead project to the HC where they establish distant pattern separated representations. Thus, the DD view suggests that the PrC supports familiarity for unitized and within-domain inter-item association whereas the HC supports recollection for intra-item, within-domain and between domain inter-item associations (Mayes et al., 2007). This theory is mainly based on findings from a patient with hippocampal lesions that showed impaired memory for between-domain associations, but relatively intact memory for intra-item and within-domain associations (Mayes et al., 2004).

When it can be assumed that within-domain associations are easier to unitize than between-domain associations, the DD and the unitization theory mostly converge except on their assumptions about whether between-domain pairs can potentially be processed as unitized associations or not (Yonelinas et al., 2010). However, two recent studies have shown that also between-domain associations can elicit familiarity. For instance, Harlow, Mackenzie, and Donaldson (2010) have shown that familiarity estimates were similar for name-name and image-name pairs. Estimates were derived from ROC or a modified R-K procedure where participants were asked to respond only familiarity-based (familiarity-only instruction). In the study of Parks and Yonelinas (2015), stimuli consisted of face-face pairs and face-hobby pairs that were studied under either a high or low unitization encoding condition. High unitization encoding boosted

familiarity for between-domain pairs, demonstrating that unitization denotes a general associative process that can occur across different stimulus domains (Parks & Yonelinas, 2015). Hence, as these results speak against the DD theory, an overview over behavioral, fMRI and ERP studies will be given that differentially manipulated unitization at encoding and could show enhanced familiarity-based recognition of unitized item pairs.

2.1.1 Manipulations of unitization and its effects on measures of familiarity

The memory advantage for unitized over non-unitized pairings – indicated by a performance increase as well as the contribution of familiarity to associative recognition - has been demonstrated for many different unitization manipulations, that can roughly be assigned to two different approaches: 1) the manipulation of stimulus characteristics (bottom-up approach) and 2) the manipulation of encoding instructions (top-down approach) (see Tibon, Gronau, Scheuplein, Mecklinger, & Levy, 2014, for a detailed illustration).

Bottom-up unitization manipulations

Bottom-up unitization manipulations focus on associative information or on overlapping item features between stimuli to produce different levels of unitization, while encoding instructions across high and low unitization conditions are held constant. One simple way to promote unitization at encoding is to employ compound words, by presenting two words that form a new meaning when combined (e.g., *land-escape*). Since compound word pairs are pre-experimentally conceptually integrated words, they are suitable to create conditions in which unitization is facilitated. Concordantly, Giovanello, Keane, and Verfaellie (2006) observed higher associative recognition for compound word pairs compared to unrelated word pairs in amnesic patients (with MTL lesions), while healthy participants demonstrated similar performance for the two types of stimulus material.

Similarly, an early frontal old/new effect has been observed for compound word pairs (e.g. *traffic-jam*), whereas semantically related word pairs (e.g., *cereal-bread*) elicited solely a late parietal old/new effect (Rhodes & Donaldson, 2007). Further, in the study of Greve et al. (2007), where category names (e.g., *animal*) preceded word pairs that were either semantically related (e.g., *rabbit-mouse*) or unrelated (e.g., *hair-bike*) to the category, associative recognition was better and additionally the early frontal old/new effect was larger for semantically related than unrelated pairs, while the late parietal old/new effect did not differ between these conditions. It is important to note, that Rhodes and Donaldson (2007) did not observe an early frontal old/new

effect for semantically related material while Greve and colleagues (2007) did. This discrepancy might be related to the contextual influences of the task: semantically related stimuli might be easier to unitize when presented together with unrelated compared to pre-experimentally unitized word pairs or when preceded by semantically related category names. Together, these findings implicate that a given relationship between stimuli, either pre-existing associatively or semantically, can promote unitized representations and enable familiarity-based recognition.

Most studies that examined the process of unitization used verbal stimuli (Diana, Van Den Boom, Yonelinas, & Ranganath, 2011; Greve et al., 2007; Kriukova, Bridger, & Mecklinger, 2013; Pilgrim, Murray, & Donaldson, 2012; Quamme et al., 2007; Rhodes & Donaldson, 2007, 2008; Staresina & Davachi, 2008; Wiegand et al., 2010), whereas unitization of visual stimuli, that are ecologically more valid than words, is less well investigated. In a recent investigation that employed ecologically valid pictorial stimuli (Tibon et al., 2014), we have used semantically related and unrelated pairs of object pictures in an associative recognition task. As such, differences in unitizability were derived from semantic regularities associated with object co-occurrences: two semantically associated objects were presented in their canonical spatial configuration (e.g., *ice cream over a cone*) or two unrelated objects were presented at the same positions (e.g., *an iron above flowers*). Due to technical reasons, most ERP studies did not include ERPs to recombined items into their analysis and based assumptions about unitization on modulations of the early frontal old/new effect associated with familiarity (Bader et al., 2010; Jäger, Mecklinger, & Kipp, 2006; Rhodes & Donaldson, 2007). In this study however, ERP indices of associative memory were more directly derived from contrasting old and recombined pairs. In contrast, retrieval of item information was assumed to be reflected in a recombined/new contrast, since the individual components but not their compositions are familiar¹. Early ERP differences between old and recombined stimuli (presumably reflecting unit familiarity) emerged at frontal recording sites for related pairs only. ERP differences between recombined and new stimuli (presumably reflecting item familiarity) were more centrally located and emerged for related and unrelated pairs. These findings are in line with the view that associative episodic recognition of semantically related visual stimuli can be supported by familiarity, perhaps because at encoding they are processed as a single unit.

However, whether or not multiple stimuli can be integrated into a unitized representation does not only depend on the type of stimulus material but also on the manner in which stimuli are encoded. In contrast to bottom-up unitization approaches, top-down manipulations

¹ For a distinction between old, recombined and new pairs on the basis of unit familiarity, one would expect an ERP pattern of old > recombined and new, while a distinction based on item familiarity is expected to elicit an ERP pattern of old and recombined > new (Tibon et al., 2014; Wiegand et al., 2010).

emphasize encoding instructions that influence whether multiple items are encoded as a unitized representation or as separate items.

Top-down unitization manipulations

One way to encourage unitization by encoding instructions is to emphasize the associative relationship between stimuli. For instance, Opitz and Cornell (2006) presented participants triplets of semantically related words (e.g. *oasis, camel, desert*) together with a filler word (e.g., *chair*) and encoding instruction focused either on associative relations between the words (“which word does not suit the context?”) or on size relations (“which word depicts the smallest object?”). The ERP correlate of recollection was observed in both conditions at retrieval, but importantly, the early frontal old/new effect only emerged for items that were encoded in an associative manner. This is consistent with the prediction that emphasizing pre-existing semantic relationships between stimuli can enhance later familiarity-based recognition. Another way to encourage unitization at encoding is the use of a strategy that allows the integration of arbitrary stimuli into a unified representation. For instance, Rhodes and Donaldson (2008) led participants learn compound and semantically related word pairs under either an interactive imagery strategy, that explicitly instructed participants to treat stimulus pairs as interacting items (high unitization encoding), or an item imagery strategy, that instructed participants to create an image for each individual word separately (low unitization encoding). They observed an enhanced early frontal old/new and old/recombined effect for semantically related word pairs encoded with an interactive imagery strategy compared to pairs encoded with an item imagery strategy, while encoding strategy had no effect on compound pairs that were already perceived as unitized and elicited these early frontal ERP effects in both encoding conditions. By contrast, semantic relationship had no effect on the late parietal old/new and old/recombined effect, but the latter one was modulated by encoding instructions, in line with the assumption that deep processing at encoding facilitates later recollection as indexed by the successful discrimination between old and recombined pairs (Rhodes & Donaldson, 2008).

Further, unitization instructions can also take the form of encoding context (colored background, e.g., red and green) and item (word, e.g., *elephant, sock*) information in an integrated (high unitization encoding) versus external (low unitization encoding) manner that supports the formation of intra- versus inter-item associations. In the former condition participants are instructed to imagine the item in the background color (e.g., “imagine the elephant being red” or “imagine the sock being green”) and in the latter condition, participants shall imagine the background color as separate contextual information of the same episode (e.g., “imagine the

elephant to be associated with a red stop sign” or “imagine the elephant to be associated with a green dollar bill”). ROC estimates, response deadline procedure and ERP measures revealed that the contribution of familiarity to recognition of word-color associations was higher under high compared to low unitization encoding (Bastin et al., 2013; Diana et al., 2011; Diana, Yonelinas, & Ranganath, 2008).

Another attempt to manipulate unitization for arbitrary word pairs that lack a pre-existing relationship is to present these stimuli together with a definition that fuses items to a new concept (high unitization encoding), e.g., “a *cloud-lawn* is a yard used for sky-gazing” (Parks & Yonelinas, 2015, p. 882), or within a sentence frame (low unitization encoding) that links the items in a way that they are processed relatively separate rather than as one unit, such as “the *cloud* could be seen from the *lawn*” (Parks & Yonelinas, 2015, p. 882). This unitization manipulation has been proven effective to facilitate the formation of unitized representations. Using this approach, which was already described in section 2.1, Bader et al. (2010) reported an early old/new effect associated with familiarity-based recognition that emerged in the high unitization condition while the late parietal old/new effect reflecting recollection only emerged in the low unitization condition. It was assumed that in cases when familiarity is sufficient to retrieve the whole word pair, the process of recollection is less required (for a similar interpretation see also Kriukova et al., 2013). Notably, while studies using stimulus material consisting of semantically related pairs or preexisting compounds observed an early frontal old/new effect for unitized pairings (Greve et al., 2007; Kriukova et al., 2013; Rhodes & Donaldson, 2007, 2008; Tibon et al., 2014), the early old/new effect in the study of Bader et al. (2010) did not exhibit the standard frontal scalp distribution but appeared as a widespread distributed effect that was maximal at posterior sites. One possible interpretation for the posterior distribution of the unit familiarity effect was given by Bader and colleagues with regard to the comparative contribution of absolute and relative familiarity to associative recognition. As described in section 1.3.8, absolute familiarity refers to baseline familiarity of an item from prior life experience and is associated with an early posterior old/new effect, while relative familiarity refers to the increment in familiarity beyond that baseline due to a presentation of the item and is associated with the early frontal old/new effect (Bridger et al., 2014; Coane et al., 2011; Mandler, 1980). It was proposed that absolute familiarity was responsible for the parietal focus of the early old/new effect, as it was more diagnostic to recognize old unitized pairings when unitization at study encouraged the formation of completely new concepts (Bader et al., 2010; Wiegand et al., 2010). Another interpretation for the posterior distribution was that the definition encoding instructions facilitated the semantic integration of item pairs into a new concept that could have led to facilitated conceptual processing at test and attenuated the N400. As outlined in section

1.3.8, since perceived conceptual fluency at test might be attributable to the study phase and contribute to familiarity-based responding (Whittlesea & Williams, 2000), these different interpretations do not contradict each other in the sense that absolute familiarity for pre-experimentally unfamiliar stimulus material might be driven by a perceived fluency signal for novel compounds due to their facilitated semantic integration during encoding (Bader et al., 2010; Wiegand et al., 2010).

That the early parietal old/new effect indeed reflects the putative ERP correlate of familiarity for newly formed concepts in unitization paradigms could be replicated in an ERP study by Wiegand et al. (2010) using the same encoding phase as in Bader et al. (2010). In this study, the early parietal old/new effect only appeared for well integrated word pairs at test that were rated as plausible during study, but not for pairings rated as implausible, providing additional evidence for an early parietal ERP correlate of familiarity specific to novel conceptual units.

Taken together, the studies reported in this section provide evidence that unitization encoding can enhance later familiarity-based retrieval. Further, depending on the type of stimulus material and the type of encoding instruction used, these studies suggest that “unitization leads to an enhancement of relative familiarity if it strengthens a pre-experimentally existing representation” (Bader et al., 2010, p. 780), leading to an increase in the early frontal old/new effect. “However, if unitization produces a novel representation, other processes—such as the assessment of absolute familiarity or the attribution of facilitated conceptual processing to a prior experience with the event—seem to be activated” (Bader et al., 2010, p. 780), that lead to an increase in the early parietal old/new effect.

2.1.2 Unitization and semantic memory

With regard to the different unitization manipulations and the observed early parietal old/new effect for novel conceptual units that was associated with conceptual fluency, it is reasonable to assume that one way through which unitization can occur is the integration of information into semantic memory for closely linked representations. It has indeed been shown, that high unitization encoding, when participants are encouraged to integrate multiple stimuli meaningfully, increases priming for associative information (i.e., more incorrect “word” responses to arbitrary words pairs learned with a definition than with a sentence in a subsequent lexical decision task; Parks & Yonelinas, 2015). This suggests that unitization can enhance semantic processing. By this, one could argue that manipulation of encoding instructions that

create different levels of unitization simply reflect levels of (semantic) processing rather than a specific form of associative learning. High unitization encoding conditions in previous studies may have involved just more elaborated semantic processing than low unitization conditions: “processing a new compound word may lead to deeper or more semantic processing than reading a sentence that includes those two words, or imagining an object in a color may be more meaningful than associating an object with a colored object” (Parks & Yonelinas, 2015, p. 883).

Parks and Yonelinas (2015) recently investigated whether high versus low levels of unitization (definition versus sentence encoding, respectively) were dissociable from deep versus shallow semantic processing (pleasantness judgement task versus vowel counting, respectively) at encoding. It was shown, that high unitization encoding selectively increased associative but not item recognition, whereas deep levels of processing benefited item and associative recognition similarly. Further, it was shown that high unitization encoding predominantly affected familiarity while deep semantic encoding affected both, familiarity and recollection. This suggests that unitization as encoding strategy is different from deep semantic processing and specific in supporting the formation of integrated representations that facilitate familiarity at retrieval (Parks & Yonelinas, 2015).

Further support for the assumption that unitization may not only act through modulation of semantic information comes from Jäger, Mecklinger, and Kipp (2006), who reported effects of unitization for stimuli that do not share a specific semantic relationship, when they are highly overlapping. In this study, associative recognition memory was tested for intra-item associations of faces, as revealed by two photographs of the same person, and for inter-item associations, as revealed by two photographs of different persons. An early mid-frontal old/new effect was obtained for intra-item associations, but not for inter-item associations. Further, Parks and Yonelinas (2015) reported that high compared to low unitization encoding (sequential versus simultaneous presentation) also increases familiarity-based recognition of pre-experimentally unknown fractal-sound pairs.

Taken together, these studies demonstrate that unitization is an effective and beneficial strategy to facilitate familiarity for associations and that it can also occur independently from semantic processing.

2.1.3 Neural basis of unitization

The view that unitization supports familiarity-based associative recognition is also supported by recent brain imaging studies. Unitization during associative encoding reduced the

recruitment of brain regions involved in recollection (including the hippocampus) and specifically engaged regions involved in the processing of unitized associations (including the parahippocampal gyrus) (Bader, Opitz, Reith, & Mecklinger, 2014). Furthermore, increased PrC activation during encoding has been shown to encourage unitization of word pairs and to covary with familiarity-based recognition of word pairs at test (Haskins, Yonelinas, Quamme, & Ranganath, 2008). Relatedly, Staresina and Davachi (2006) observed PrC activity during encoding to be correlated with later recognition of word-color associations when color was encoded as an item detail (Staresina & Davachi, 2008, 2010, 2006) but not when the encoding task required item-context binding (Staresina & Davachi, 2008).

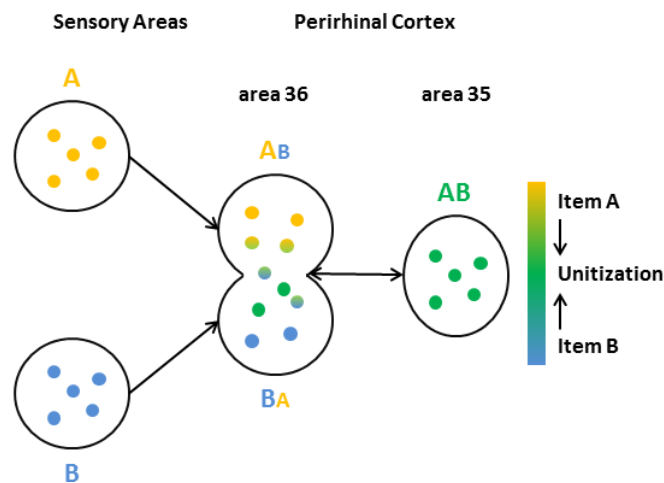


Figure 6 - Illustration of the hierarchical organization for unitization processing in the PrC (adapted from Fujimichi et al., 2010). Two objects (A and B) are represented in A 36 as two associated stimuli. In contrast, in A 35, these two objects are represented as one single representation.

Recently, Fujimichi et al. (2010) recorded single-unit activity within the PrC of primates while performing a paired associate task, in which a cue object is followed by two alternative choice objects consisting of the paired associate (target) and a distractor. The response of certain PrC neurons (within area 35) was very similar to paired associate stimuli, suggesting that these stimuli are treated as one single unitized item, while other PrC neurons (within area 36) differentiated between them, suggesting that these stimuli are more treated as two associated items. Thus, the different representations of associative memory within PrC neurons suggest a hierarchical processing for unitization (see Figure 6). This is in line with the assumption, that unitization processing occurs along a continuum of different levels of unitization (Parks & Yonelinas, 2015; Yonelinas et al., 2010).

2.1.4 Costs of unitization

One important feature of hippocampus-dependent associative bindings is that memories are highly flexible. Flexibility of memory representation is the crucial basis for mental time travel, future planning and creativity (Clayton, Bussey, & Dickinson, 2003; Henke, 2010). Flexibility permits the rearrangement of components of one episode to recollect the initial information. “This means that the elements of a relation retain their identity in any binding, i.e. the representation of an element remains the same irrespective of the actual binding demands, so the representation of “your colleague” is the same regardless of the meeting situation” (Opitz, 2010, p. 1038). Therefore, memoranda can flexibly be triggered by many cues (Henke, 2010). Bunsey and Eichenbaum (1996) showed that rats that performed a paired associate task for trained odor-odor associations were able to recollect the correct association when the single odor components were presented in reversed order (symmetry) or when the associated component was not the same as during training but shared a common element with the cue odor (transitivity). By contrast, rats with hippocampal lesions showed neither symmetry nor transitivity. Relatedly, it has been demonstrated that recall performance of paired associates (A - B) is nearly identical for forward (when A is the cue to recall B: $A \rightarrow B$) and backward ($B \rightarrow A$) recall (Kahana, 2002).

In contrast to flexible hippocampus-dependent associations, unitized associations are assumed to be inflexible and more rigid (Bader et al., 2014; Henke, 2010). For instance, Rhodes and Donaldson (2008) observed that test response accuracy for recombined pairs was reduced when they were studied under high unitization encoding but not when they were studied under low unitization encoding. It was suggested that unitized representations are “difficult if not impossible to break up once established” (Rhodes & Donaldson, 2008, p. 882). Correspondingly, Wiegand et al. (2010) observed an early parietal old/new effect (ERP correlate of unit familiarity when unitization encoding encourages the formation of novel conceptual units) only for old (e.g., *milk-taxi*), but not for reversed items (e.g., *taxi-milk*), suggesting that reversing the order of two associates within one pair would disrupt the unit. Thus, unitization is not only beneficial, in the sense that it encourages the contribution of familiarity to associative memory, but it also comes with costs, namely the inflexibility of associations.

Further, Pilgrim and colleagues (2012) observed that the ERP correlate of familiarity was selectively reduced for single words of a pairing that was previously studied under high unitization compared to low unitization encoding, indicating detrimental effects of unitization on familiarity for the single components of a unitized association (Mayes et al., 2007). Effects of costs of unitization have also been observed with regard to recollective processing of unitized associations. It was also shown that unitization encoding can produce activity reductions in the

HC (Bader et al., 2014; Ford, Verfaellie, & Giovanello, 2010) and reduce the ERP correlate of recollection (Bader et al., 2010; Kriukova et al., 2013). A possible interpretation for the differential effect of unitization on familiarity and recollection for associations implied that in such cases, when familiarity might have been sufficiently diagnostic to correctly recognize item pairings, there is no further need for additional recollection (Bader et al., 2010; Kriukova et al., 2013).

Taken together, unitization can be beneficial in the sense that it facilitates the contribution of familiarity to associative recognition and by this enhances associative memory performance. Besides, there are also findings that suggest that unitization can also come with costs. These costs are quantifiable as a reduced familiarity signal for the single components of unitized pairs and a reduced contribution of recollection to recognition, namely when unit familiarity is sufficiently diagnostic to retrieve the association.

III FACTORS THAT MODULATE THE AGING EPISODIC MEMORY

In chapter I, empirical evidence from behavioral and ERP studies was gathered showing that recollection is impaired in elderly while familiarity remains comparatively intact (Ally et al., 2008; Bastin & Van der Linden, 2003; Friedman et al., 2010; Guillaume et al., 2009; Schiltz et al., 2006), suggesting that effortful, strategic compared to rather automatic processing becomes less efficient with age. By this, it has been shown that performance differences between young and old adults are particularly pronounced when the task requires the self-initiation of effortful and controlled processing as in recall and associative recognition tasks (Craik & Byrd, 1982; Craik & McDowd, 1987; Craik, 2005). These findings are important as they suggest that observed episodic memory declines in old adults are highly task-dependent. From the viewpoint of Craik (1992, 2005), mental operations involve the interaction between internally generated and externally triggered processes, and when the task does not provide support, one must self-initiate the relevant mental operations. Therefore, due to reduced self-initiated controlled processing with age, older adults rely more on external environmental factors (see Figure 7).

Thus, according to Craik (1983, 1986, 2005), older adults are less likely to self-initiate controlled memory processes spontaneously, but still have the potential to engage in strategic processing, when provided with adequate environmental support, that can effectively guide encoding and retrieval. In virtue of the environmental support hypothesis, certain manipulations and conditions can be useful to counteract age-related memory impairments by reducing demands on self-initiated processing and by this particularly benefit older adults' memory (Craik & Bosman, 1992; Craik, 2005).

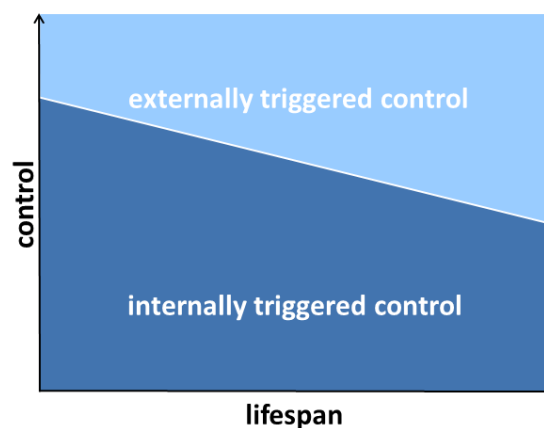


Figure 7 - Link between internally and externally driven cognitive operations (adapted from Lindenberger & Mayr, 2014).

As outlined in 1.2, older adults engage in less elaborative encoding generating less distinctive memory representations, and effortful retrieval operations are less likely to be self-initiated in old adults, resulting in a specific deficit of processing associative information and of recollection-based remembering. Thus, environmental support manipulations aim at facilitating encoding conditions, that allow deeper processing of the to-be-learned information, and retrieval conditions, that enhance the recapitulation of learned information. Different environmental support manipulations focus on task format and the type of stimulus material. By this, a distinction between environmental support and schematic support was proposed, referring to supportive information in the outside environment, i.e. manipulation of the task format, or internal support based on stock of well-learned schema information, i.e. manipulation of the stimulus material (Bialystok & Craik, 2005). It was suggested that environmental support denotes the broader term of supportive conditions whereby schematic support can be understood as the “mental equivalent of environmental support” (Craik & Bosman, 1992, p. 85). Since many studies also manipulate strategy instructions at encoding, which reflects per definition support by environmental context, we will refer to it as strategic support throughout the thesis, because it depicts a further specific class of task manipulation (Naveh-Benjamin et al., 2007). In the following, different implementations of support during encoding and retrieval are described that provide evidence for a successful reduction of the recollection deficit in old adults.

3.1 Environmental support

One manipulation that can be understood as environmental support and that reduces age-related performance differences is the use of a recognition task rather than testing older adults’ memory with recall (Botvinick & Storandt, 1980; Chalfonte & Johnson, 1996; Craik & McDowd, 1987; see section 1.2.1 for a detailed description of studies). That is, because in recognition tasks the previously encoded information is presented as reinstated at test and further self-initiated processing to complete the original pattern of learned information is less required than in recall tasks (Craik & Bosman, 1992) (see Figure 8). This finding corresponds to the *encoding specificity principle* that states that memory benefits from information being available at test that was also present during encoding (Tulving & Thomson, 1973). Similarly, Craik and Schloerscheidt (2011) tested young and older adults item memory on words that were studied superimposed on different backgrounds and which were presented at test within the same background from the study episode, a switched background from the study episode or no background. They observed that older adults benefitted more from context reinstatement at test (same > switched > no background) than young adults. Moreover, it has been reported, that age-related performance

differences in a word-stem cued recall task are eliminated when high retrieval support is provided compared to low support (the retrieval cue consisted of a four rather than three letter stem, Angel et al., 2010b). Additionally, in the more supportive condition the late parietal old/new effect associated with recollection was observed to be similar between young and old adults (Angel et al., 2010b). This suggests that the amount of environmental support by means of encoding specificity is particularly beneficial for older adults and can aid their otherwise impaired recollection-based memory retrieval.

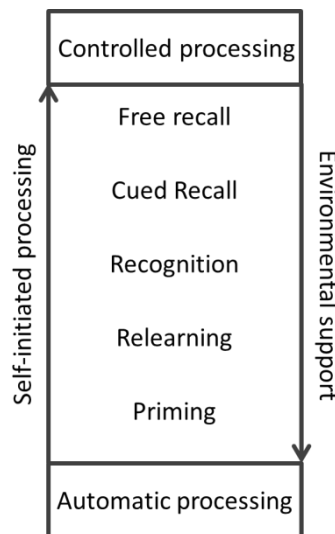


Figure 8 - Rank-ordered amount of environmental support and requirement of self-initiated processing for different memory tasks (adopted from Craik, 2005).

3.2 Schematic support

Schematic information that denotes the stock of an individual's mental schemes and habits can support learning and retrieval by providing a basis for meaningful interpretations of the to-be-learned information.

When young and older adults learned items associated with realistic and unrealistic grocery prices, performance between age groups was similar for cued recall performance of realistic but not for unrealistic grocery prices (Castel, 2005). This suggests that reliance on schema knowledge can disproportionately benefit the elderly. In a similar vein, the associative memory deficit in older adults was reported to be reduced for semantically related in comparison to unrelated pairs (Badham, Estes, & Maylor, 2012; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005; Naveh-Benjamin, 2000; Patterson, Light, Van Ocker, & Olfman, 2009), because semantic relations

between items reduce the need for self-initiated strategic processing since learning can be based on pre-existing relations. In cases of congruency between the actual information and pre-existing schemes, well-established neocortical semantic representations are activated that support memory, whereas schema incongruent information, as is the case for arbitrary item pairs or unrealistic grocery prices, is highly dependent on hippocampal binding mechanisms (Van Kesteren et al., 2012, see also section 1.3.3), that are severely reduced in old adults (Giovanello & Schacter, 2012).

Moreover, the use of colored pictorial rather than simple word stimuli can be understood as another instantiation of schematic support since colored pictures are perceptually rich that allow deep levels of processing and the formation of distinctive mental representations (Gallo et al., 2008; Paivio & Csapo, 1973; Paivio, 1991; Shepard, 1967). It was shown that this so-called picture superiority effect disproportionately favors older compared to younger adults (Ally et al., 2008; Craik & Schloerscheidt, 2011). The color and object details of pictorial information may provide more external cues than for instance word stimuli and by that support effective processing without much cognitive effort (Craik, 2005). In the study of Craik and Schloerscheidt (2011) (see section 3.1), the effect of context reinstatement was not only tested with words but also pictures of objects superimposed on different backgrounds. It was shown, that the use of pictorial stimuli reduced the effect of context and eliminated the age-related performance decrement. In an ERP study by Ally et al. (2008), testing item recognition for words and pictures, age-related recognition memory differences were observed in the word but not in the picture condition and the memory benefit of pictures was larger in old than young adults. Suitably, age-related differences in the early frontal and late parietal old/new effect only emerged in the word, but not in the picture condition. It was suggested that pictures enriched memory representations and by this enabled elderly to compensate for diminished episodic memory functioning (Ally et al., 2008).

3.3 Strategic support

Finally, providing participants with strategies that support deep elaborative encoding can reliably reduce the associative memory deficit in older adults. In support of this, it was demonstrated that the utilization of a relational strategy at encoding (i.e., to create sentences to bind the two words) diminishes the associative memory deficit for arbitrary word pairs in older adults (Giovanello & Schacter, 2012; Naveh-Benjamin et al., 2007) and can even eliminate it when strategies are provided at encoding and retrieval (Naveh-Benjamin et al., 2007). Importantly, when the strategy instructions are just intentional by means of instructing

participants to best possibly memorize word pairs for a later cued recall (Naveh-Benjamin et al., 2005) or associative recognition test (Naveh-Benjamin et al., 2009), then strategy instructions do not disproportionately favor old adults and reduce age differences (Naveh-Benjamin et al., 2009), but can benefit young and older adults similarly (Naveh-Benjamin et al., 2005). This suggests that when intentional instructions still require the self-initiation of controlled and strategic operations, age-related differences will persist. Therefore, to provide sufficient strategic support it might be important to provide a strategy that allows deep relational encoding (Giovanello & Schacter, 2012; Naveh-Benjamin et al., 2007) and to inform elderly about how to effectively utilize the strategy (Shing & Lindenberger, 2011).

Taken together, findings from strategic support suggest that appropriate support at encoding and/or retrieval can compensate for reduced recollection in older adults. However, there is increasing evidence that impairments in recollection can be effectively compensated by reliance on intact familiarity (Ahmad, Fernandes, & Hockley, 2014; Bastin & Van der Linden, 2003; Bastin et al., 2013; Zheng, Li, Xiao, Broster, & Jiang, 2015). By this it has been shown that age-related episodic memory impairments are particularly reduced in conditions that foster familiarity-based memory.

3.4 Compensation for impaired recollection: the potential role of familiarity in environmental support

It was shown, that older adults are impaired to recollect qualitative information about a prior event and thus are less likely to base their recognition decisions on recollection but instead rely predominantly on less specific memory signals, such as familiarity. Consequently, reduced recollection-related hippocampal activity together with increased familiarity-related PrC activity has been reported during episodic recognition tasks, suggesting that older adults greater reliance on familiarity-based recognition may be due to reduced recollection (Cabeza et al., 2004; Daselaar et al., 2006a).

Bastin and Van der Linden (2003) demonstrated that age-related performance differences are largely reduced in a forced-choice compared to an item recognition task (see also 1.2 and 1.3.2 for a discussion of this study). While recollection and familiarity can contribute to recognition in both tasks, familiarity-based responding is assumed to be facilitated in the forced-choice task (Shepard, 1967; Westerberg et al., 2006). In a forced-choice task, where the old item is presented simultaneously with lure items, participants can choose the one item among the others for which the familiarity-strength signal in a direct comparison is the greatest. However, in

an item recognition task when items are presented sequentially, also lures might elicit a familiarity signal that can exceed decision criterion when no other item is available for a direct comparison of the familiarity strength and produce an incorrect ‘old’ response. Thus, the assessment of familiarity alone might not be sufficient to guide accurate performance in item recognition tasks (Shepard, 1967; Westerberg et al., 2006). Importantly, in the study of Bastin and Van der Linden (2003) age-related decreases in recollection (indicated by the proportion of correct ‘remember’ responses) were observed in both tasks, whereas a significant increase in correct familiarity-based ‘know’ judgements in older adults was particularly pronounced in the forced-choice task (Bastin & Van der Linden, 2003). This suggests, that older adults’ overreliance on intact familiarity in tasks that foster familiarity-based retrieval can reliably compensate for deficient recollective processing and reduce age-associated episodic memory differences.

Further, it has been shown that age differences in associative memory are reduced by encoding manipulations that encourage unitization and later familiarity-based retrieval of unitized associations. Evidence in favor of preserved memory for unitized representations in old adults comes from three recent associative memory studies using compound words (Ahmad et al., 2014; Zheng, Li, Xiao, Broster, & Jiang, 2015a) and item-color associations (Bastin et al., 2013). Ahmad et al. (2014) and Zheng et al. (2015a) found the age-related associative deficit to be alleviated when memory was tested for unitized pre-existing associations of a compound word (e.g., *landscape*) compared to a non-compound word (e.g., *needle-birth*). Additionally, Zheng et al. (2015a) reported an early ERP old/new effect to be similar in old and young adults for unitized pairings but not for non-unitized pairings. It was proposed that the compound words – being pre-experimentally related - provide schematic support and as a consequence help older adults to build integrated representations (Ahmad et al., 2014) that allowed enhanced contribution of familiarity to associative recognition (Zheng et al., 2015a). Evidence for a unitization benefit for item-color associations in older adults was provided by the study of Bastin et al. (2013). Young and older participants studied words that were presented on a colored background (red or green) under two different encoding conditions that either promote unitization (by creating intra-item associations) or not (by creating inter-item associations). In a subsequent source memory task, age differences were reduced in the former (high unitization) but not in the latter condition (low unitization). Additionally, ROC curves of the older adults revealed a greater reliance on familiarity in the high unitization compared to the low unitization encoding condition. Therefore, conditions that promote unitization at encoding can encourage the contribution of familiarity to associative recognition at test and, by doing so, effectively alleviate the age-related associative memory deficit.

To summarize findings reported in chapter III, the environmental support hypothesis suggests that age differences depend on the extent to which a certain task requires self-initiated processing. By providing support in terms of reduced task requirements, such as schematic information or strategy utilization, older adults can make up for reduced processing resources and enhance their memory performance. Importantly, reduced age-related performance differences have also been reported for experimental manipulations that enable elderly to mainly capitalize on intact familiarity.

IV RESEARCH QUESTIONS

The major proposition from the theoretical introduction given in chapter I to III is that deficiencies in associative binding and self-initiated processing are important contributors to the episodic memory impairment in old adults. Consequently, elderly face difficulties in creating associative links between multiple information units and in (spontaneously) executing effective encoding and retrieval operations. By this, a vast amount of behavioral studies revealed that aging particularly disrupts recollection-based remembering but leaves familiarity rather intact. In contrast, findings on the ERP correlate of familiarity are less clear and the early frontal old/new effect was on the one hand reported to be intact and on the other hand to be absent in elderly. What makes the picture of the aging episodic memory look generally less negative is the finding that various manipulations can support memory in elderly and counteract the age-related episodic memory deficit.

The very crux of this thesis is to (a) examine experimental implementations that facilitate recognition based on familiarity and by this successively support episodic memory performance in old adults and (b) to more systematically explore how the ERP correlate of familiarity is affected by age under conditions which best foster familiarity-based recognition. For this endeavor, we additionally recorded ERP old/new effects to investigate age-related differences in the underlying contribution of familiarity and recollection to recognition under such conditions.

Environmental and schematic support manipulations were performed in two major ERP experiments. We used colored object stimuli for which detailed and vivid memoranda can be formed and that were shown to disproportionately benefit memory in older adults (Ally et al., 2008; Craik & Schloerscheidt, 2011) in all experiments.

In Experiment 1, we additionally manipulated response speed at test to best foster familiarity-based processing and to explore age-differences in item recognition and the emergence of the ERP correlate of familiarity in elderly under such conditions.

Then, in Experiment 2, we tested the ability of older adults to form associations between arbitrary object stimuli that were positioned, relative to each other, in either spatially plausible or implausible locations (e.g., an axe oriented towards or away from a hamburger), the former of which was expected to promote unitization at encoding. We thus hypothesized age-related associative memory differences to be reduced in the plausible condition that was expected to facilitate unitization at encoding and familiarity-based memory at retrieval.

We additionally performed an Experiment 3 to follow-up on results in Experiment 2. The rationale for conducting Experiment 3 will be discussed subsequent to the two major experiments.

V EXPERIMENT 1

5.1 Introduction

In line with the assumptions that recollection is impaired in older adults, ERP studies, as discussed in 1.3.9, mainly report the late parietal old/new effect to be diminished or absent in elderly (Eppinger et al., 2010; Friedman et al., 2010; Wegesin et al., 2002). In contrast however to the assumed intactness of familiarity in elderly, the early frontal old/new effect has not unequivocally been reported to be preserved from aging (Duarte et al., 2006; Guillaume et al., 2009; Wang et al., 2012). In studies where the early frontal old/new effect was concordantly reported to be comparable in young and older adults groups, perceptually rich colored pictures of nameable objects were employed as test stimuli (Ally et al., 2008; Dulas & Duarte, 2013; Eppinger et al., 2010; Morcom & Rugg, 2004). In those studies where the early frontal old/new effect was not observed in elderly, stimuli consisted of greyscale pictures of faces or of meaningful objects (Duarte et al., 2006; Guillaume et al., 2009), or word stimuli (Wang et al., 2012; Wolk et al., 2009). Colored picture stimuli may induce high levels of memory strength (Wang et al., 2012) and have previously been shown to disproportionately benefit memory for older adults (Ally et al., 2008; Craik & Schloerscheidt, 2011).

First, one goal of the present study was to more systematically explore how the ERP correlate of familiarity is affected by aging by providing conditions which best foster familiarity-based recognition. One way in which familiarity-based processing was supported, was the use of perceptually-rich colored picture stimuli for which detailed and highly distinctive memories can be easily formed (Ally et al., 2008). If familiarity is less modulated by old age, as suggested by the majority of behavioral studies, then the ERP correlate of familiarity should be preserved in old age, at least under conditions that are likely to support familiarity-based processing. Second, as a corollary to this, the present study also tested the assumption that age-related recognition impairments should be reduced or eliminated under conditions for which recognition should primarily be driven by familiarity. This was implemented by employing an item recognition memory task for which ERP effects of familiarity and recollection are usually found and adding a manipulation of response speed. Studies employing response deadlines have shown that limiting the time to respond attenuates the contribution of recollection but leaves familiarity largely unaffected (Boldini et al., 2004) and a recent ERP study with young adults revealed that the ERP correlate of familiarity was preserved whilst the correlate of recollection was eliminated when speeded recognition decisions had to be given (Mecklinger et al., 2011). Based on the aforementioned aging studies, we expected larger age differences in memory performance in a non-speeded recognition memory task (in which recognition judgments can be supported by

familiarity and recollection) than in a speeded version of this task (in which the contribution of recollection is attenuated and recognition should be mainly supported by familiarity).

The use of ERP measures in combination with a response deadline procedure to explore age differences in familiarity and recollection presupposes that age-associated differences in the ERP measures are not confounded with differences in the strength of the underlying memory signal. Addressing this is important because age-related changes in the ERP correlates of familiarity and recollection might not necessarily reflect differences in the underlying memory processes but could also result from behavioral differences in memory performance between age groups. This is problematic because memory performance is remarkably variable in old age (Morse, 1993) and a large number of studies have shown that the late parietal old/new effect is modulated by memory performance (see Friedman & Johnson, 2000, for a review). As outlined above, the use of perceptually-rich colored picture stimuli which are more memorable was expected to disproportionately strengthen recognition memory in old adults (Ally et al., 2008; Craik & Schloerscheidt, 2011). To further ensure that any age-related changes in the amplitude of ERP old/new effects are unlikely to be a consequence of declines in memory strength, the number of elderly who participated was larger than that of younger participants in order to account for the greater variability in memory performance of older adults and to allow an age-group comparison for which memory performance was matched. In line with a stronger age-related decline in recollection than in familiarity we predicted that the ERP correlate of familiarity should show less age-related differences than the ERP correlate of recollection under these conditions.

5.2 Method

5.2.1 Participants

Twenty younger adults (YA *mean age* = 24.15, *SD* = 2.76; 10 females) and 36 older adults (OA *mean age* = 69.75, *SD* = 3.71; 15 females) recruited from within Saarland University and via local newspaper advertisement in the wider community, took part in this study. Participants gave informed consent and were reimbursed € 8 per hour. Groups did not differ in their sex distribution ($\chi^2(1) = 0.36, p = .55$). Data from seven additional older participants had to be excluded from analysis due to high amount of eye and body movement artifacts (> 30% rejected trials, $n = 2$) and poor performance (accuracy < 0.50, $n = 5$). All participants were right-handed, native German speakers and reported themselves to be in good health (no depression or previous neurological problems).

5.2.2 Neuropsychological screening

All participants underwent a comprehensive neuropsychological test-battery that was conducted separately from the electroencephalography (EEG) session and lasted approximately 1½ hours. This consisted of 14 tests to assess potential cognitive ability: (1) semantic fluency (2) phonemic fluency (3) the Boston Naming Test (4) the Trail Making Test part A and B (5) word-list memory (recall, recognition) (6) and constructional recall, all subtests of the CERAD-Plus 1.0 (Memory-Clinic-NPZ, 2005) (7) mental control (8) logical memory (9) verbal paired associates (10) visual paired associates (encoding, recall) (11) and backward digit span, all subtests of the WMS-R battery (Härting, Markowitsch, Neufeld, Calabrese, & Deisinger, 2000). An operation span task (adapted from Turner & Engle, 1989, 12) and the digit symbol of the HAWIE-R (Tewes, 1991, 13) were also completed. The demographic and neuropsychological data for the two age groups are presented in Table 1. A one-way ANOVA was used to assess group differences on standardized test scores. Older adults were additionally tested with the Mini-Mental State Examination (MMSE, subtest of the CERAD-Plus 1.0) and scored within the average range ($M = 29.3$, $SD = 0.88$; the standardized z -value is not different from 0, $p = .43$).

5.2.3 EEG Session

Stimuli

Stimuli consisted of 256 colored pictures of the Snodgrass and Vanderwart object drawings (Rossion & Pourtois, 2004) and were divided into two study-test blocks of 128 items each. One half of the pictures in each block were randomly attributed to the study phase and the other half were assigned as new items to the test phase so that old/new status and block assignment was balanced across subjects. The pictures within a block were pseudo-randomly ordered for each participant with the constraint that a maximum of four items with the same old/new status could occur in a row. To familiarize subjects with the task we used a practice session before each block containing additional 40 line-drawing pictures that were taken from the database of the International Picture Naming Project (Bates et al., 2003; Székely et al., 2004) and were colored using Adobe® Photoshop® CS6.

5.2.4 Procedure

Participants were seated comfortably in a sound- and electrically-shielded room with a distance of approximately 80 cm from a 17"- display monitor. All stimuli were presented against a white background subtending a visual angle of approximately $3.6^\circ \times 5.0^\circ$. The procedure was adapted from Mecklinger and colleagues (2011). Participants were instructed to respond to stimuli by pressing the right (m) or left button (c) on a computer keyboard with the corresponding hand. Response assignment was counterbalanced across participants. The task was performed in two study-test cycles and a practice block was performed before each study-test cycle. This contained 10 study and 20 test trials in the non-speeded study-test cycle and twice as many items in the speeded study-test cycle. Different practice lengths were used because elderly participants took more time to adapt to the speeded response deadline. To avoid asymmetric carry-over effects between response conditions, the non-speeded condition was always performed first.

In both study phases, 64 object pictures were presented consecutively and subjects were told to memorize each picture and to decide by button-press whether the object was smaller or bigger than the size of the computer monitor in real life. A study trial consisted of a fixation cross (400 ms), a study picture (2000 ms) and a fixed intertrial interval (1400 ms). Between study and test phase there was a retention interval that lasted approximately five minutes while subjects performed an easy arithmetic task in which they counted backwards for 30 sec in steps of three from a random number between 300 and 900. At test, subjects were instructed to make old/new recognition decisions for each sequentially presented picture. Participants were given a break after half of the trials were performed. A test trial consisted of a fixation cross (500 ms), a test picture (750 ms for younger and 1050 ms for older adults) and a feedback stimulus (smiley or frowning face for 1000 ms) that appeared on screen 200 ms after the response. The intertrial interval was 2000 ms. In the non-speeded condition, subjects were allowed to respond during test picture presentation and were given an additional 5000 ms if they did not respond while the picture remained on screen. A response after picture presentation would terminate the trial. In the speeded condition, subjects were instructed to respond during picture presentation. If the response was given after the presentation of the picture, subjects heard a brief complex sound (main frequency band 100 to 3000 Hz, ~ 58 db, 140 ms) and the trial was discarded from analysis. To account for the generally slower processing speed in the older adult group, different response deadlines were used for younger (YA: 750 ms) and older adults (OA: 1050 ms). These values were estimated from a pilot study that revealed that elderly took approximately 300 ms longer for correct responses in a non-speeded version of an item recognition memory task with pictorial stimuli (see Mecklinger et al., 2011, for the same approach).

EEG recording

EEG was recorded from 27 Ag/AgCl-electrodes embedded in an elastic cap according to the extended international 10-20 system (American Clinical Neurophysiology, 1994). An additional four electrodes were placed above and below the right eye and at the outer canthi of both eyes to record vertical and horizontal electrooculograms (EOGs). Two electrodes were placed bilaterally on the mastoid processes, with on-line reference from the left-mastoid and off-line re-referencing to linked mastoids. Electrode impedance was kept below 5 k Ω . EEG signals were band-pass filtered from DC-100 Hz and digitized at a sampling rate of 500 Hz with a notch filter of 50 Hz. Trials were epoched and baseline corrected off-line with a 200 ms pre-stimulus period and a 1200 ms post-stimulus period. Trials containing eye movement artifacts were corrected using a linear regression approach (Gratton, Coles, & Donchin, 1983) while trials containing other artifacts (whenever standard deviation in a 200 ms time interval exceeded 25 μ V in either Fz or any of EOG channels) were discarded from further analyses. Off-line data processing further involved band-pass filtering from 0.03 to 30 Hz. After elimination of artifact trials, mean averages were computed for correct old and new responses in the two response conditions for each participant at all recording sites. In the non-speeded condition, the mean numbers (and range) of hit trials that entered ERP calculation were 45 (28-53) for young and 41 (20-57) for old adults; mean trial numbers for correct rejections were 47 (24-58) for young and 42 (24-56) for old adults. In the speeded condition, mean trial numbers for hits were 37 (24-46) for young and 40 (21-56) for old adults; mean trial numbers for correct rejections were 38 (22-57) and 40 (24-58) for young and old adults, respectively.

ERP data analysis

ERP analyses were focused on assessing group differences in the ERP correlates of recollection and familiarity in the speeded and/or the non-speeded response condition. We used 15 electrodes over frontal (F3/Fz/F4), fronto-central (FC3/FCz/FC4), central (C3/Cz/C4), centro-parietal (CP3/CPz/CP4) and parietal (P3/Pz/P4) regions for all statistical analyses. Mean amplitude data were taken from early (300 to 500 ms) and late (500 to 700 ms) time windows for both response conditions to quantify the early mid-frontal and the late parietal old/new effect, respectively. Consistent with previous research, statistical analysis of the ERP old/new effects were performed separately for recording sites and time windows, where old/new differences associated with either familiarity or recollection were expected (for a similar approach see Ally et al., 2008; Curran & Doyle, 2011). Regions included in the ANOVA depended on the time window of interest, such that only ERP amplitudes at anterior recording sites (frontal and fronto-

central electrodes) in the early time window were used for the quantification of the early frontal effect and only data from posterior recording sites (centro-parietal and parietal electrodes) in the late time window were used for analysis of the late parietal effect. In each time window an ANOVA with the factors Response Condition (non-speeded, speeded), Item Status (hits, crs), Location (early time window: frontal, fronto-central; late time window: centro-parietal, parietal), Laterality (left, midline, right) and the between-group factor Group (YA, OA) was conducted. Interactions involving the factor Response Condition, Group and Item Status were analyzed separately for each response condition and followed-up in separate group-specific ANOVAs that were broken down by levels of Location and Laterality.

To compare effect sizes across factor-levels partial eta squared (η_p^2) was calculated (Tabachnik & Fidell, 2007, pp. 54-55). Violations of homogeneity of variances in ANOVAs were adjusted using the Greenhouse-Geisser correction (Greenhouse & Geisser, 1959) and in t-statistics using Welch's t-test that allows different population standard deviations (Bortz, 2005, p. 141). If necessary, corrected p -values are reported alongside uncorrected degrees of freedom.

5.3 Results

5.3.1 Neuropsychological test performance

As can be seen from Table 1, the two age groups were matched for all neuropsychological test scores except verbal fluency, verbal recall and visual pair associates. This was tested with one-way analyses of variance (ANOVAs) performed on standardized test scores. Verbal fluency was higher in the older adults ($F(1,54) = 4.38, p < .05$). In contrast, older participants showed lower scores of verbal recall ($F(1,54) = 4.72, p < .05$) and visual pair associates performance ($F(1,54) = 7.91, p < .01$).

Table 1 - Demographic and neuropsychological test results (\pm SD) for the two age groups.

	Younger Adults	Older Adults	<i>p</i> -value
Age	24.2 (2.8)	69.8 (3.8)	
Education	16.6 (2.4)	15.1 (3.4)	.08 +
Verbal Fluency	23.5 (3.8)	25.0 (6.5)	.04 *
Phonemic Fluency	16.0 (3.5)	15.2 (5.2)	.87
Boston Naming	14.9 (0.4)	14.4 (1.0)	.14
Wordlist Memory			
<i>Verbal Recall %</i>	97.4 (9.8)	87.0 (14.3)	.03*
<i>Verbal Recognition %</i>	99.5 (1.5)	99.2 (1.9)	.81
Constructional Recall %	97.7 (8.3)	89.5 (18.9)	.19
Mental Control	5.5 (0.9)	5.4 (0.7)	.17
Logical Memory	34.9 (5.3)	28.3 (6.3)	.86
Visual Pair Associates			
<i>Encoding</i>	16.7 (1.7)	11.9 (3.6)	.01 **
<i>Recall</i>	6.0 (0.2)	5.3 (0.9)	.60
Verbal Pair Associates			
<i>Encoding</i>	22.7 (1.4)	20.1 (2.6)	.09 +
<i>Recall</i>	8.0 (0.0)	7.4 (0.9)	.18
Operation Span	34.1 (4.5)	28.3 (4.1)	1.0
Digit Symbol	42.1 (7.7)	30.0 (5.6)	1.0
Backward Digit Span	7.5 (1.8)	7.1 (2.1)	.16
Trail Making Test (B-A)	1.9 (0.8)	2.3 (0.7)	.12

Note. The standard deviation of the means are given in parentheses.

Oneway ANOVA *s* for test scores were performed with standardized (z -) values according to age and education.

+marginal significant, *significant, ** highly significant.

5.3.2 Behavioral results

Memory performance (Pr = hit rate – false alarm rate), response bias (Br = false alarm rate / (1- Pr)) (Snodgrass & Corwin, 1988) and reaction time (RT) for both groups and response conditions are summarized in Table 2.

Pr values were subjected to an ANOVA with the factors Response Condition and Group. A main effect of Response Condition ($F(1,54) = 40.86, p < .001$) indicated that memory accuracy was higher in the non-speeded than speeded response condition and the interaction of Response Condition by Group ($F(1,54) = 18.36, p < .001$) reflected the fact that younger adults

outperformed older adults in the non-speeded condition ($t(54) = 2.35, p < .05$), whereas group differences in the speeded response condition were marginally significant in the opposite direction ($t(54) = -1.75, p = .09$). The interaction of Response Condition and Group was further broken down by follow-up group-specific analyses. Young participants showed significantly better performance in the non-speeded condition ($t(19) = 6.22, p < .001$), the same pattern was only marginally significant in the older subjects ($t(35) = 1.84, p = .08$).

Table 2 - Mean RTs, proportion of hits and correct rejections, Pr and Br (\pm SEM) for the two age groups in the speeded and non-speeded condition.

	Younger Adults	Older Adults
RT Non-speeded		
<i>HITs</i>	897 (49)	1015 (39)
<i>CRs</i>	888 (57)	991 (37)
RT Speeded		
<i>HITs</i>	594 (6)	782 (10)
<i>CRs</i>	598 (6)	792 (8)
Proportion HITs		
<i>Non-speeded</i>	0.87 (0.02)	0.84 (0.01)
<i>Speeded</i>	0.81 (0.02)	0.84 (0.01)
Proportion CRs		
<i>Non-speeded</i>	0.91 (0.03)	0.87 (0.01)
<i>Speeded</i>	0.79 (0.01)	0.83 (0.01)
Performance Estimate (Pr-Score)		
<i>Non-speeded</i>	0.78 (0.04)	0.71 (0.02)
<i>Speeded</i>	0.60 (0.03)	0.67 (0.02)
Bias Estimate (Br-Score)		
<i>Non-speeded</i>	0.44 (0.04)	0.46 (0.03)
<i>Speeded</i>	0.51 (0.04)	0.52 (0.03)

Note. Reaction times are displayed in ms and standard errors of the means (SEM) are given in parentheses.

A Response Condition \times Group ANOVA was performed on mean reaction times to correct responses (RTs) and revealed main effects of Group ($F(1,54) = 19.47, p < .001$) and Response Condition ($F(1,54) = 73.47, p < .001$) that indicated that younger adults responded

faster than older adults and that both groups took more time to respond in the non-speeded compared to the speeded response condition as expected.

To determine whether response bias differed between groups and/or conditions, Br was subjected to a Response Condition \times Group ANOVA. There was only a marginally significant main effect of Response Condition ($F(1,54) = 3.76, p = .058$) that indicated that participants in both groups tended to adapt a more conservative bias in the non-speeded than in the speeded response condition (see Table 2).

Consistent with our hypothesis, younger subjects performed better than older subjects in the non-speeded response condition. Performance differences were much smaller in the speeded response condition in which elderly adults tended to perform better than young adults. In addition, condition-specific analyses revealed that young participants performed better in the non-speeded than in the speeded response condition, whereas this difference was only marginally significant for elderly participants.

It is conceivable that the use of different response deadlines in the speeded condition for the two groups may have resulted in a greater relative time pressure for the young participants. If this is the case, then this group should have made significantly more timeouts than older adults. A Chi-Square analysis for the mean number of time-out responses (YA: $M = 14.80, range = 2-33$; OA: $M = 11.72, range = 2-31$) revealed no group differences for the number of timeouts ($\chi^2(19) = 21.88, p = .29$). Additionally if older adults benefited from the extra response time in the speeded condition they should have made disproportionately more correct responses at the upper end of their response time distribution (i.e. later in the time window in which they were allowed to respond). Hence, older adults should show worse performance when slow responses are excluded from analysis. In order to determine how to eliminate such “slow responses” in the elderly, we calculated the between-group response time differences in the non-speeded condition, because this should reflect general slowing differences between the two groups when there was no time pressure. By adding this between-group RT difference to the response deadline given to young adults ($750 \text{ ms} + 111 \text{ ms} = 861 \text{ ms}$) we derived an approximate time-point beyond which responses could be deemed ‘slow’ or to have benefited from the different response deadlines. All correct responses beyond this point were thus removed and new Pr-scores in the elderly group were calculated. The subsequently corrected Pr-Scores for the speeded condition of the older adults was 0.70 which is greater than the initial Pr-value (0.67). Removing slow responses should have either reduced or not impacted Pr if older adults had benefited from extra time. The artificial deadline reduction thus led to the exclusion of mainly incorrect responses at the upper

end of the response window, suggesting that older adults gave the majority of correct decisions towards the beginning of the response window.

Together with the initial data of the young group and the non-speeded data of the older adults, the corrected speeded-Pr-score was submitted to a Response Condition \times Group ANOVA, for which the main effects and interaction remained significant. Concordant with the initial pattern, the main effect of Response Condition ($F(1,54) = 27.19, p < .001$) indicated better performance across groups in the non-speeded response condition. The interaction of Response Condition by Group ($F(1,54) = 21.19, p < .001$) was followed-up by condition- and group-specific analyses. Contrasting group performance within the speeded response condition revealed better performance for older over young adults ($t(54) = -2.26, p < .05$) and contrasting response conditions within the older group revealed no significant result ($t(35) = 0.51, p = .62$). These data, together with the observation that the mean number of timeout responses did not differ across age groups, suggest that the older adults' comparable performance across the two conditions was not the result of relatively greater exposure and response time in the speeded condition.

5.3.3 ERP results

The grand mean ERP waveforms of the mean amplitude measures are illustrated in Figure 9 separately for each group and response condition.

In the non-speeded response condition, both groups show a frontally distributed old/new effect in the early time window which is slightly right lateralized for old adults. In the late time window young adults display a positivity that is larger for old than new pictures and distributed over central and parietal electrodes. Conversely, old/new effects in the late time window in older participants were virtually absent at posterior recordings. In the speeded response condition in the early time window, young and old adults again show an early frontal old/new effect and for old adults an additional posteriorly distributed negativity to old items emerges. In the late time window, old/new differences are present in the younger adult group, though they are smaller than in the non-speeded condition. For older adults the posterior negativity is again present. To examine these observations, global ANOVAs comprised comparisons between ERPs of each Item Status in each time window and the outcomes of these ANOVAs are reported below.

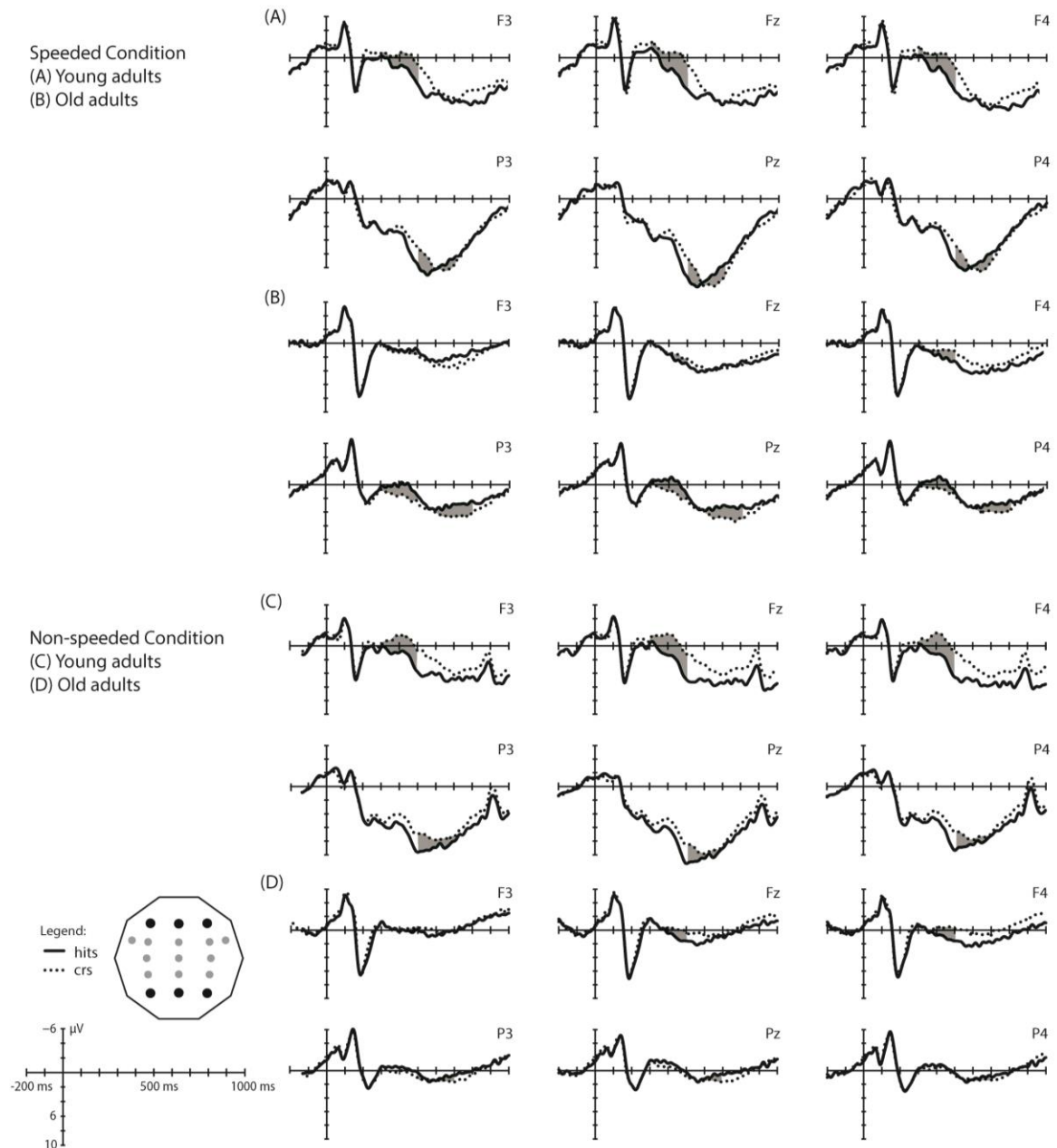


Figure 9 - ERP waveforms associated with hits and correct rejections for young (A) and old adults (B) in the speeded condition (upper panel) and for young (C) and old adults (D) in the non-speeded condition (lower panel). Data are depicted at frontal and parietal electrodes. Gray shading denotes old/new differences in the investigated time windows (adopted from Scheuplein, Bridger, & Mecklinger, 2014).

Early frontal ERP effects (300 - 500 ms)

To investigate the early frontal effect, an ANOVA with the factors Response Condition (non-speeded, speeded), Item Status (hits, crs), Location (frontal, fronto-central), Laterality (left, midline, right) and the between-group factor Group (YA, OA) was performed for the mean ERP

amplitude in the early time window over anterior scalp sites. There was a main effect of Item Status ($F(1,54) = 48.77, p < .001$) and a marginally significant interaction between Response Condition and Item Status ($F(1,54) = 3.85, p = .06$) that was followed-up by condition-specific analyses reflecting greater Item Status effects in the non-speeded ($\eta_p^2 = .41$) than in the speeded ($\eta_p^2 = .31$) response condition. The global ANOVA also revealed an Item Status by Group interaction ($F(1,54) = 27.44, p < .001$) and a marginally significant Item Status, Laterality and Group interaction ($F(2,108) = 3.23, p = .06$). These interactions suggest that Item Status effects differ as a function of Response Condition, Group and Laterality. To explore how the early frontal effect differs between the two age groups, the three-way interaction was broken down for each level of Response Condition and Laterality and two-way ANOVAs with factors Item Status and Group were conducted for each response condition at each level of the laterality factor. In the non-speeded condition significant Item Status by Group interactions were observed at all levels of the Laterality factor across left, midline and right lateral sites (all p -values $< .01$). At the left anterior recording sites the Item Status effect was significant for young adults ($p < .001$) but not for old adults ($p = .48$). At the midline and right anterior recording sites the Item Status effects were significant in both age groups (p -values $< .01$) with larger effect sizes for young (midline: $\eta_p^2 = .50$; right: $\eta_p^2 = .57$) than old adults (midline: $\eta_p^2 = .21$; right: $\eta_p^2 = .28$).

Similarly, in the speeded response condition interactions of Item Status and Group were evident at all levels of Laterality (all p -values $< .01$). At left anterior sites the Item Status effect was significant for young adults ($p < .001$) and marginally significant for old adults ($p = .054$). At midline recording sites the Item Status effects were significant for young adults ($p < .001$) but not for old adults ($p = .94$), whereas at right anterior sites the Item Status effect was significant in both groups (p -values $< .05$) with larger effect sizes for young ($\eta_p^2 = .50$) than for old adults ($\eta_p^2 = .15$).

To explore whether Item Status effects in the elderly group were overestimated due to their greater group size, we randomly selected twenty elderly among the older participants (non-speeded: YA: $M = 0.78, SD = 0.11$; OA: $M = 0.71, SD = 0.11$; $t(38) = 2.10, p < .05$; speeded: YA: $M = 0.60, SD = 0.17$; OA: $M = 0.68, SD = 0.10$; $t(38) = -1.84, p = .08$). For the older adults we then conducted three-way (Item Status \times Location \times Laterality) ANOVAs separately for each condition. The resulting pattern did not change (Item Status effect at right anterior sites: non-speeded, $p < .01$ and speeded, $p < .001$), indicating that the early frontal effect is not overestimated in elderly despite their greater group size.

To summarize, in the early time window, we found a reliable frontal old/new effect in both groups, assumed to reflect the ERP correlate of familiarity. This effect was smaller in

amplitude and right-lateralized for older adults, but most importantly was elicited by both groups in both response deadline conditions.

Late parietal ERP effects (500 - 700 ms)

In the late time window the overall global ANOVA with factors of Response Condition, Item Status, Location, Laterality and Group, conducted on ERPs from posterior recording sites, revealed interactions between Item Status and Group ($F(1,54) = 6.79, p < .05$), Response Condition and Item Status ($F(1,54) = 4.04, p = .05$), and Response Condition, Item Status, Location, Laterality and Group ($F(2,108) = 4.82, p < .05$). Follow-up analyses were performed separately for both response conditions and age groups. For young adults there was an effect of Item Status in the non-speeded response condition ($F(1,19) = 8.49, p < .01$) but this was not significant in the speeded response condition ($p = .46$). We explored the possibility that polarity changes in the old minus new differences in the late portion of the 500 to 700 ms time windows may have cancelled out this effect for the young group in the speeded condition. Separate analyses of the Item Status effects in time windows from 500 to 600 ms and 600 to 700 ms revealed a significant Item Status effect in the former ($F(1,19) = 5.68, p < .05$) but not in the latter of these two time windows ($p = .17$). Item Status effects for young adults in the speeded condition were not only less temporally extended than in the non-speeded condition but also smaller in magnitude (speeded 500-600 ms: $\eta_p^2 = .23$, non-speeded 500-700 ms: $\eta_p^2 = .31$). Group-specific analysis for old adults revealed no effect of Item Status in the non-speeded response condition ($p = .57$). Notably, for older adults in the speeded response condition, the polarity of the Item Status effect reversed with hit responses showing more negative-going waveforms than correct rejections ($F(1,35) = 3.43, p = .07$). This negativity was significant at parietal ($F(1,35) = 4.98, p < .05, \eta_p^2 = .13$) but not at centro-parietal electrodes ($p = .17$).

Summing up the results of the late time window, the late parietal old/new effect, the ERP correlate of recollection, was evident for young adults in both response conditions. Consistent with the assumption that recollection is attenuated in the speeded response condition it was smaller and restricted to a shorter time window in this condition. For older adults, the ERP correlate of recollection was absent in the non-speeded response condition, whereas in the speeded condition the waveforms were more negative for hits than for correct rejections at parietal recording sites.

5.4 Post hoc analysis

5.4.1 Late parietal and early frontal ERP effects with performance matched age groups in the non-speeded condition

The late parietal old/new effect was not observable in the non-speeded condition for the older adults. Given previous reports in which the magnitude of the parietal old/new effect covaried with the amount of information recollected (Vilberg & Rugg, 2009) it is conceivable that older adults recollected less information and that this is reflected in the attenuated effect for this group. To test this assumption we matched the two age groups in performance in the non-speeded condition by selecting data from the largest number of elderly participants ($n = 28$) for which it was possible to statistically equate performance in the non-speeded condition (OA mean performance: $M = 0.75$, $SD = 0.07$; YA: $M = 0.78$, $SD = 0.11$; $t(46) = 1.04$, $p = .30$; see Wang et al., 2012, for a similar approach). An Item Status \times Location \times Laterality \times Group ANOVA for the mean waveforms in the 500 to 700 ms time interval in the non-speeded condition revealed a significant main effect of Item Status ($F(1,46) = 4.56$, $p < .05$) and an interaction of Item Status and Group ($F(1,46) = 4.71$, $p < .05$). A group-specific break-down of the interaction revealed an Item Status effect in young ($F(1,20) = 8.49$, $p < .01$) but not in older adults ($p = .98$).

To see whether performance differences in the non-speeded condition contributed to the smaller early old/new effect shown for old adults, we conducted the same analysis at frontal electrodes in the early time window. The data from the non-speeded condition, for the same selection of older adults ($n = 28$) for whom performance in the non-speeded condition was equated to performance of the young adults, were entered into an Item Status \times Location \times Laterality \times Group ANOVA. There was a significant main effect of Item Status ($F(1,46) = 31.28$, $p < .001$), an interaction of Item Status and Group ($F(1,46) = 11.28$, $p < .01$) and an interaction of Item Status by Laterality ($F(2,92) = 12.95$, $p < .001$). Group-specific analysis for each level of laterality revealed significant Item Status effects in young adults at all levels of laterality (left: $\eta_p^2 = .51$, midline: $\eta_p^2 = .50$ and right: $\eta_p^2 = .57$). In contrast, in old adults Item Status effects were significant at midline ($\eta_p^2 = .22$) and right ($\eta_p^2 = .28$) (each p -value $< .05$), but not at left frontal recording sites ($p = .68$). This pattern resembles that repeated for the entirely elderly sample, suggesting that the smaller early frontal old/new effect in old adults is not modulated by their poorer performance.

5.4.2 Analysis of the posterior negativity

As is apparent in Figure 9, an additional ERP effect was also evident for older adults over electrode regions that did not enter the global ANOVAs reported above. First, in the early time window (300-500 ms) in the speeded response condition there was more negative-going activity for hits than for correct rejections at posterior recordings. This negativity was left-lateralized and continued for several hundred milliseconds and was thus also observable in a later time period where it might have overshadowed the late parietal old/new effect. Negative-going effects of this kind were not observed for old adults in the non-speeded condition.

To further explore this unexpected posterior negativity for older adults, 4-way ANOVAs with factors of Response Condition, Item Status, Location and Laterality were conducted on ERPs from posterior recording sites. Given the extended nature of the effect ANOVAs were conducted over two time windows (300-500 and 600-800 ms) where the effect was most pronounced. For the earlier time window there was a main effect of Item Status ($F(1,35) = 20.64$, $p < .001$) and interactions between Response Condition and Item Status ($F(1,35) = 7.82$, $p < .01$) and between Item Status, Location and Laterality ($F(2,70) = 4.53$, $p < .05$). Separate analyses for each response condition revealed a main effect of Item Status for the speeded condition ($F(1,35) = 42.15$, $p < .001$) but not for the non-speeded condition ($p = .23$). In the speeded condition, the effect was significant at all combinations of Laterality and Location factors (all p -values $< .01$), and was smallest at CP4 ($\eta_p^2 = .29$) and largest at P3 ($\eta_p^2 = .60$). For the 600-800 ms time window a similar picture emerged. There was a main effect of Item Status ($F(1,35) = 7.62$, $p < .01$), a marginally significant interaction between the factors Response Condition and Item Status ($F(1,35) = 3.88$, $p = .06$) and a significant interaction between Response Condition, Item Status, Location and Laterality ($F(2,70) = 3.63$, $p < .05$). Follow up analyses revealed significant effects of Item Status for the speeded ($F(1,35) = 12.27$, $p < .01$), but not for the non-speeded condition ($p = .14$). Again, the effect in the speeded condition was significant at almost all combinations of the Laterality and Location factors except at CP4 ($p = .37$, all other p -values $< .05$) and was largest at P3 ($\eta_p^2 = .30$) and Pz ($\eta_p^2 = .31$). The left-lateralized distribution of the posterior negativity in the speeded condition was thus highly similar in both time windows, suggesting that it reflects a functionally homogeneous and temporally extended process.

5.5 Discussion

The present study investigated age differences in the ERP correlates of episodic recognition processes. We used perceptually rich pictorial stimuli and an item recognition

memory task with a response deadline procedure that imposed low demands on effortful, self-initiated retrieval processes to explore whether age differences in recognition memory performance are smaller when recognition decisions have to be given quickly and the contribution of recollection to these decisions is assumed to be minimal. We also sought to determine whether, under the current conditions which were designed to specifically enhance familiarity-based responding, the putative ERP correlate of familiarity, would be detectable in elderly participants.

5.5.1 Behavioral results

In the non-speeded response condition where time to respond was not restricted, it was assumed that recognition decisions could be based on both familiarity and recollection. Younger participants performed better than older participants in this condition. This is presumably because elderly participants could use recollection to a lesser extent than young adults, basing their responses primarily on familiarity, whereas younger participants are able to use both processes. This interpretation meshes with the assumption that impaired recollection is one of the main mediators of age-related episodic memory impairments.

In contrast, participants were forced to respond quickly in the speeded response condition and had to rely primarily on fast-acting familiarity. There is increasing evidence that familiarity is largely unaffected by aging (Bastin et al., 2013; Yonelinas, 2002) and that older adults' episodic memory impairment is attenuated under conditions that reduce the need for recollection processes because intact familiarity can still support memory for individual items (Bastin et al., 2013; Cohn, Emrich, & Moscovitch, 2008; Naveh-Benjamin et al., 2009). Thus, it was expected that age-related performance differences would be smaller or even diminish in the speeded response condition. In line with this, age-related differences in memory performance were much smaller in the speeded response condition and old adults, in contrast to younger adults, did not show a performance decrement from non-speeded to speeded responding. By this, our behavioral findings confirm those of other researchers, who also report age differences in memory performance to be diminished with short deadlines that allow familiarity (as reflected in elevated false alarm rates to rearranged word pairs or plurality reversed words) to dominate (Light et al., 2004, 2006, see section 1.3.2).

The finding that age effects on memory performance were much smaller in the speeded than in the non-speeded condition should be interpreted with caution, however, because of the use of age-specific response deadlines which allow for the possibility that old adults benefited

from extra response time in the speeded condition. However, the older adults' recognition performance remained on a level comparable to the non-speeded condition even when their slowest responses were eliminated to adjust for aging-related processing differences. It is unlikely therefore that the absence of performance differences in the speeded condition is due to the extended response deadline allowing more recollective processing for the older adults (as does the absence of significant late old/new effects for the elderly in the speeded condition). The post-hoc exclusion of slow responses revealed that performance of elderly participants actually decreased, when responses were made towards the end of the response deadline. A positive relationship between speed of responding and accuracy of this kind may be consistent with the notion that this group predominantly uses fast familiarity-based processing, for which additional post-retrieval processing may not necessarily be beneficial. Broadly in line with this is data from Angel et al. (2013), who tested participants with a R-K paradigm on pictures that were either presented once (hard) or twice (easy) during encoding. Accuracy of the familiarity index did not differ between the two age groups for either difficulty condition, but of most interest was the observation that older adults were actually faster than young participants in producing these correct 'know' responses in the hard condition. These latter results confirm the view that older compared to younger adults rely primarily on fast-acting familiarity. The differential age effects in the two response conditions of the present study are thus likely to have stemmed from age-related differences in the underlying memory processes. From this perspective the age-related decline in the non-speeded condition is derived from the decreased availability of recollection for the elderly whilst performance in the speeded condition would be less affected by aging because these same participants could rely on intact familiarity. Another related possibility is that the time pressure induced elderly participants to invest additional effort in the speeded condition. This group is likely to be particularly motivated to perform well, especially in the more challenging speeded condition given that they were aware that the study was concerned with memory in old age. The analysis of the ERP old/new effects in the early time window of the current study provides some support for the former of these interpretations.

5.5.2 Early mid-frontal old/new effect

The early mid-frontal old/new effect, the putative ERP correlate of familiarity, was present in both, young and older participants, in the speeded and the non-speeded response condition. This finding adds to those reports in which it was possible to detect an ERP correlate of familiarity in older adults when perceptually rich stimuli were used (Ally et al., 2008; Eppinger et

al., 2010; Morcom & Rugg, 2004) which are inherently more memorable and more distinctive than verbal stimuli (Gallo, Weiss, & Schacter, 2004; Paivio & Csapo, 1973).

Although it is important to note the observation of a significant early old/new effect for the elderly group (in contrast to the finding for the late parietal effect), the early effect differed from that of the young participants in two important ways. Firstly, the early old/new effect was right-lateralized in the older adults. A more right-lateralized topography for the ERP correlate of familiarity in older adults is consistent with previous reports (Ally et al., 2008; Morcom & Rugg, 2004; Wegesin et al., 2002). The second important difference between groups was that the early frontal old/new effect was smaller in amplitude for old adults in both response conditions. On the one hand, these findings suggest that familiarity is preserved in older subjects under conditions that support familiarity-based responding. On the other hand, the observation that the effect is attenuated in old age and limited to electrodes over the right side of the scalp, even when stimuli and response requirements that engender high levels of memory strength are employed, suggests that the neural generators of the early frontal old/new effect change with age and that familiarity-related processing may not comprise entirely the same operations across these age groups. It further suggests that its neural generators are degraded in old adults, though to a lesser extent than the generators of the parietal old/new effect, which was virtually absent in the elderly.

Whereas the direct index of familiarity used in this study, the amplitude of the early frontal old/new effect, was diminished for the elderly group compared to young adults, there were no behavioral age differences in the condition assumed to depend predominantly on familiarity-based processing. This extends observations derived from other aging studies using a response deadline procedure (Light et al., 2004), because it indicates that age-related reductions in familiarity can come about, and that these are not necessarily the result of impaired memory performance or memory strength of old adults (see section 8.3 for a detailed discussion). Despite this disconnect, the behavioral data in the speeded response condition nonetheless indicate that familiarity-based processing is an important contributor to the disproportionately good memory performance of the elderly in the fast response condition.

5.5.3 Late parietal old/new effect

Consistent with an increasing number of ERP studies reporting that aging is associated with recollective impairments, much larger age-related differences were found for the parietal old/new effect, the putative ERP correlate of recollection. For young adults the effect was

present in the non-speeded condition and, albeit smaller in amplitude and restricted to a smaller and earlier time window, also in the speeded condition. The latter result suggests that the deadline manipulation in young adults did not eliminate the use of recollection completely although it did substantially attenuate its contribution to recognition decisions in this condition.

The results of an additional subgroup analysis indicated that the between-group differences in the parietal old/new effect do not result from behavioral differences in memory performance. When the group of elderly participants was equated for memory performance with the younger group, the effect was still absent for older adults. These results thus add to the increasing amount of evidence that recollection-based processes are reduced in old age (Friedman, 2013; Wang et al., 2012). In addition, the finding that age differences in memory performance and the ERP correlate of recollection were most pronounced in the non-speeded condition is consistent with models of cognitive aging that assume that effortful memory operations that entail self-initiated strategies to search through memory or to generate retrieval cues are more vulnerable to aging than more automatic processes (Craik, 1994; Morcom & Rugg, 2004; Yonelinas, 2002).

Observing an early frontal old/new effect but failing to detect a late parietal old/new effect in older adults with the current stimuli may also be taken to be consistent with the view that familiarity is more dependent on perceptual processes than recollection (Yonelinas, 2002). These results diverge to some extent from the findings of Ally et al. (2008), however, who also used perceptually rich stimuli but reported age invariance in the ERP correlates of both familiarity and recollection. It is conceivable that the use of both words and pictures in that study and the potential for perceptual mismatch between study and test cues, encouraged more conceptually-driven processing, in turn causing elderly participants to be less reliant on familiarity-supporting perceptual representations than would be the case for participants in the present study.

5.5.4 Posterior negativity

In the speeded response condition pronounced age-related differences emerged at posterior recording sites. In older adults at these sites a sustained left-lateralized negative-going deflection was elicited by hit responses that started around 300 ms and extended for several hundred milliseconds.

Similar negative-going slow waves have been reported in other ERP aging studies. Duarte et al. (2006) observed a broadly distributed but right-frontally accentuated negative slow wave for remember responses selectively for a low performing subgroup of participants. In a similar vein,

Friedman et al. (2010) also observed a left-frontal negative slow wave for low performing elderly and speculate that this effect reflects the attempt to compensate for a decline in recollective processing in this group. To explore whether the posterior negative slow wave was modulated by memory performance in a similar way in the current study, we divided the sample of old adults according to their performance scores in the speeded condition into high- (mean Pr = 0.75) and low performing (mean Pr = 0.60) subgroups of old adults by median split (Median = 0.68). We compared the mean negativity in the 300-500 ms and the 600-800 ms time window at parietal electrodes in the two subgroups of old adults. An ANOVA with the factors Item Status (hits, crs), Laterality (left, midline, right) and Subgroup (high, low performer) was performed for parietal electrodes only (P3, Pz, P4) where the negativity in the early (300-500ms) and late (600-800ms) time window was largest. As the posterior negativity has a highly similar left-lateralized distribution across time windows, we conducted the analyses on the mean amplitude measures averaged across both time windows. The analyses revealed a main effect of Item Status ($F(1,34) = 35.69, p < .001$) and a marginally significant interaction of Item Status by Subgroup ($F(1,34) = 3.68, p = .06$). Subgroup-specific analyses, collapsed across the Laterality factor, showed a greater Item Status effect for low ($F(1,17) = 25.05, p < .001, \eta_p^2 = .60$) than high performing old adults ($F(1,17) = 10.87, p < .01, \eta_p^2 = .39$).

As illustrated in Figure 10, high performing older participants showed a smaller posterior negativity to hits relative to correct rejections than low performing older participants, collapsed across all levels of laterality. As was the case in Friedman et al. (2010), the current negativity was larger for poorer performing old adults.

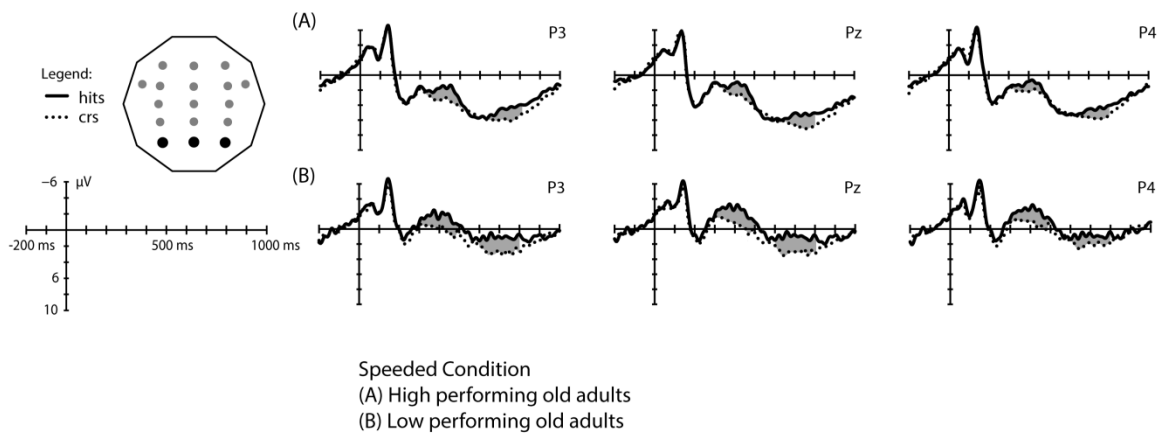


Figure 10 - ERP waveforms associated with hits and correct rejections in the speeded condition for high performing (A) and low performing (B) old adults. As in Figure 9, gray shading denotes differences between hits and correct rejections in the investigated time windows.

In addition we conducted ascendant regression analyses to explore whether, besides memory performance, other variables like age, MMSE and years of education additionally accounted for variance of the posterior slow wave. We identified and excluded one participant from this analysis whose memory performance was more than three standard deviations from the mean of the older adults (Aggarwal, 2013, pp. 6-12). The results of the regression analyses with the remaining 35 older adults show that only memory performance contributed to the variance in the posterior slow wave in the early time interval at the midline (Pz: $R^2 = .13$; $F(1,34) = 5.05$, $p < .05$) and right parietal (P4: $R^2 = .16$; $F(1,34) = 6.29$, $p < .05$) electrodes. There was no reliable relationship between the other variables and the posterior slow wave at these two recording sites (all p -values $\geq .15$). No effects were obtained in the regression analysis for the slow wave at the left posterior recording site in the early time window (P3: $R^2 = .08$; $F(1,34) = 2.68$, $p = .11$) or at any recording site in the late time interval (all p -values $\geq .22$).

On the basis of this relationship between memory performance and the posterior negativity, it is worth speculating whether the current negativity reflects attempts to recruit alternative retrieval strategies to cope with the high task demands or to invest additional effort in the more challenging speeded condition (see section 8.5 for a detailed discussion).

5.5.5 Conclusions

Taken together, the present results correspond well with the assumption that recollection is more affected by aging than familiarity. Performance differences between both age groups were pronounced in the non-speeded condition in which recollection can contribute to memory performance. When response time was limited and memory performance relied to a larger extent on familiarity, performance differences between groups were negligible, in line with preserved familiarity supporting memory performance of the elderly in this condition. The data show that under conditions designed to foster familiarity-based responding, elderly participants show equal performance to young adults, in line with a greater reliance on familiarity in old age. By showing ERP correlates of familiarity in both age groups in both conditions and the selective absence of the ERP correlate of recollection in the non-speeded condition in older adults, the ERP results complement the aforementioned pattern of behavioral results. At the same time, however, the results indicate a reduction in the amplitude of the early frontal old/new effect even when experimental parameters (including highly distinctive picture stimuli and a response deadline) induce comparable performance between elderly and young participants. An additional posterior negativity in the elderly, which varied across participants, may reflect the tendency of elderly participants to base their memory decisions more on visual perceptual rather than abstract

information or to engage in more effortful processing in the more demanding speeded response condition. The results suggest that the effects of aging on memory are not uniform. They show that testing conditions and stimulus characteristics play an important role when studying the effects of aging on episodic memory. Understanding the conditions under which age-related memory impairments can be reduced or even eliminated remains an important endeavor for further studies.

VI EXPERIMENT 2

6.1 Introduction

As discussed in section 1.2.2, older adults are particularly impaired in memory for associations, while memory for single item information remains relatively intact (Chalfonte & Johnson, 1996; Duarte, Henson, & Graham, 2008; Naveh-Benjamin et al., 2003). This associative memory deficit has been related to deficiencies in strategic processes and binding mechanisms that allow the integration of separate information into a coherent memory representation (Cohn et al., 2008; Shing et al., 2010). It has been proposed that these deficiencies reflect neural changes in the HC and the PFC (Shing et al., 2010).

While both recollection and familiarity can support recognition of item information, recognition of associated information depends primarily on recollection (Yonelinas et al., 2010). However, when the components of an association are unitized, i.e. processed as a single coherent representation, familiarity can also contribute to associative recognition (Bader et al., 2010, 2014; Quamme et al., 2007; Rhodes & Donaldson, 2007, 2008; Tibon et al., 2014). Several lines of evidence support the view that unitization facilitates familiarity-based associative memory (see section 2.1.1 for a detailed description). However, most studies that examined the process of unitization have used verbal stimuli, such as word pairs (Ahmad, Fernandes, & Hockley, 2014; Bader et al., 2010; Greve et al., 2007; Kriukova et al., 2013; Pilgrim, Murray, & Donaldson, 2012; Quamme et al., 2007; Rhodes & Donaldson, 2007, 2008; Wiegand, Bader, & Mecklinger, 2010; Zheng, et al. 2015) or word-source (i.e., color) associations (Bastin et al., 2013; Diana et al., 2011; Staresina & Davachi, 2006), whereas unitization of visual stimuli, that are ecologically more valid than words, is less well investigated. In a recent investigation that used pictorial stimuli (Tibon et al., 2014), we manipulated unitizability by presenting two objects in their canonical spatial configuration being either semantically related (e.g., *a lamp over a table*) or unrelated (e.g., *a key-ring over an apple*) and investigated the effects of unitization in young adults. Early ERP differences between intact and recombined stimuli (presumably reflecting unit familiarity) emerged at fronto-polar recording sites for related pairs only. Early ERP differences between recombined and new stimuli (presumed to reflect item familiarity) were more centrally located, and emerged for both related and unrelated pairs. The ERP correlate of recollection also appeared in both conditions. These findings are in line with the view that associative episodic recognition of semantically related visual stimuli can be supported by familiarity and suggest that familiarity can also support memory for associations in the pictorial domain.

It has been shown that unitization facilitates familiarity-based associative memory and by this reduces the age-related associative memory deficit (see section 3.4). For instance, Zheng et al. (2015a) observed similar memory performance for compound word pairs, that provide schematic support due to being pre-experimentally related, compared to arbitrary word pairs and additionally reported the early frontal old/new effect to be comparable in both age groups for unitized pairings only. Further, Bastin et al. (2013) observed the associative deficit to be alleviated in old adults, when a strategy is provided that facilitates unitization of item-color associations (by promoting intra-item versus inter-item associations, e.g. “imagine the elephant being red” versus “imagine the elephant to be associated with a red stop sign”, respectively, see section 2.1.1). Thus, schematic and strategic support, that promote unitization can encourage the contribution of familiarity to associative recognition at test, and by doing so, effectively alleviate the age-related associative memory deficit.

Similarly to the study of Tibon et al. (2014), we used pairs of pictorial stimuli presented above and below fixation. Expanding upon the findings of that study, we wished to determine whether spatial configuration plausibility could engender unitization even of semantically unrelated object pictures, and in turn benefit older adults’ associative memory. Thus, rather than manipulating their semantic relations, we manipulated the plausibility of their spatial relations. That is, two semantically unrelated objects were positioned relative to each other in either spatially plausible or implausible locations, e.g. an axe oriented towards or away from a hamburger (see Figure 11). Prior studies have shown that objects, either related or unrelated, positioned for a potential interaction, can be perceptually grouped and processed configurally (Riddoch et al., 2006, 2011; Roberts & Humphreys, 2011). Thus, this location-related associative information might facilitate the generation of a unified contextual representation of the scene. To ensure that the two conditions differed solely in the plausibility of their arrangement, the same object pairs accompanied by the same encoding instructions were used in both conditions. ERPs were recorded during the memory recognition test to derive correlates of familiarity and recollection.

Our main hypothesis was that plausibly and implausibly situated object pairs would differentially modulate the contribution of familiarity and recollection to associative recognition memory. Specifically, since arbitrary object pairs lack a pre-existing relationship, we expected that plausible location-based information in the absence of a semantic relationship between these objects would encourage unitization and by this lead to the creation of novel conceptual units. Thus, in the plausible condition we expected unit familiarity to support associative recognition (along with recollection), whilst in the implausible condition, recollection was expected to be the main contributor to associative memory. We further assumed that spatially plausible pairings

would facilitate unitization at encoding and promote familiarity at retrieval, leading to a reduction of the age-related associative memory deficit relative to the spatially implausible pairings.

On the basis of prior studies that observed an early parietal old/new effect to be elicited specifically by novel conceptual units that were formed of arbitrary items during encoding (Bader et al., 2010; Wiegand et al., 2010), we expected item familiarity to be represented in an early anteriorly distributed old/new effect and unit familiarity to be represented by ERP differences between old and new picture pairs that are posteriorly distributed. Consistent with previous findings and results of Experiment 1 showing that the ERP correlate of familiarity can be reliably recorded in old adults whereas the ERP correlate of recollection is virtually absent in this age group, we expected the early old/new effect to be present in the item and unit familiarity contrast in both age groups. If familiarity is sufficiently diagnostic to guide recognition judgments for unitizable pairings, the late parietal old/new effect should be reduced in the condition with spatially plausible relative to implausible pairings (Bader et al., 2010; Kriukova et al., 2013). For old adults we did not expect to observe an ERP correlate of recollection in either condition.

6.2 Stimulus material and pre-experimental rating

The current experiment required a sufficient number of semantically unrelated pictures that could be arranged in either a plausible or an implausible spatial configuration and recombined with another pairing in such a manner that intact and recombined stimuli did not differ in their relatedness and associative strength (see Figure 11 for examples of such stimulus quadruplets and appendix B for all stimuli). Stimuli consisted of pictures of objects including vegetables, fruits, various foods, beverages, animals, insects, clothing, tools, furniture and appliances, and were collected from the Hemera Photo-Objects Collection (Hemera Photo Objects, Gatineau, Quebec, Canada) as well as diverse free internet sources, before being edited with Adobe® Photoshop® CS6. 278 stimulus quadruplets were created and were rated for semantic relatedness (“How meaningful are the two objects related with each other, disregarding their spatial plausibility? I.e., *dog-cat* are both animals; *table-chair* are kinds of furniture.”) and spatial plausibility (“How plausible is the arrangement of two objects, disregarding their semantic relatedness? I.e., a kangaroo on top of a bicycle is plausible because it is suggestive of a performed action.”) on a scale from 0 (“very low”) to 5 (“very high”) (see appendix A for the rating questionnaire). Pairings were also screened for nameability of the single components by asking respondents to “Please mark all individual objects that you cannot identify.” We built four versions of the rating questionnaire. Each version was built upon half of the stimulus material and included two pairings (old and recombined) of one quadruplet (either plausible or

implausible) and thus contained 278 pictures pairings in total, with half of the questionnaire pictures belonging to the plausible or implausible category. This pilot rating was performed by 42 participants, psychology students at Saarland University or adults from the local community (*mean age* = 25.0, *range* = 19 – 60). We removed all pairs for which one component was not identifiable by five or more of the raters (21 rater per picture pairing), and those pairs for which the majority of participants did not confirm the attribution of spatial plausibility and/or lack of relatedness (e.g. that received a mean score of < 3 on the plausibility scale and/or > 3 on the relatedness scale), leaving 154 quadruplets. Since this number was insufficient, we conducted with the same procedure a second rating questionnaire containing 148 quadruplets (built from different pictures of the same sources) rated by additional 22 participants, leaving 110 quadruplets. Thus, in total 264 quadruplets were employed in the associative memory test. All confirmed objects were then fully counterbalanced across experimental conditions (plausible/implausible and old/recombined/new), with each stimulus pair of one quadruplet associated with one plausible and one implausible pair and with one intact and one recombined test response condition. Each participant saw the two corresponding stimuli of each quadruplet in only one of these conditions. Those items that were not seen during study served as new items.

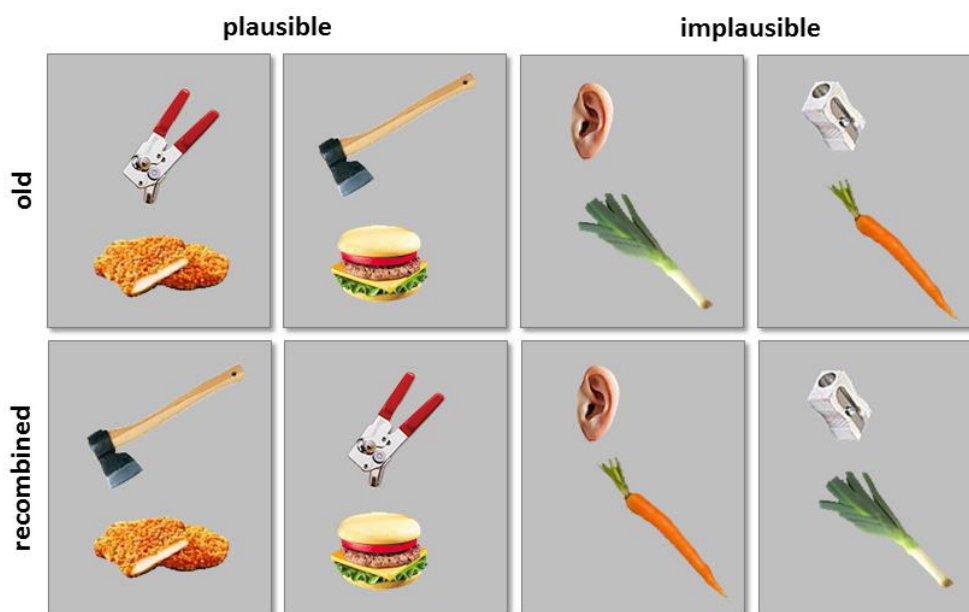


Figure 11 - *Examples of plausible or implausible stimulus configurations depicted as old pairings or as a recombined pair.*

6.3 Method

6.3.1 Participants

Sixty-five adults (25 young and 40 older adults) participated in this study. All were recruited at Saarland University or in the local community. Four younger and ten older participants had to be excluded because of a high amount of eye and body movement artifacts (> 32% rejected trial; $n = 3$), technical problems during EEG recording ($n = 2$), use of ataractics ($n = 2$) or due to high misclassifications at study that suggest a lack of understanding the task ($n = 7$). The final sample that entered behavioral analysis included 21 younger adults (YA *mean age* = 23.7 *SD* = 3.1; 8 females) and 30 older adults (OA *mean age* = 71.7, *SD* = 4.5; 16 females). All participants were right-handed (all scored positively on the Edinburgh Handedness Inventory; Oldfield, 1971), with normal or adjusted-to-normal vision and no signs of color-blindness. None of the participants reported a psychiatric or neurological disorder that could affect their cognitive functioning. On average, groups did not differ in years of education² (YA $M = 16.5$, $SD = 2.5$; OA $M = 15.6$, $SD = 3.8$; $t(48) = 0.92$, $p = .36$) or in their sex distribution ($\chi^2(1) = 1.15$, $p = .28$). All participants gave informed consent prior to participation and were reimbursed at a rate of 8 € per hour. To test whether our older participant sample was representative regarding normal age-related cognitive changes, all participants were tested on three psychometric tests subsequent to the associative recognition task: (1) the digit symbol (DS) of the HAWIE-R (Tewes, 1991) that tests for speed of processing and (2) a counting span task (CST, adapted from Wechsler, 1955, 2008) that measures working memory capacity; both of these tests were used to test for fluid intelligence. The third task was the Multiple-Choice-Knowledge-Test (MWT, Lehrl, 1977; Lindenberger, Mayr, & Kliegl, 1993) which uses measures of verbal knowledge as a proxy for crystallized intelligence (see Ferdinand and Kray, 2013; Schmitt et al., 2014, for the same approach). In line with the expectation that fluid but not crystallized intelligence should decrease with aging (see Baltes, Staudinger, & Lindenberger, 1999), younger adults showed better performance in the DS ($F(1,49) = 89.71$, $p < .001$) and CST ($F(1,49) = 12.28$, $p < .01$), whereas older adults performed better in the MWT ($F(1,49) = 8.16$, $p < .01$). To grade their cognitive state, older adults were additionally tested with the Mini-Mental State Examination (MMSE, subtest of the CERAD-Plus 1.0 that is used as a dementia screening; Memory-Clinic-NPZ, 2005) and scored within the average range ($M = 29.22$, $SD = 0.86$; the standardized z -value is not different from 0, $p = .14$), suggesting that none of them showed signs of severe cognitive impairment. These results indicate that our sample was indeed representative. The results together with demographic characteristics of the participants are displayed in Table 3.

² This information was missing for one older participant, so only 50 participants entered analysis.

Additionally, one young and two older participants that entered behavioral analysis were excluded from ERP analysis because of a very low trial number in one of the task conditions (< 10 trials), leaving 20 young and 28 old adults whose data entered ERP analysis (the pattern of significant and insignificant results for all subsequent behavioral analysis and the psychometric test results did not change without these individuals).

Table 3 – Sample characteristics and psychometric test results.

	Younger Adults	Older Adults
<i>N</i>	21	30
Gender distribution (m/f)	8/13	16/14
Mean age (years)	23.7 (3.1)	71.7 (4.5)
Age range (years)	19-30	60-79
Education (years)	16.5 (2.5)	15.6 (3.8)
<i>Cognitive Variables</i>		
Digit Symbol	47.1 (5.6)	30.4 (6.6)
Counting Span	5.5 (2.2)	3.6 (1.7)
Multiple-Choice Knowledge Test	24.0 (4.9)	27.1 (3.1)

Note. Standard deviations are given in parentheses.

6.3.2 Procedure

Participants were seated comfortably in a sound- and electrically-shielded room at a distance of approximately 65 cm from a 17" display monitor. On-screen size of the stimulus pairings varied from 3 to 7 cm in length and from 4 to 8 cm in height, with a distance of approximately 1 cm between stimuli. Thus, horizontal and vertical visual angles ranged from approximately 2.6° to 6.2° and 3.5° to 7.0°, respectively. All objects were presented against a gray background.

A total of 176 stimulus pairs served as pictures in the study phase. Half of the stimuli were presented in a plausible and half in an implausible spatial configuration. The plausibility factor was kept constant from study to test. During the recognition test phase, half of the encoded stimuli (88) were presented as old (intact) and half as recombined pairs, and 88 additional picture pairs (half plausible, half implausible) served as new items. Thus, at test, stimuli could appear as one of 44 items in each of the following six conditions: plausible-old, implausible-old, plausible-

recombined, implausible-recombined, plausible-new, implausible-new. Stimulus assignment to these conditions was completely counterbalanced across participants.

The experimental procedure was adapted from Tibon et al. (2014). Before the main phase of the experiment, instructions were read to participants by the experimenter and a practice session with study and test phases was performed, to assure that participants understood the procedure correctly. If participants were uncertain about the task, the practice session could be repeated as necessary. For the practice session, 44 additional picture pairings were used as practice items³.

In the study phase, participants saw pictures pairs and were told to rate (from 0 ‘absolut nicht möglich’/‘absolutely impossible’ to 5 ‘sehr gut möglich’/‘very well possible’) on a response pad whether the stimulus array represented a possible interaction or not, and they were further told to memorize the pairings⁴. Study picture pairs were presented on the screen for 2500 ms. If no response was given during this time a blank screen appeared for 2000 ms, during which a response could also be provided. A subsequent 700 ms blank screen was then followed by a 1000 ms fixation cross. Every 44 trials participants were given self-paced breaks. The interval between study and test phase lasted approximately five minutes in which subjects performed an arithmetic distractor task (counting aloud backwards for 60 sec in steps of three from a random number between 300 and 900).

In the test phase, each trial began with a 500 ms fixation cross, after which picture pairs (each belonging to one of the six described test conditions) were shown until a response was made. Participants had to indicate for each pair whether it was old, recombined, or new by pressing a corresponding key on a response pad. Response assignments were counterbalanced across participants. After a response was provided, a blank screen appeared for 1000 ms. During the test phase, participants were given self-paced breaks every 88 trials.

During practice, participants were given specific feedback on their old/recombined/new response. In case of a correct response, this took the form of a smiley and the sentence

³ These items were taken from those excluded in the pre-experimental rating because of problems with nameability (in this case improved pictures were substituted) or high rankings on semantic relatedness. The assignment to conditions was not counterbalanced in the practice session; 22 were assigned to old, 12 to recombined and 10 to the new condition (with half of the stimuli corresponding to the plausible and half to the implausible array in each condition). There were twice as many old items than new and recombined, because piloting revealed that participants were less likely to give an old response when they were unsure. We assumed that this “response bias” would diminish with unbalanced conditions, because participants received specific feedback on each response in the practice session and would have been advised more often that they should have pressed the ‘old’ button.

⁴ We used the term “interaction possible or not” instead of “plausible or implausible configuration”, because during piloting elderly had severe problems to understand the plausible-instructions, as they tended to confuse “plausibility” with “possibility in reality” despite instructing them profoundly otherwise, and rated the majority of pictures as “implausible”.

“correct!”, and in case of an incorrect response, a frown and the sentence “old/recombined/new would have been the correct response!” was presented for 1500 ms. No such feedback was provided during the actual test phase.

6.3.3 EEG recording

EEG recording and data processing was completely the same as in Experiment 1 (see section 5.2.3). Impedance of electrodes was kept below 7 k Ω .

We did not analyze ERPs to recombined items because the number of artifact free trials was insufficient. Focusing on ERP old/new effects in tasks of associative recognition is however comparable with previous ERP studies that did not include recombined items in analysis of ERP data for similar reasons (Kriukova et al., 2013; Bader et al., 2010, Greve, van Rossum and Donaldson, 2007; Rhodes and Donaldson, 2007). To retain a sufficient signal-to-noise ratio, the minimum number of old and new trials contributing to each average ERP was 10. The mean trial number and range of each condition that entered analysis were as follows: plausible-old (YA: 22 (18-41); OA: 25. (13-38)), implausible-old (YA: 22 (10-39); OA: 20 (10-31)), plausible-new (YA: 29 (21-41); OA: 25.7 (15 - 39)), implausible-new (YA: 22 (19-39); OA: 27 (15-42)).

6.3.4 Data Analysis

Main analysis employed repeated measure of analysis of variance (ANOVA) on behavioral and ERP data and univariate ANOVAs or t-tests were conducted for subsequent contrasts. To account for violations of homogeneity, p -values were corrected using the Greenhouse-Geisser method (Greenhouse & Geisser, 1959). In such cases, uncorrected degrees of freedom are reported. To draw comparisons on significant effects in ANOVAs, partial eta squared (η_p^2) is provided for subsequent main effects whenever required (Tabachnik & Fidell, 2007, pp. 54-55).

Behavioral data analysis

Recognition accuracy rates and reaction times to correct responses (RTs) were subjected to a $2 \times 3 \times 3$ ANOVA with the within-subject factors of Encoding Condition (plausible, implausible) and Item Status (old, recombined, new) and the between-subject factor of Group (YA, OA). Furthermore we computed performance scores for item memory [PrI = hit rate

(old/'old') – false alarm rate (new/'old')] and associative memory [$PrA = \text{hit rate (old/'old')} - \text{false alarm rate (recombined/'old')}$] (Snodgrass & Corwin, 1988), collapsed across encoding conditions, to analyze age-related performance differences on item and associative memory. Towards that end, Pr-scores were subjected to a 2×2 ANOVA with the within-subject factor Pr Type (PrI, PrA) and the between-subject factor Group (YA, OA). We further calculated the number and type of error responses for each of the encoding conditions (e.g. responding 'old' or 'new' to a recombined pairing) and subjected this data to a 2 Encoding Condition (plausible, implausible) \times 2 Error Type (recombined, new for old pairs; old, new for recombined pairs; and old, recombined for new pairs) \times 2 Group (YA, OA) ANOVA, that was performed separately for old, recombined and new pairings (see Tibon et al., 2014, for the same procedure).

We also analyzed plausibility judgments in the study phase, to test whether age groups gave the same proportions of congruent (i.e. judging a plausible configuration with 3, 4 or 5) and incongruent judgments (i.e. judging a plausible configuration with 0, 1 or 2). Study responses were subjected to a $2 \times 2 \times 2$ ANOVA with the between-subject factor Group (YA, OA) and the within-subject factors Encoding Condition and Judgment (congruent, incongruent). To test whether age group differences during study explain variance in associative memory recognition at test, we added rating congruency as covariate to the initial Encoding Condition \times Item Status \times Group ANOVA with accuracy as dependent variable. Rating congruency was defined as the difference between congruent and incongruent judgments at study collapsed across conditions.

ERP data analysis

ERP contrasts were restricted to trials elicited by correct responses to old and new items. For statistical analysis of the ERP old/new effects, mean amplitudes from 9 representative electrodes covering frontal (F3/Fz/F4), central (C3/Cz/C4) and parietal (P3/Pz/P4) scalp regions in two time windows (early: 300 - 500 ms, late: 500 - 700 ms) associated with familiarity and recollection were used. Selection of time windows was based on Experiment 1 and on visual inspection. ANOVAs included the between-subject factor Group (YA, OA) and within-subject factors Encoding Condition (plausible, implausible), Item Status (old, new), Location (frontal, central, parietal) and Laterality (left, midline, right) and Time Window (early, late). Only main effects and interactions including the factor Item Status are reported. Subsidiary analyses of interactions involving Item Status, Encoding Condition and Group were broken down for each encoding condition and followed-up in separate group-specific analysis.

Importantly, the critical distinction between item and associative recognition is that the latter one can distinguish old from recombined pairings while memory for individual items cannot. Thus, firm conclusions about the contribution of unit familiarity to associative recognition can only be drawn from ERPs elicited by old and recombined items. ERP old/new comparisons alone do not allow for strong conclusions about the extent to which observed encoding condition-specific old/new differences relate to unit rather than item familiarity. Since we did not include recombined items, we analyzed item-status-specific differences between plausible-old and implausible-old pairings instead. By doing so, we can control for effects of item familiarity, because encoding conditions presumably differed solely in the spatial arrangement of the two object pairings that was assumed to either facilitate familiarity or not, while the individual stimuli were the same across conditions. We thus expected that any differences between ERPs elicited by plausible-old and implausible-old pairs would arise from underlying differences in processing associations between the two conditions, i.e. unitization.

6.4 Results

6.4.1 Recognition accuracy, error responses and response times

Table 4 shows means and standard errors of the mean (SEMs) of accuracy, Pr-scores and RTs to correct responses of the test phase.

Proportion of correct responses were subjected to an ANOVA with factors Encoding Condition, Item Status and Group and revealed main effects of Encoding Condition ($F(1,49) = 95.95, p < .001$) and Group ($F(1,49) = 35.24, p < .001$) that reflect the overall better memory performance in the plausible than implausible condition and in young than old adults. There was also an interaction between these two factors ($F(1,49) = 23.60, p < .001$), that was followed up by group-specific and encoding-condition-specific contrasts. A main effect of Encoding Condition was larger in younger adults ($F(1,20) = 88.20, p < .001, \eta_p^2 = .82$) than older adults ($F(1,29) = 15.17, p < .01, \eta_p^2 = .34$), indicating a greater memory benefit from plausible pairings in the former group. In addition, age differences were more pronounced in the plausible ($F(1,49) = 48.56, p < .001, \eta_p^2 = .50$) than the implausible condition ($F(1,49) = 18.98, p < .001, \eta_p^2 = .28$). There was also an interaction between Encoding Condition and Status ($F(2,98) = 50.09, p < .001$). A main effect of Encoding Condition was revealed for old ($F(1,49) = 137.53, p < .001, \eta_p^2 = .74$) and recombined pairings ($F(1,49) = 12.04, p < .01, \eta_p^2 = .20$), suggesting better performance in the plausible than the implausible condition for these pairings, whilst the opposite pattern emerged for new items ($F(1,49) = 6.42, p < .05, \eta_p^2 = .12$).

Separate Pr-scores were calculated for item memory and associative memory to explore general age differences for both memory types and subjected to an ANOVA with the factors Pr-Type and Group. There was an interaction between Pr-Type and Group ($F(1,49) = 14.89, p < .001$). Pr-type-specific follow-up analysis revealed main effects of Group for the associative ($F(1,49) = 43.64, p < .001, \eta_p^2 = .47$) and item Pr-Score ($F(1, 49) = 10.82, p < .01, \eta_p^2 = .18$). To test whether the associative memory deficit was significantly bigger in old compared to young adults, we subjected the differences of these scores (PrI minus PrA) to an ANOVA with the factor Group that revealed a main effect of Group ($F(1,49) = 14.89, p < .01, \eta_p^2 = .23$). These results suggest that age differences were larger for associative than item memory and confirms the frequently reported finding of larger age-related differences in tests for associative than item memory (Chalfonte & Johnson, 1996; Naveh-Benjamin et al., 2003).

Table 4 – Behavioral performance measures for young and old adults.

	Young Adults		Old Adults	
	Plausible	Implausible	Plausible	Implausible
Accuracy				
<i>old</i>	0.81 (0.02)	0.59 (0.04)	0.67 (0.03)	0.52 (0.03)
<i>recombined</i>	0.68 (0.03)	0.58 (0.04)	0.47 (0.03)	0.46 (0.03)
<i>new</i>	0.88 (0.02)	0.89 (0.02)	0.71 (0.03)	0.76 (0.03)
Pr-score				
<i>Item (PrI)</i>	0.79 (0.02)	0.58 (0.04)	0.59 (0.03)	0.48 (0.03)
<i>Associative (PrA)</i>	0.60 (0.04)	0.38 (0.04)	0.25 (0.03)	0.16 (0.03)
RT				
<i>old</i>	1777 (175)	2242 (182)	2047 (118)	2384 (168)
<i>recombined</i>	2314 (158)	2685 (221)	2688 (179)	2767 (210)
<i>new</i>	1808 (132)	1816 (135)	2050 (145)	2144 (200)

Note. SEMs are given in parenthesis.

We additionally analyzed error responses separately for old, recombined and new pairings (see Table 5).

Table 5 – Error types.

Item Status		Old		Recombined		New	
Error Type		“recombined”	“new”	“old”	“new”	“old”	“recombined”
PL	YA	13.96 (1.82)	4.76 (0.97)	21.75 (2.27)	9.74 (1.36)	1.95 (0.77)	9.63 (1.87)
	OA	23.34 (2.10)	8.79 (1.39)	40.61 (3.07)	12.80 (1.82)	6.06 (0.97)	22.42 (2.30)
IMPL	YA	26.84 (2.38)	14.50 (2.38)	20.24 (2.57)	21.32 (2.91)	1.08 (0.40)	9.96 (2.10)
	OA	16.52 (2.38)	29.85 (1.97)	35.39 (2.75)	19.17 (2.20)	3.93 (0.69)	20.0 (2.15)

Notes. Error responses are displayed in %. SEMs are given in parenthesis.

PL = plausible condition, IMPL = implausible condition.

For old pairings, the analysis revealed a main effect of Encoding Condition ($F(1,49) = 132.68, p < .001$), indicating that more errors were made in the implausible than plausible condition, a main effect of Error Type ($F(1,49) = 53.64, p < .001$), reflecting more erroneous ‘recombined’ than ‘new’ responses and a main effect of Group ($F(1,49) = 4.88, p < .05$), suggesting more errors made by old than young adults. There was also an interaction of Encoding Condition and Group ($F(1,49) = 8.15, p < .01$), whose decomposition for each encoding condition revealed age effects in the plausible ($F(1,49) = 12.01, p < .01$), but not the implausible condition ($p = .84$). For recombined items, the analysis revealed also a main effect of Encoding Condition ($F(1,49) = 12.03, p < .01$), with the same plausible < implausible pattern, a main effect of Error Type ($F(1,49) = 31.45, p < .001$), reflecting a ‘old’ > ‘new’ error pattern and a main effect of Group ($F(1,49) = 18.47, p < .001$), suggesting more errors by old than young adults. There was also an interaction of Encoding Condition by Group ($F(1,49) = 7.64, p < .01$), stemming from larger group differences in the plausible than implausible condition (plausible: $F(1,49) = 24.99, p < .01$; implausible: $F(1,49) = 8.89, p < .01$) and from young ($F(1,20) = 11.14, p < .01$) but not old adults ($p = .51$) making less errors in the plausible compared to the implausible condition. Analysis of recombined pairs further revealed an Error Type by Group ($F(1,49) = 11.14, p < .01$) and an Encoding Condition by Error Type interaction ($F(1,49) = 18.20, p < .001$). An error-type-specific follow-up of these interaction revealed for the former one that older compared to young adults made more erroneous ‘old’ responses to recombined items ($F(1,49) = 21.76, p < .001$), whereas there were no age differences with respect to erroneous ‘new’ responses ($p = .86$), and for the latter one suggesting more ‘new’ errors to recombined pairs in the implausible than plausible condition ($F(1,49) = 32.45, p < .001$), while there is a reversed trend

(plausible > implausible) for erroneous ‘old’ responses ($F(1,49) = 3.78, p = .06$). For new item pairs, the analysis revealed again a main effect of Encoding Condition ($F(1,49) = 5.52, p < .05$) with the plausible > implausible pattern and a main effect of Error Type ($F(1,49) = 67.44, p < .001$), reflecting a ‘recombined’ > ‘old’ error pattern and a main effect of Group ($F(1,49) = 20.09, p < .001$), suggesting more errors by old than young adults. There was also an interaction between Error Type and Group ($F(1,49) = 7.03, p < .05$), stemming from older adults making much more erroneous ‘recombined’ than ‘old’ responses to new pairings ($F(1,29) = 56.47, p < .01$) than young adults ($F(1,20) = 21.07, p < .01$).

For RTs to correct responses there was a main effect of Encoding Condition ($F(1, 49) = 31.91, p < .001$), indicating overall faster responses in the plausible than implausible condition, and a main effect of Item Status ($F(2,98) = 45.90, p < .001$) that was followed-up by separate contrasts: new versus old ($F(1,49) = 4.28; p < .05$), old versus recombined ($F(1,49) = 56.44; p < .001$) and new versus recombined ($F(1,49) = 83.44; p < .001$) that imply a new < old < recombined response pattern for both age groups. There was also an interaction of Encoding Condition by Item Status ($F(2,98) = 13.27, p < .001$) and an interaction between Encoding Condition, Item Status and Group ($F(2,98) = 3.91, p < .05$). Decomposition of the three-way interaction by the Group revealed Encoding Condition by Item Status interactions in young ($F(2,40) = 7.22, p < .01$) and old adults ($F(2,58) = 8.32, p < .01$) that were followed up separately for each level of the factor Item Status. Young individuals responded faster to plausible than to implausible old and recombined items, whereas their response times did not differ between plausible and implausible new items (YA: old: $F(1,20) = 34.45, p < .001$; new: $p = .91$; recombined: $F(1,20) = 11.21, p < .01$). In contrast, older individuals showed faster responses to plausible than to implausible old items and no condition-related RT differences for new and recombined items (OA: old: $F(1,29) = 16.26, p < .001$; new: and recombined: all p -values $\geq .13$).

6.4.2 Plausibility ratings

Participants’ plausibility judgments at study (from 0 to 5) were sorted according to whether they were congruent or incongruent with the stimulus pair assignment to the encoding condition, i.e. rating a (pre-experimentally defined) plausible pair with 3, 4 or 5 would be a congruent, with 0, 1 or 2 an incongruent plausibility judgement. The mean number of plausibility judgments to each encoding condition is summarized in Table 6. The proportions of plausibility judgments were then submitted to an ANOVA with the factors Encoding Condition, Judgment (congruent, incongruent) and Group. The analysis revealed a marginal main effect of Encoding Condition

($F(1,49) = 3.62$; $p = .06$) and significant main effects of Group ($F(1,49) = 8.17$, $p < .01$) and Judgment ($F(1,49) = 458.05$, $p < .001$). A Judgment \times Group interaction ($F(1,49) = 14.01$, $p < .001$) broken down by the factor Judgment revealed main effects of Group for congruent ($F(1,49) = 14.44$, $p < .001$) and incongruent plausibility judgements ($F(1,49) = 13.53$, $p < .001$). This demonstrates that young participants made significantly more congruent and less incongruent plausibility judgments than old adults. To test whether these group differences in experienced plausibility at study can explain age-related differences in recognizing plausible and implausible pairs at test, we defined a variable “Rating Congruency” as the difference between congruent and incongruent judgments at study collapsed across conditions and added this variable as covariate to the initial Encoding Condition \times Status \times Group ANOVA with accuracy as dependent variable. The ANCOVA revealed that there was no significant effect of rating congruency ($p = 0.72$) or interaction with it (all $p \geq .28$). The Outcomes of the initial ANOVA with main effects of Encoding Condition and Group and the interaction of Encoding Condition and Pair Status remained the same. Controlling for rating congruency as a covariate did not change the result pattern of the initial ANOVA (reported above).

Table 6 – Plausibility judgments during study.

	Plausible condition		Implausible condition	
	Young Adults	Old Adults	Young Adults	Old Adults
<i>plausible judgment</i>	90.14 (1.29)	78.61 (3.03)	7.97 (2.12)	20.56 (2.79)
<i>implausible judgment</i>	9.86 (1.29)	21.39 (3.03)	92.03 (2.12)	79.44 (2.79)

Note. Plausibility judgements to each encoding condition in %. SEMs are given in parenthesis.

To briefly summarize, the behavioral results showed that age differences were larger for associative than item memory and more pronounced in the plausible than in the implausible condition. Importantly, older adults were less able to perceive inherent plausibility at study (as it was defined from the pre-experimental rating), but when controlled for this discrepancy, initial result pattern did not change, suggesting that incongruencies in perceived plausibility do not explain the increased aging effect for plausible pairings.

6.4.3 ERP results

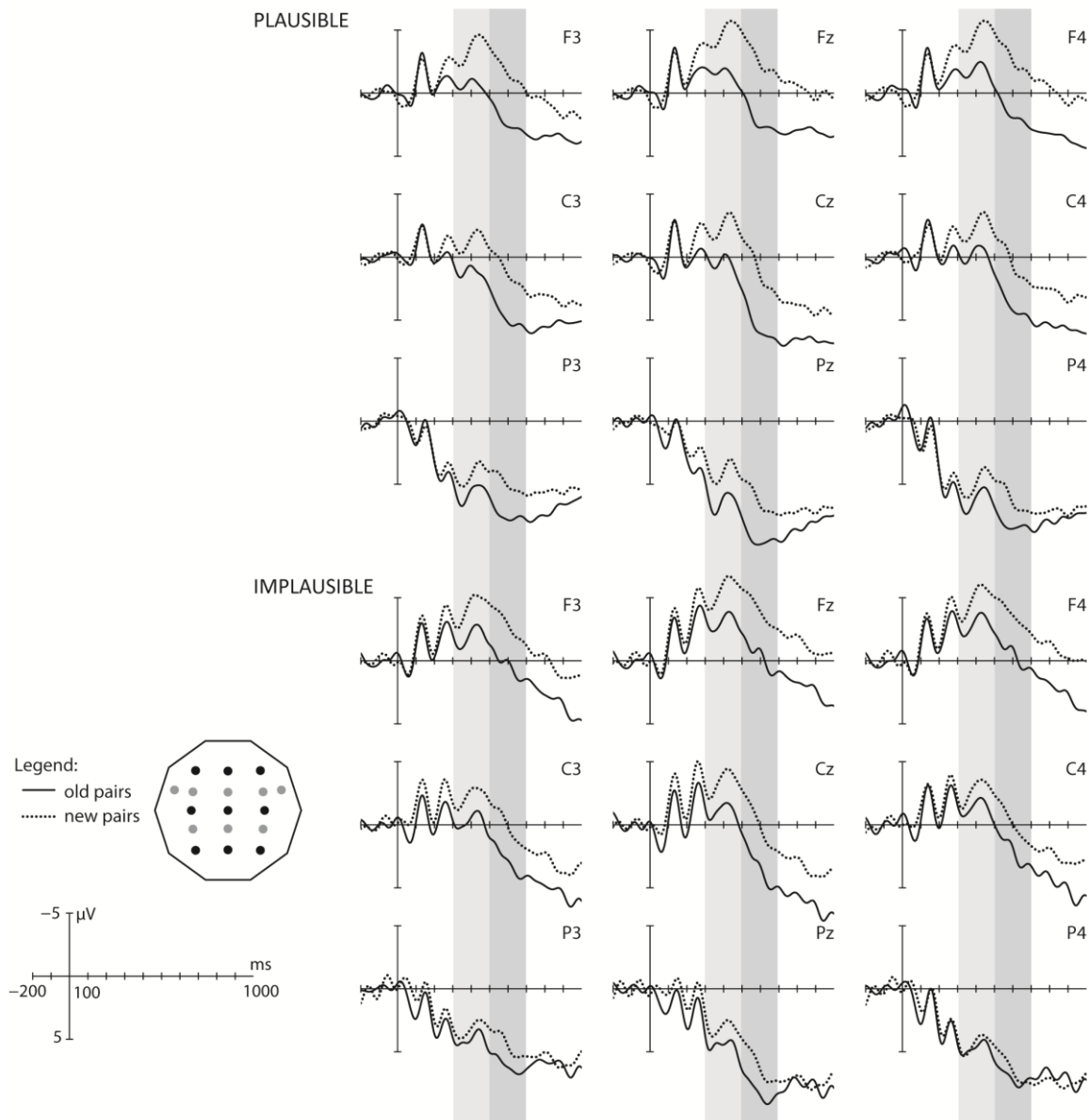


Figure 12 – ERP waveforms of old and new items, depicted for young adults in the plausible condition and the implausible condition. Light-grey shading denotes the 300-500 ms time-window and dark-grey shading the 500-700 ms time window.

Figure 12 and 13 illustrate averaged ERPs for each group and encoding condition. Visual inspection reveals that early old/new effects differ across conditions and age groups: in young adults, old/new differences appear with a frontal maximum in both encoding conditions in the early and late time window, albeit more widely distributed in the early time window in the plausible condition. In old adults, similar but substantially smaller old/new effects appear in the

early time window only, whereas no differences in the ERPs elicited by old and new pairings were visible in the late time window at posterior sites.

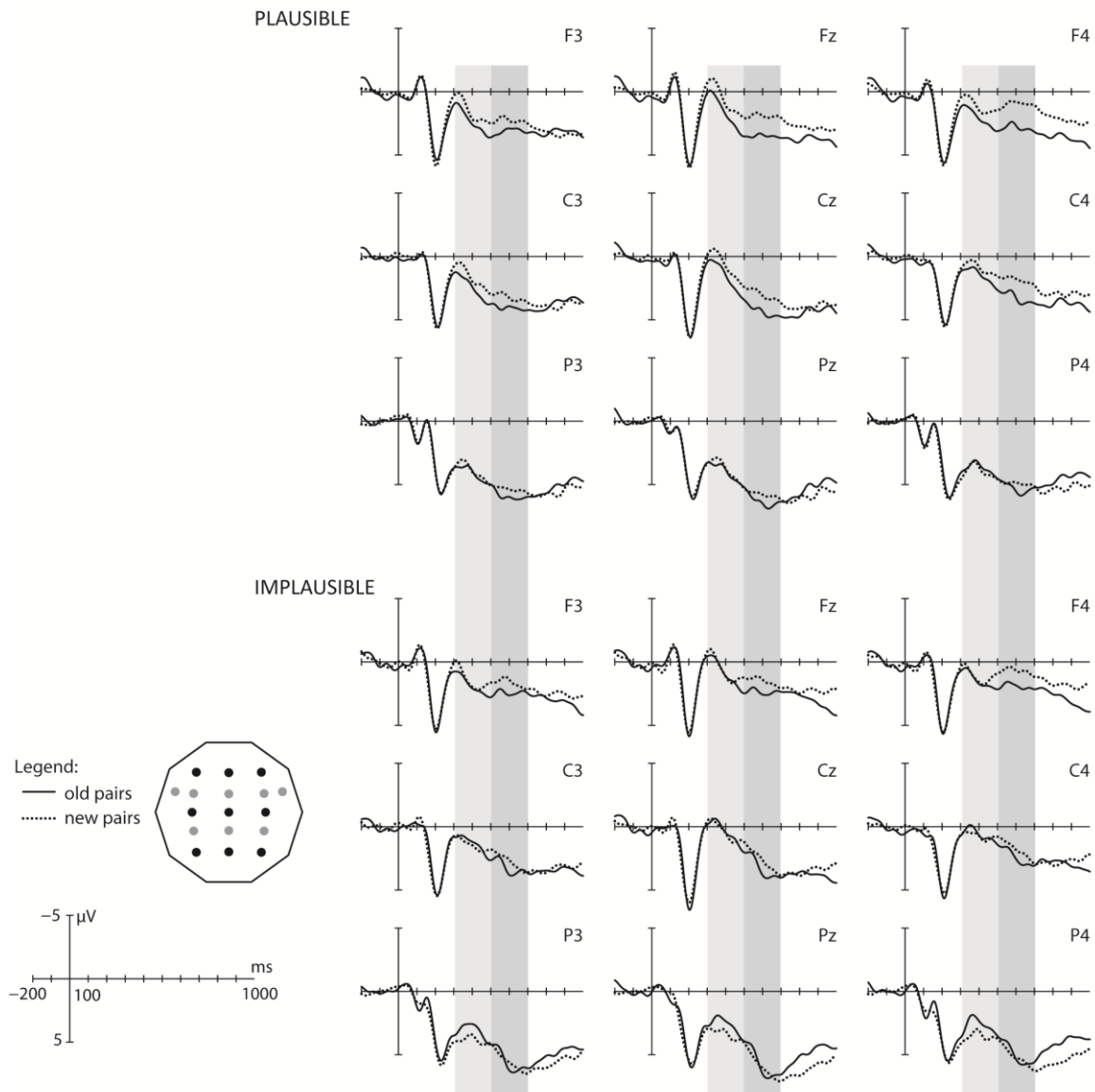


Figure 13 - ERP waveforms of old and new items, depicted for old adults in the plausible condition and the implausible condition. Light-grey shading denotes the 300-500 ms time-window and dark-grey shading the 500-700 ms time window.

The outcome of the global ANOVA with the factors Encoding Condition (plausible, implausible), Item Status (old, new), Location (frontal, central, parietal), Laterality (left, midline, right), Time Window (early, late) and Group (YA, OA) is summarized in Table 7. These outcomes demonstrate that effects of item status differ in their size according to age group and encoding condition and that effects of item status and encoding condition differ in their

distribution according to the time window. Given these interactions and licensed by the specific directed hypotheses about effects of age and encoding condition on the early and late old/new effects, we performed separate follow-up analyses, even though the six-way interaction was not significant ($p = .17$). We performed time-window- and encoding-condition-specific follow-up analyses with the factors Item Status, Location, Laterality and Group to investigate age-related differences in encoding condition-specific old/new effects. We also performed time-window- and item-status-specific follow-up analyses with the factors Encoding Condition, Location and Laterality separately for each group to investigate item status-specific differences across conditions.

Table 7 – Outcomes of the global ANOVA and time-window- and encoding-condition-specific follow-up analyses.

The global ANOVA	<i>F</i> -value			
IS, $F(1,46)$	61.94 ***			
IS × GP, $F(1,46)$	29.12 ***			
EC × IS, $F(1,46)$	3.29, $p=.08$			
IS × Lat × GP, $F(2,92)$	7.85 **			
EC × Loc × Lat × TW, $F(4,184)$	4.60 **			
IS × Loc × Lat × TW, $F(4,184)$	13.02 ***			
IS × Lat × TW × GP, $F(4,184)$	2.65, $p=.09$			
EC × IS × Loc × Lat × TW × GP, $F(4,184)$	1.71, $p=.17$			
Follow-up by TW and EC	300 – 500 ms		500 – 700 ms	
	PL	IMPL	PL	IMPL
IS, $F(1,46)$	33.74 ***	7.06 *	48.45 ***	17.83 ***
IS × GP, $F(1,46)$	12.79 **	9.81 **	14.90 ***	8.56 **
IS × Loc, $F(2,92)$	14.15 ***	14.53 ***		
IS × Lat, $F(2,92)$	6.38 **	6.47 **		
IS × Lat × GP, $F(2,92)$		4.32 **	3.30 *	5.52 **
IS × Loc × Lat, $F(4,184)$			6.53 ***	3.89 **
IS × Loc × Lat × GP, $F(4,184)$	2.25 +			

Note. Shown are only significant effects and interactions including the factor Item Status (IS) of the global ANOVA and subsequent follow-up analysis.

IS = Item Status, GP = Group, EC = Encoding Condition, Loc = Location, Lat = Laterality, TW = Time Window.

+ $p = .07$, * $p < .05$, ** $p < .01$, *** $p < .001$.

Early ERP effects (300-500 ms): Condition-specific old/new comparison

Significant interactions of the follow-up analysis that included the factors Item Status and Group were further broken down by the factor Group and analyses were performed separately for each group.

In the plausible condition, a break-down of Item Status \times Group of the global ANOVA revealed effects of Item Status in both groups (YA: $F(1,19) = 27.98, p < .001, \eta_p^2 = .60$; OA: $F(1,27) = 3.96, p = .06, \eta_p^2 = .13$), indicating larger old/new effects in young than old adults. Further, the follow-up of the Item Status \times Laterality \times Location \times Group interaction revealed for young adults an interaction of Item Status and Location ($F(2,38) = 5.71; p < .05$) that was further broken down by the factor Item Status. This revealed old/new differences along frontal ($F(1,19) = 34.61, p < .001, \eta_p^2 = .65$), central ($F(1,19) = 25.71, p < .001, \eta_p^2 = .58$) and parietal electrodes ($F(1,19) = 11.18, p < .01, \eta_p^2 = .37$), with largest effect sizes at anterior sites. In young adults, Item Status further interacted with Laterality ($F(2,38) = 6.15; p < .01$), because of the left-lateralized distribution of the effect (left: $F(1,19) = 29.30, p < .001, \eta_p^2 = .61$; central: $F(1,19) = 29.02, p < .001, \eta_p^2 = .60$; right: $F(1,19) = 20.52, p < .001, \eta_p^2 = .52$). There was also an Item Status by Location by Laterality interaction in young adults ($F(4,76) = 2.61, p = .05$), such that the largest effect sizes were found at F3 ($F(1,19) = 42.76, p < .001, \eta_p^2 = .69$), C3 ($F(1,19) = 27.45, p < .001, \eta_p^2 = .59$) and Pz ($F(1,19) = 15.79, p < .001, \eta_p^2 = .45$). Similarly, in old adults, there was an interaction between Item Status and Location ($F(2,54) = 8.72, p < .01$) and between Item Status, Location and Laterality ($F(4,108) = 2.48; p \leq .05$), such that the largest effect sizes were found at Fz ($F(1,27) = 9.82, p < .001, \eta_p^2 = .27$) and C3 ($F(1,27) = 7.57, p < .001, \eta_p^2 = .22$) and no significant old/new effects at posterior sites (all F -values $\leq .61$, all p -values $\geq .44$).

In the implausible condition, the interaction of Item Status and Group was followed-up group-specifically and revealed main effects of Item Status that were substantial in young adults ($F(1,19) = 9.52, p < .01, \eta_p^2 = .33$) and not apparent in old adults ($p = .65$). Additionally, the decomposition of the three-way Item Status, Laterality and Group interaction revealed main effects of Items Status in young adults at all levels of Laterality (left: $F(1,19) = 10.71, p < .01, \eta_p^2 = .36$; central: $F(1,19) = 10.56, p < .01, \eta_p^2 = .36$; right: $F(1,19) = 5.95, p < .01, \eta_p^2 = .24$) and no effects in old adults in any Laterality condition (all p -values $\geq .54$). This indicates that old adults showed no old/new effects in the implausible condition, while old/new effects in young adults were lateralized to left and central sites. The Item Status \times Location \times Group interaction was not significant ($p = .66$), but since we did find two-way interactions between Item Status and Group and between Item Status and Location and since we had proposed a specific hypothesis regarding the different distribution of old/new effects between conditions, we conducted group-

specific follow-up contrasts on the Item Status by Location interaction (YA: $F(2,38) = 4.13$; $p < .05$; OA: $F(2,54) = 6.15$; $p < .05$). In young adults, effects of Item Status were significant at frontal ($F(1,19) = 13.72$, $p < .01$, $\eta_p^2 = .42$) and central ($F(1,19) = 11.10$, $p < .01$, $\eta_p^2 = .37$), but not at parietal electrodes ($F(1,19) = 2.68$, $p = .12$). In old adults, old/new contrasts were not significant at frontal and central sites (all p -values $\geq .34$) but appeared as a negative going deflection for old relative to new items that started at around 300 ms at parietal sites ($F(1,27) = 4.40$, $p < .05$; $\eta_p^2 = .14$).

Summing up the results of the early time window, we found larger early old/new effects, associated with familiarity, in young than in old adults. In young adults, this effect was observed in both encoding conditions, though it was topographically more extensive in the plausible compared to the implausible condition. In older adults, the early old/new effect was only apparent in the plausible condition, showing a fronto-central distribution, whilst ERPs were more negative going for old than new items at posterior sites in the implausible condition (see Figure 13).

Early ERP effects (300-500 ms): Item-specific plausible/implausible comparisons

Since the recombined condition did not yield enough artifact-free trials for analysis, we attempted to gain more direct traction on processing differences between conditions by comparing ERPs evoked by plausible-old and implausible-old pairs. Since the same objects were used in both of those conditions, and they differed solely in their spatial arrangement, we assumed item familiarity to be constant across conditions. As such any difference between plausible-old and implausible-old ERPs would ostensibly be due to differences in plausibility-engendered associative processing, i.e. unitization. Figure 14 illustrates the plausible-old/implausible-old effect in young and old adults, which is shown as mean amplitude scores for plausible and implausible old pairs collapsed across all frontal, central and parietal recording sites.

ANOVAs with the factors Encoding Condition, Location and Laterality for old items in the early time window were conducted separately for young and old adults. For young adults, the old item analysis revealed a main effect of Encoding Condition ($F(1,19) = 4.54$, $p < .05$; $\eta_p^2 = .19$) and no interaction of Encoding Condition with any of the other factors (all p -values $\geq .40$). In the same manner for old adults, the analysis revealed a main effect of Encoding Condition ($F(1,27) = 6.85$, $p < .05$; $\eta_p^2 = .20$) and no interaction of Encoding Condition with any of the other factors (all p -values $\geq .24$). Thus, the early plausible-old/implausible-old differences in both age groups depict a widely distributed effect, with plausible pairings showing a more positive

going deflection. Below (see discussion) we will argue that taking this finding together with the widely distributed early old/new effect in younger adults may indicate a contribution of unit familiarity to associative recognition.

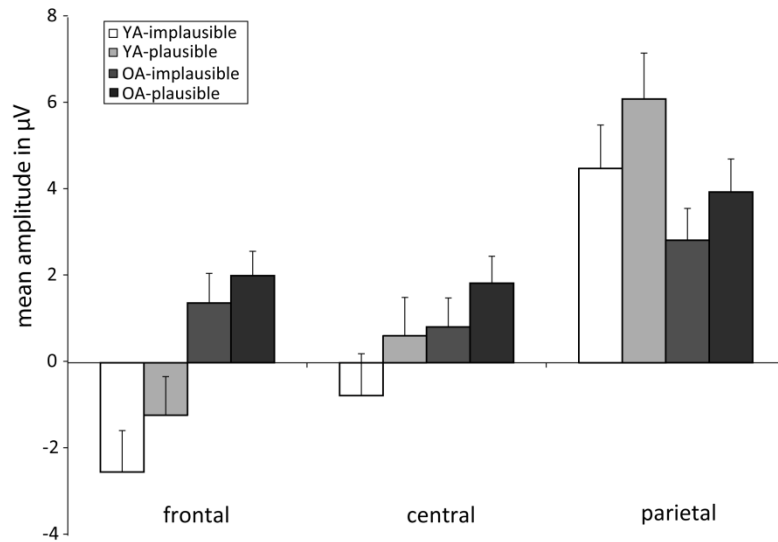


Figure 14 - Mean amplitude of plausible old and implausible old pairs in the early time window (300-500 ms), collapsed across frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) electrodes. Error bars depict the standard error of the mean.

Late ERP effects (500-700 ms)

In the plausible condition, a group-specific breakdown of the Item Status \times Group interaction revealed main effects of Item Status in both groups, that indicate a larger old/new effect in young ($F(1,19) = 35.66, p < .001, \eta_p^2 = .65$) than old adults ($F(1,27) = 8.09, p < .01, \eta_p^2 = .23$). Further, the Item Status \times Laterality \times Group and the Item Status \times Location \times Laterality interaction suggest that effects of Item Status vary in their distribution and with age group and were thus followed-up separately for the two age groups and all levels of Location and Laterality. In young adults, old/new effects were significant at all levels of Location and Laterality (all p -values $\leq .01$), but differentially left-lateralized, with largest effect sizes at F3 ($\eta_p^2 = .73$), C3 ($\eta_p^2 = .70$) and P3 ($\eta_p^2 = .53$). In older adults, late old/new effects were right-lateralized and only evident at frontal and central electrodes (all p -values $\leq .01$; F4: $\eta_p^2 = .45$; Fz: $\eta_p^2 = .31$; C4: $\eta_p^2 = .34$; Cz: $\eta_p^2 = .25$) and not significant at left-sided (all p -values $\geq .07$) or parietal electrodes (all p -values $\geq .15$).

In the implausible condition, decomposing the Item Status \times Group interaction revealed that old/new differences were large in young adults ($F(1,19) = 13.70, p < .01, \eta_p^2 = .42$) and

virtually absent in old adults ($p = .20$). Interactions between Item Status, Laterality and Group and between Item Status, Location and Laterality were decomposed for young and old adults, revealing for the former group a left-lateralization of the late old/new effect in the implausible condition (all p -values $\leq .05$, but P4: $p = .38$), in which it was largest at F3 ($\eta_p^2 = .49$), C3 ($\eta_p^2 = .50$) and Pz ($\eta_p^2 = .25$) for each level of Location. In old adults, old/new effects are only observable at F4 ($F(1,27) = 6.14$, $p < .05$, $\eta_p^2 = .19$) and not significant at any other level of Laterality and/or Location (all p -values $\geq .09$).

To summarize, in the late time window where the ERP correlate of recollection is expected to occur, old/new effects were distributed across the scalp but differentially left-lateralized, and evident at parietal sites in young adults in both encoding conditions, though somehow larger in the plausible than implausible condition. In line with an assumed recollection deficit in old adults, no late old/new effect was observable in old adults at parietal sites in both encoding conditions.

6.5 Post hoc analysis

6.5.1 Posterior negativity

As reported above, a negativity for old relative to new pairings appeared for older adults in the implausible condition in the 300-500 ms time window. As can be seen in Figure 13, the negativity onsets in posterior sites around 300 ms and extends for several hundred milliseconds. Similarly, a negative going slow waves in older adults has been observed in Experiment 1 and in previous studies (Duarte et al., 2006; Friedman et al., 2010) that was particularly pronounced for low performing elderly and that has been interpreted as attempts to recruit alternative retrieval strategies to compensate for impoverished recollection in situations with high task demands (for a thorough discussion of the posterior negativity see section 5.5.4). To explore whether the posterior negativity in this study resembles the one observed in Experiment 1 and previous studies, we tested whether the posterior negativity in the implausible condition varied with older adults' memory performance.

First, mean difference scores for the ERP effect in the 300 – 500 ms time window (old minus new) collapsed across posterior sites (Mean difference (P3, Pz, P4) in the implausible encoding condition and an associative memory score (PrI minus PrA, reflecting the magnitude of the associative memory deficit) in the implausible encoding condition were built. Then, a bivariate correlation between these two measures in older adults was performed. The magnitude

of the associative memory deficit in the implausible condition was correlated negatively with the old-new difference ($r(28) = -.46$; $p < .05$) showing that older adults with the larger associative memory deficit tended to display a larger negativity (see Figure 15).

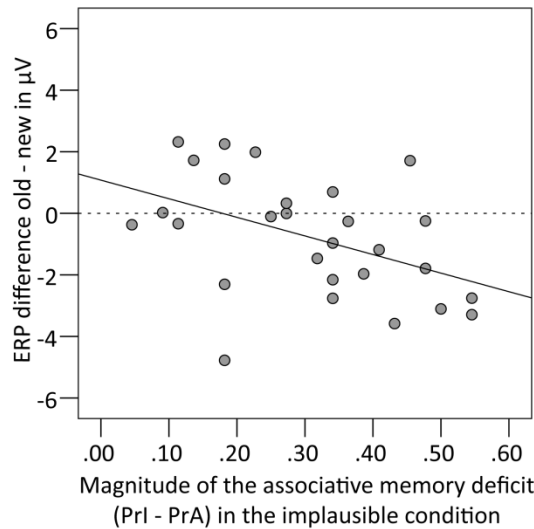


Figure 15 - ERP old-new differences in old adults in a 300-500 ms time window at posterior sites correlates with magnitude of the associative memory deficit in the implausible condition ($r(28) = -.46$; $p < .05$).

6.5.2 ERP old/new effects with performance matched groups

A possible caveat of age-related ERP comparisons is that overall memory performance is usually lower in older than younger adults, and the possibility remains that attenuations of old/new effects in older participants could be a result of this (Wang et al., 2012). We therefore re-conducted the foregoing ERP analysis for the largest subset of young ($n = 16$) and old ($n = 18$) participants for whom item memory scores were comparable (PrI plausible: OA: $M = 0.70$, $SD = 0.10$; YA: $M = 0.76$, $SD = 0.10$; $t(32) = 1.55$, $p = .13$ / PrI implausible: OA: $M = 0.55$, $SD = 0.13$; YA: $M = 0.53$, $SD = 0.17$; $t(32) = -0.40$, $p = .69$). The pattern of main effects and interactions in the early and late time windows did not change: In the 300-500 ms time window in the plausible condition, effects of Item Status appeared for young adults at frontal ($\eta_p^2 = .60$), central ($\eta_p^2 = .58$) and parietal electrodes ($\eta_p^2 = .50$), whereas in older adults, old/new effect were apparent at frontal ($\eta_p^2 = .35$) and central sites ($\eta_p^2 = .25$). In the implausible condition, young adults' old/new effects were attenuated compared to the plausible condition and present at frontal and central, but not parietal locations ($\eta_p^2 = .32$; $\eta_p^2 = .29$; $p = .29$; respectively). In old adults, early old/new effects in the implausible condition solely displayed a negativity at posterior

sites ($\eta_p^2 = .21$). In the 500-700 ms time window, left parietal old/new effects were only evident in young adults in both conditions (plausible at P3: $\eta_p^2 = .70$; implausible at P3: $\eta_p^2 = .27$; OA: all p -values $\geq .38$). To summarize, the subgroup analysis indicated that the between-group differences in the early frontal and late parietal old/new effects are unlikely to result from differences in memory performance.

6.6 Discussion

In the current study we used pairs of semantically unrelated objects that were positioned relative to each other at either spatially plausible or implausible locations to either encourage or discourage unitization at encoding. Contrary to our hypothesis that unitization would attenuate age-related associative memory differences, age-related performance differences were actually increased for plausible compared to implausible pairings. In contrast, ERP results indicated that the early old/new effect was attenuated and only present in the plausible condition at frontal ($\eta_p^2 = .27$) and central recording sites ($\eta_p^2 = .22$) and absent in the implausible condition. In young adults, the early old/new effect was larger and topographically more widespread distributed for plausible than implausible pairings: in the former condition the effect is most pronounced at frontal electrodes ($\eta_p^2 = .69$) but extends through centro-parietal sites ($\eta_p^2 = .45$), while in latter condition it occurs at frontal ($\eta_p^2 = .42$) and central electrodes ($\eta_p^2 = .37$) only. Further plausible-old items widely elicited a more positive going deflection than implausible-old items in young and older adults. Additionally, older adults showed a posterior negativity in the more demanding implausible condition that was larger in those elderly that exhibited more of an associative memory deficit. In the late time window, generally associated with the ERP correlate of recollection, young adults exhibit a late left-lateralized old/new effect with a broad distribution in both conditions (plausible: $\eta_p^2 = .65$; implausible: $\eta_p^2 = .42$). In old adults, late old/new effects were right-lateralized and not apparent at posterior sites in both conditions.

6.6.1 Behavioral results

We start with discussing the results of the reaction times first, since these findings were least complex. We found that responses at retrieval were faster for plausible than implausible pairs. In young but not old individuals, this effect interacted with memory: the speed-up in the plausible condition was evident for old and recombined but not new items. This indicates that processing of plausibly organized pictures is accelerated when either the items comprising the

pair or the pair itself have been learned previously, leading to faster recognition decisions for these items in young adults.

Analysis of performance scores revealed poorer associative memory performance by old relative to young adults, and larger group differences for associative memory than item memory. This pattern provides further support for the associative memory deficit hypothesis (Naveh-Benjamin et al., 2007; Naveh-Benjamin, 2000). The current study was designed to investigate the impact of conditions that encourage unitization on older adults' associative memory. Memory appeared to benefit from unitization at encoding for both young and old adults, as performance was higher for plausibly than implausibly situated stimuli in both groups. Based on findings that unitization disproportionately favors old individuals (Ahmad et al., 2014; Badham et al., 2012; Bastin et al., 2013; Naveh-Benjamin et al., 2007), we had expected that older adults would profit to a greater extent than young adults in the condition designed to encourage unitization. Unexpectedly, however, the recognition advantage for plausible over implausible pairs was greater in young than older adults, and as a consequence age differences were more pronounced in the plausible than in the implausible condition. Age differences in the implausible condition were expected to arise from elderly participants' recollection impairment that impeded retrieval of associative information. In the plausible condition, we expected older adults to benefit from the plausible location-based information that encourages unitization, which in turn would have enabled unit familiarity to compensate for age-related reductions in recollection.

The greater age differences in the plausible condition might have occurred because all the stimulus pairs were semantically unrelated and therefore especially difficult for the elderly to process. In this vein it is important to note that during the study phase older adults made more incongruent plausibility rating judgments compared to young adults. However, as revealed by an ANCOVA, when these age differences in perceived plausibility were taken into account, the disproportionately larger age decrement for plausible pairs remained. This suggests that the age difference in perceived plausibility is not the main factor behind the age group differences in memory performance and the observed pattern most likely reflects the old adults' general decrement in associative memory.

It is important to note that, contrary to other aging studies which manipulated unitizability of word stimuli by encoding instructions (Bastin et al., 2013) or stimulus pairs containing pre-experimental associations (Ahmad et al., 2014), we used unrelated pictures whose spatial arrangement was expected to inherently enable unitization. These former studies have in common that unitization easily supported the cohesion of two components to one single item, so that the two items may not even be perceived as two separate items at all, by this reducing the

demands on effortful encoding strategies. Ofen & Shing (2013) suggested that older adults find it hard to create memory associations according to arbitrary rules, which was especially needed to engender unitization within the current paradigm, since all pairings were semantically unrelated. In line with this assumption is the finding, that older adults made more erroneous ‘old’- and ‘recombined’ responses than young adults in both conditions, reflecting their difficulty in creating and retrieving associations (see Table 5). Importantly, it has repeatedly been shown that providing appropriate strategy instruction about how to encode and integrate two arbitrary words meaningfully can reliably decrease the associative memory deficit (Naveh-Benjamin et al., 2007, 2005). The present unitization manipulation of the spatial arrangement of unrelated pictures might have provided insufficient schematic support, such that older adults might have faced problems to self-generate a unitized representation when no top-down encoding instructions were provided.

ERP results may outline more directly to what extent the reported behavioral results stem from differences in unitization processing and consequently from different contributions of familiarity and recollection that underlie participants’ recognition decisions and the large age-related memory deficit in the plausible condition.

6.6.2 Early ERP effects

Since ERPs largely differ between conditions and groups, the findings and their implications in the context of behavioral results are discussed separately for young and old adults.

Young adults

For young adults, the early old/new effect was observable for spatially plausible and implausible pairings, though larger and topographically more widespread in the former condition. Consistent with prior studies that showed that an early ERP effect associated with familiarity-based remembering can be observed in associative memory tasks (Bader et al., 2010; Greve et al., 2007; Tibon et al., 2014) early ERP old/new effects were found in the plausible and implausible condition. The early old/new effect in the plausible condition was topographically widespread, whereas in the implausible condition it displayed a fronto-central maximum. Additionally, categorical amplitude differences between plausible-old and implausible-old ERPs were obtained in the form of a more positive-going deflection for plausible than implausible pairs.

We hypothesized that the ERP difference between plausible-old and implausible-old pairs most likely reflects unit familiarity, since encoding conditions only differed in the presence of spatially congruent contextual information that encourage unitization at encoding and were matched for item familiarity and response type. Thus, the plausible-old/implausible-old ERP effect suggests that young adults used location-based associative information to form unitized representations at encoding. This early plausible-old/implausible-old ERP effect together with the larger early old/new effect and the associative recognition benefit in the plausible condition in young adults supports the notion that the plausible encoding condition encouraged unitization and facilitated familiarity-based associative recognition judgments.

However, there is also another interpretation likely for the observed early ERP effects in young adults. The larger early old/new effect in the plausible compared to the implausible condition may simply reflect greater memory strength for plausible pairings and the plausible/implausible ERP effect to old items may reflect more fluency-based processing due to facilitated semantic access of plausible compared to implausible pairings. Moreover, since the late parietal old/new effect – the putative ERP correlate of recollection - is also slightly larger in the plausible than implausible condition one could argue that the increased memory benefit for plausible pairs may reflect contributions from recollection rather than familiarity. To test whether the observed differences in early old/new effects between conditions in young adults are influenced merely by differences in performance scores rather than differences in unitization, we performed a repeated measure ANCOVA controlling for variance in performance scores⁵. The ANCOVA was calculated on old-new differences collapsed across laterality with the within-subject factors Encoding Condition (implausible, plausible), Location (frontal, central, parietal) and the mean performance scores (Mean PrI, PrA) of the plausible and implausible condition as covariates. The analysis reveals that ERPs still differ (marginally significant) between encoding conditions when we control for differences in performance scores (between subject contrasts: performance plausible condition: $p = .96$; performance implausible condition: $p = .19$; within subject contrast: main effect Encoding Condition $F(1,17) = 4.18$, $p = .057$, $\eta_p^2 = .20$; no interaction with any of the covariates, all p -values $\geq .16$). These results suggest that the initially observed result pattern remains rather stable when ERP effects are controlled for variance in performance within the young adults. It is thus unlikely that the observed ERP differences are confounded memory strength differences between conditions in young adults. Further, if the early ERP difference between plausible-old and implausible-old pairings would reflect enhanced processing fluency, it should also show up for plausible pairings without any memory history. But given that differences in response latencies between conditions only emerged for old and

⁵ An ANCOVA was performed, because it was impossible to match younger adults' performance across conditions without excluding a sustainable number of participants.

recombined, but nor for new responses, it is reasonable to assume that there is more than semantic fluency to this effect. We therefore assume, that condition-related early ERP differences are likely produced by different levels of unitization processing, rather than memory strength and semantic fluency differences. Moreover, a recent study, comparing associative recognition in young adults for compound (e.g., *greek-mythology*) and unrelated word pairs (e.g., *pool-letter*), also observed unitization encoding to enhance the contribution of both familiarity and recollection to later recognition (Zheng et al., 2015b). It was suggested that when familiarity is also high for recombined pairs (e.g., *greek-letter*) it is not sufficient for recognizing unitized associations and recollection might then be additionally required for discriminating old from recombined pairings (Zheng et al., 2015b). This assumption would also hold for the current data. We used semantically unrelated pairings whose configuration was manipulated and unitization of plausible pairs was likely to occur by means of gist information (e.g., action relations). Since these pairings were pre-experimentally rated to be equally plausible in the original (e.g., an axe above a hamburger) or recombined (e.g., a can opener above a hamburger) configuration (see Figure 11 in section 6.2), it is likely that gist information, and hence familiarity, was similar between old and recombined items, thus requiring additional recollection in the plausible condition.

The early difference between plausible-old and implausible-old pairings as well as the early old/new difference for plausible pairings were topographically more widespread as compared to the mid-frontal old/new effects typically observed in item recognition memory task. The more posterior distribution of the early old/new effect in the plausible condition may be due to the differential contribution of absolute and relative familiarity (see section 1.3.8). Absolute familiarity refers to the pre-experimental baseline semantic familiarity of an item, and relative familiarity to the episodic increment in familiarity beyond that baseline after the item has been presented in the study phase (Bridger et al., 2014; Mandler, 1980). These two signals are associated with topographically distinct early old/new effects: a frontal old/new effect reflecting relative familiarity and a posterior effect reflecting absolute familiarity (Bader et al., 2010; Bridger et al., 2014; Stenberg, Hellman, Johansson, & Rosén, 2009; Wiegand et al., 2010). It was proposed that absolute familiarity is very useful for recognition memory decisions in situations in which all stimuli are novel during learning, and the low absolute familiarity in turn is highly diagnostic for the recent occurrence in the study phase. In this vein, it is reasonable to assume that two unrelated objects positioned to each other in a spatially plausible way (e.g., a drill oriented towards a donut) are unique and engender a low sense of absolute familiarity that was highly diagnostic for the previous occurrence in the study phase and therefore associated with a more posterior distribution of the early old/new effect. Notably the posterior distribution of the old/new effects for spatially plausible pairs differs from the distribution of the early associative

familiarity effect for semantically related object pairs reported in our previous study (Tibon et al., 2014). One reason for this discrepancy could be that absolute familiarity was rather high for the semantically related pairs (e.g., a lamp on a table) in the latter study and by this less diagnostic for prior occurrence than the unique pairings in the present study. Accordingly, associative recognition of the related pairs in the Tibon et al. (2014) study may have relied more on relative familiarity, which is indexed by the early frontal old/new effect.

A related interpretation for the posterior distribution of the old/new effect in the plausible condition is that the processes that gave rise to the absolute familiarity effect are similar to those that give rise to the N400, an ERP component related to semantic access (Kutas & Federmeier, 2000, see section 1.3.7 for a discussion of the N400). Spatially plausible location-based information may have facilitated semantic access for these pairings and this facilitated semantic processing is reflected in the observed plausible-old/implausible-old ERP difference. To address this possibility, we performed the item-type-specific ERP contrast reported above for old items for new items as well. To this end, ERP waveforms evoked by new items were contrasted for plausible and implausible pairings in an Encoding Condition \times Location \times Laterality ANOVA in the early time window in young adults. The analysis revealed a marginally significant Encoding Condition by Laterality interaction ($F(2,38) = 3.11, p = .056$) that reflects an effect of Encoding Condition (plausible $>$ implausible) that was marginally significant at left hemisphere recordings ($F(1,19) = 3.86, p = .06, \eta_p^2 = .17$) but not at central and right recordings (p -values $\geq .17$). The topography of this Encoding Condition effect for new items together with the corresponding effect for old items for young adults (as reported in the result section 6.4.3) in the 300 to 500 ms time interval are illustrated in Figure 16. This comparison indicates that the item-specific ERP contrast for new items revealed more positive-going waveforms for plausible pairs, an effect that resembles the N400 which is always attenuated for semantically accessible items (Kutas & Federmeier, 2011). The corresponding effect for old pairings was larger and topographically more widespread, suggesting that the assessment of absolute familiarity for plausible pairs partly relies on processes that facilitated semantic access of completely new pairs without study history, as reflected in the N400, but cannot be equated with these processes.

Given that the plausible/implausible ERP contrast for old pairs was topographically different from that of new pairs, we suggest that our data speak more in favor of the unitization rather than memory strength/semantic fluency interpretation. Importantly, given that ERP effects do not differ as largely between conditions as reported in other unitization studies using encoding manipulations or related stimulus material (Bader et al., 2014; Rhodes & Donaldson, 2007; Tibon et al., 2014), we suggest that the current unitization manipulation engendered generally lower levels of unitization as compared to those studies.

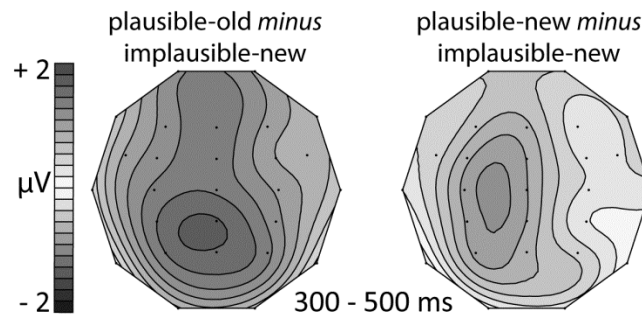


Figure 16 - Topographic maps of the plausible – implausible differences for old and new items in young adults.

Old adults

In old adults, the early old/new effect was present in the plausible condition only. Similar to Experiment 1, the early old/new effect was diminished in the elderly, suggesting an age-related degradation of its neural generators. Compared to the effect in young adults, it was also less topographically widespread and pronounced only at frontal and central electrodes. Additionally, as for younger adults, plausible-old items elicited a widespread and more positive-going deflection than implausible-old items in the early time window. Replicating findings from Experiment 1, the observed negativity in older adults for the implausible pairings in the early time window was modulated by memory performance, being larger in old adults that showed more of an associative memory deficit in the implausible condition. This suggests that subgroups of older adults engaged in qualitatively different strategies to retrieve associative information or to invest additional effort to cope with high task demands in the more difficult implausible condition, where reliance on familiarity was presumably less successful (Zheng et al., 2015a; Duarte et al., 2006; Friedman et al., 2010).

The diminished early old/new effect for plausible pairings together with the smaller plausibility benefit in old adults suggests that unitization-based familiarity is attenuated in old adults, and might contribute less to associative memory recognition than in young adults. The attenuated early old/new effects together with the smaller behavioral effect of spatially plausible object pairs on associative memory suggest that old adults benefit to a much lesser extent from the opportunity to create unitized representations during encoding, and have a weaker absolute familiarity signal to judge the prior occurrence of spatially plausible object pairings. Even though the exact reasons for this differentially small effects of plausibility-engendered unitization on associative memory and the corresponding ERP correlates remain to

be elucidated in further studies, we assume that the evident attenuation of these effects in old adults results from the way we manipulated unitizability. Given that unitizability critically depended on the processing of location-based information which is especially vulnerable in old age (Moffat, Zonderman, & Resnick, 2001; Klencklen, Després, & Dufour, 2012), probably due to a reduced hippocampus-dependent processing (Wimmer, Hernandez, Blackwell, & Abel, 2012), and was not supported by semantic factors such as the frequency of co-occurrence of two objects, the two objects may have been treated as two separate objects. This weak unitization strength may have imposed large demands on associative memory, which is in general strongly affected by old age. The data indicate that the effectiveness of unitization on old adults depends both on the type of materials to be encoded and on the methods of unitization.

Notably, in the implausible condition, no typical ERP old/new effect was observable in old adults, but rather a negative going old/new deflection at parietal sites, similar to the posterior negativity observed in Experiment 1 and previous studies (Duarte et al., 2006; Friedman et al., 2010; Zheng et al., 2015a). Since prior studies indicate that item familiarity is not affected (Eppinger et al., 2010) or only partly affected by aging as observed in Experiment 1, why was an early frontal old/new effect related to item familiarity in old adults not observed in the implausible condition? One explanation why we failed to observe an early frontal old/new effect for implausible pairs in old adults could be that encoding of objects oriented towards each other in an implausible layout was more shallow and less detailed, leading to variations in memory strength of the single components. Thus, without location-based contextual information that encourages unitization at encoding, memory strength for the single items would be weaker and less sensitive to differences in recognition memory strength. Another explanation for the failure to find the ERP correlate of familiarity in the implausible condition could be due to large opposing effects of the posterior negativity. This negativity could have overshadowed the early frontal positivity in the implausible condition, making it impossible to draw firm conclusions about its presence or absence in this condition. Moreover, controlling for variance of performance (as was done for young adults) to test for memory strength differences is also difficult, since the negativity is correlated with performance. Thus, we can only guess that the absence of an early frontal old/new effect in the implausible condition is likely produced by differences in memory strength, the posterior negativity or a combination of both. In light of the posterior negativity, an interpretation of the observed item-type-specific ERP difference between plausible-old and implausible-old in older adults is also problematic, as this difference is also likely provoked by the more negative going deflection of implausible-old pairs.

Given the limited topographical expansion of the old/new effect in the plausible condition and the difficulty to interpret old/new effects in the implausible condition, it is hard to say

whether older adults acquired unit familiarity or not. However, the observed ERP correlate of familiarity in the plausible condition in older adults together with their better memory performance in this condition suggests that encoding manipulations that encourage unitization indeed benefit older adults, but that it is not sufficient to overcome the age-related memory deficit, especially when young adults engage in unit familiarity and recollection to retrieve associative information at test.

6.6.3 Late ERP effects

In line with the assumption that recollection is more impaired by aging than familiarity, age differences in memory-related ERPs were particularly evident in the late time window, in which the ERP correlate of recollection can be observed. In both conditions, young adults showed a left parietal old/new effect, the ERP correlate of recollection related to the retrieval of associative information about the corporate appearance of components of the stimulus pair. In contrast, Bader et al. (2010) and Kriukova et al. (2013) reported an attenuated late parietal old/new effect in associative recognition tasks in situations in which unit familiarity is mnemonically diagnostic. This suggests that recollection may be dispensable when familiarity can contribute to associative recognition. In the current study, the ERP correlate of recollection was similarly observable in both conditions, though slightly larger in the plausible condition, despite the occurrence of unit familiarity in the plausible condition. Of note, Tibon et al. (2014), who used highly similar pictorial stimuli, similarly observed ERP correlates of recollection regardless of unit familiarity contributing to associative recognition. It was proposed that pictorial stimuli yield rich and vivid memory representations that are easily accessible via recollection as opposed to the word pair associates used in the Bader et al. (2010) and Kriukova et al. (2013) studies. Therefore participants might engage in recollective processing without extra effort, irrespective of whether unit familiarity is available to support recognition judgments.

As expected, older adults showed no ERP correlate of recollection. The absence of a late parietal old/new effect cannot be attributed to component overlap with the posterior negativity for old implausible pairings, as that negativity was most pronounced in the early time interval, and confined to implausible pairings. Rather, the absence of the ERP correlate of recollection together with the observation of an attenuated early old/new effect in old adults correspond with findings of larger age-related memory impairments of recollection than familiarity, and further add evidence to the assumption that strategic and effortful memory operations, such as recollection, are particularly vulnerable to aging (Craik, 1994; Friedman, 2013). These current findings, together with the larger age differences in associative than item memory, support the

view that impaired recollection is one of the main factors behind the associative memory deficit in older adults.

6.7 Conclusion

Taken together, our ERP findings reveal that the spatial-coherence associative information inherent in object pairs benefits associative recognition in young adults, but less so in older adults. Most strikingly, the ERP findings revealed that spatially coherent encoding manipulation affected the contributions of familiarity and recollection to associative recognition at retrieval. The early old/new effect, typically associated with familiarity, was attenuated in old adults, but importantly, the effect was larger and topographically different for plausible than implausible picture pairings in young adults. This suggests that an arrangement of objects in spatially plausible locations can encourage unitization at encoding and the contribution of familiarity to associative recognition in young adults. Even though familiarity signals degrade with age, the observed albeit smaller memory benefit and ERP correlate of familiarity in the plausible encoding condition in old compared to young adults advise the assumption that older adults also benefit from unitization engendered by spatial coherence even in the absence of semantic relatedness. Additionally, the posterior negativity in low performing older adults in the more difficult implausible condition suggests that aging is not uniform and performance variability in older adults might reflect the attempt to recruit alternative retrieval strategies or to invest additional effort when task demands are high.

VII EXPERIMENT 3

7.1 Introduction

The preceding unitization experiment revealed ERP differences between conditions for old (unit familiarity) and new (N400) item pairings in young adults that displayed a larger positivity for items of the plausible compared to the implausible category (see Figure 14). The item-specific ERP contrast of old items is assumed to reflect unit familiarity, since item information is assumed to be the same for plausible and implausible pairings and any ERP differences should thus be a product of enhanced associative strength between objects. The observed item-specific ERP contrast of new items, the N400, reflects the facilitated semantic integration of plausible compared to implausible pairings. The N400 is a negative going component that is reduced when semantic processing is facilitated and can be observed for all sorts of meaning-related stimuli (Kutas & Federmeier, 2011; see also 1.3.7). The N400 is not only sensitive to explicit but also to implicit manipulations, the latter of which are usually studied in priming paradigms (Kutas & Federmeier, 2011). The unit familiarity effect in Experiment 2 was dissociable from the N400, which made it rather unlikely that unit familiarity was confounded by fluency effects to plausible configurations. However, the N400 observation in the associative recognition task leads to the assumption that objects in a plausible arrangement can be integrated more semantically meaningful than objects in an implausible arrangement. More fluent processing of plausible pairings is presumably induced by the location-based or functional relationship between the single components, because the spatial layout of the objects was the only manipulation that differentiated a plausible from an implausible pairing. It is thus reasonable that the proper spatial arrangement inherently activated object schemata and facilitated encoding/recognition of plausible pairings. Since the N400 signal is typically investigated in priming paradigms comparing semantically related and unrelated material (see Kutas & Federmeier, 2011, for a review), it remains unresolved what exactly triggered the effect in the precedent experiment. To resolve this question it is important to understand how objects are processed in memory.

It is assumed that our memory is organized in structures that constitute typical scenes (Bar, 2004; Gronau & Bar, 2008). These structures are characterized by different types of object relations within scenes such as the co-occurrence of objects and its' functional and spatial relations. Semantic regularities exist about what kind of objects tend to appear together, how they are used and how they need to be located relative to each other in order to be useful. According to the functional grouping hypothesis (Green and Hummel, 2004) object schemata represent objects in spatial and functional relations, and due to experience with these objects, inter-object

relations are abstract and connected to variable arguments. Thus, functional relations between objects represent an important factor for the organization of the semantic network system.

Thus, object schemata place emphasis on meaningful spatial object relations (Mandler & Johnson, 1976) and guide information search in order to facilitate encoding and recognition (Bar & Ullman, 1996; Bar, 2004; Biederman, Mezzanotte, & Rabinowitz, 1982; Vö & Wolfe, 2013b). It is thus reasonable to assume that an object invokes expectations about the kind, location and orientation of other possible objects occurring in the same scene. Vö and Wolfe (2013b) showed that eye movements in a visual search paradigm are strongly guided by the semantic information provided by a scene (Vö & Wolfe, 2013b) and that violations of relations, i.e. when objects are located in a spatially improper manner within a scene, provoke slower target detectability (Bar & Ullman, 1996; Biederman et al., 1982; Vö & Wolfe, 2013b) and more erroneous target identification (Bar & Ullman, 1996; Bar, 2004; Biederman et al., 1982). Hence, schema consistent information is processed more efficiently than inconsistent information provoking memory differences at retrieval (Gronau & Shachar, 2015).

Semantic priming effects have been shown for different materials and object relations. For example, N400 effects differentiated between sequentially presented related (e.g., *knife-fork*) and unrelated (e.g., *cup-leave*) pictures. Further, Bach, Gunter, Knoblich, Prinz, and Friederici (2009) showed N400-like negativities for two objects in proper spatial relations, when either the functional relation (e.g., opening a *keyhole* with a *screen*) or the orientation between objects was mismatching (e.g., opening a vertical *keyhole* with a horizontally oriented *key*) compared to the match condition (e.g., opening a vertical *keyhole* with a vertically oriented *key*). Similarly, an enhanced N400 has also been observed during processing of incongruous compared congruous scenes (e.g., a soccer player shooting toilet paper rather than a ball) (Ganis & Kutas, 2003; Mudrik, Lamy, & Deouell, 2010; Vö & Wolfe, 2013a). Thus an “appropriate context may prime relevant semantic representations” (Ganis & Kutas, 2003, p. 142), thereby producing an attenuated N400. Priming effects have not only been observed on a conceptual level for semantically or functionally related material. For instance, Kan et al. (2011) investigated effects of novel associative priming for arbitrary object pairs that were presented simultaneously on the horizontal axis in either spatial separation or proximity. Associative priming is typically assessed in two steps including a study phase that exposes participants to the item pairs and subsequent test phase, that quickly (33 ms in the study of Kan et al., 2011) presents studied pairs in different combinations (old, recombined or new) and participants have to perform an unrelated task (e.g., perceptual identification as in Kan et al., 2011). Successful priming of associations is reflected in higher accuracy or shorter reaction times to old as compared to recombined pairs. Kan et al. (2011) reported enhanced test performance for arbitrary object pairs that were presented in

spatial separation. Importantly, this effect of associative priming was enhanced by spatial contiguity between objects, suggesting that spatial proximity of object pairs can facilitate the establishment of perceptually unitized representations (Kan et al., 2011).

Further, it has been shown, that also the orientation of objects influences whether they are processed conjointly or rather separately (Riddoch et al., 2011). Participants with parietal, frontal or subcortical lesions that suffered from spatial extinction showed reduced extinction effects under bilateral presentation (more detection of objects presented at contralesional sites), when (semantically related) objects were positioned in a plausible configuration, depicting an action (“e.g. the teapot was positioned as if it was pouring into a cup”, Riddoch et al., 2011, p. 581). Similarly, smaller extinction effects for action related objects were observed in patients regardless of the familiarity of the action (“e.g., wine bottle pouring into a wine glass” [or] “into a bucket”, Humphreys & Riddoch, 2007, p. 540). This indicates that attention switches from the ipsi- to contralesional presented stimulus were facilitated when objects were positioned in plausible locations for action. It was suggested that plausible action relations, regardless of the familiarity of the action, enable participants to encode object pairs as a unit configuration and overcome the extinction deficit (Humphreys & Riddoch, 2007). Healthy young participants also showed cueing effects for action-related objects when the cue portrayed a possible action, but not when the action was impossible (e.g., a whisk pointing upwards, since it is usually used in the opposite direction; Roberts and Humphreys, 2011). However, cueing and semantic priming reflect different aspects of cognition, namely attentional and meaning-related processing, but these processes seem to interact (Kutas & Federmeier, 2011): In a cueing paradigm, Roberts and Humphreys (2011) showed larger location cueing benefits for semantically related cue-target pairs, when the task instruction emphasized this relationship. In a semantic priming paradigm of selective attention, McCarthy and Nobre (1993) observed N400 effects only for words appearing in an attended spatial location, suggesting that the N400 is not automatically elicited but requires attention directed to the stimuli. Thus, attention can be guided by a manipulable object towards the second object and distributed to both members of the pair, supporting the configural encoding of the ensemble (Riddoch & Humphreys, 2011). Such object cues might activate action schemata that concern characteristics of objects such as information about its traditional purpose and where they are spatially located (Gallese & Lakoff, 2005). From this it is reasonable to assume that it is the action relation between objects that determines its’ encoding as unit. However, Gronau and Shachar (2015) showed that it is not the implied action that facilitates encoding of details and associative grouping of briefly glimpsed object pairings. Participants encoded object pairings that were semantically related or unrelated and part of an active (e.g., a teapot above a cup) or passive (e.g., a lamp above a desk) relation. Recognition performance was

better for semantically related than unrelated pairings and not influenced by action relations, suggesting that scenic information rather than action relations facilitates generating associative representations (Gronau & Shachar, 2015). However, Experiment 2 of this thesis showed that associative memory can also be improved when no semantic relation but rather a spatial plausible configuration is provided.

Taken together, there is evidence that different forms of object relations such as semantic, proper functional and/or spatial relations can facilitate object processing. Schematic scene information seems to allow each object within a scene to elicit expectations about the occurrence of other related objects. It is thus possible that the one object in the previous experiment could have acted as a prime for the second object in the plausible condition, even though they have been presented simultaneously. In contrast, an implausible array may have provided misleading cues violating expectations. To test whether solely the spatial arrangement of objects inherently activates schema knowledge and effectuates processing fluency, we conducted a sequential location priming experiment on the same stimulus material as in Experiment 2. We expected that location-based or functional priming facilitates object processing resulting in enhanced priming effects – that is faster response times and an attenuated N400 effect - for targets appearing in a plausible compared to implausible location.

7.2 Method

7.2.1 Participants

Twenty-five undergraduates from Saarland University participated in this study (10 males, 15 females). All participants gave their informed consent. To test whether the participants of the current priming experiment were comparable to those of Experiment 2 by means psychometric test performance, participants performed the same tests as in Experiment 2 subsequent to the priming task (1) the DS of the HAWIE-R (Tewes, 1991) (2) CST (adapted from Wechsler, 1955, 2008) and (3) the MWT (Lehrl, 1977; Lindenberger et al., 1993). The test results together with demographic characteristics of the participants are displayed in Table 7.

One participant was excluded from subsequent analysis, because of problems understanding the task, and three further participants that performed low on neuropsychological tests were excluded to statistically equalize performance on measures of fluid and crystallized intelligence between participants of Experiment 2 and 3. Thus, the final sample consisted of 21 participants (*mean age* = 24.3, *SD* = 2.7; 12 females). These participants showed same performance on the MWT and the CST as participants of Experiment 2 (all *p*-values \geq .39).

Despite excluding low performing participants, group differences in the digit symbol task that measures processing speed was still marginal significant ($F(1,40) = 3.18, p = .08$), revealing the tendency of participants of Experiment 2 to be better in that task. All 21 participants of the current experiment were right-handed (positive score on the Edinburgh Handedness Inventory; Oldfield, 1971), had normal or adjusted-to-normal vision and showed no signs of color-blindness or any psychiatric or neurological disorder. Participants did not differ from participants of Experiment 2 in their age and years of education (all p -values $\geq .52$) or in their sex distribution ($\chi^2(1) = 0.1, p = .75$).

Table 8 – Sample characteristics and psychometric test results for young adults of Experiment 2 and Experiment 3.

	Younger Adults Experiment 2	Younger Adults Experiment 3
<i>N</i>	21	21
Gender distribution (m/f)	8/13	9/12
Mean age (years)	23.7 (3.1)	24.3 (2.7)
Age range (years)	19-30	19-30
Education (years)	16.5 (2.5)	16.1 (2.3)
<i>Cognitive Variables</i>		
Digit Span Task	47.1 (5.6)	43.8 (6.5)
Counting Span	5.5 (2.2)	5.7 (2.1)
Multiple-Choice Knowledge Test	24.0 (4.9)	22.7 (6.6)

Note. Standard deviations are given in parentheses.

7.2.2 Stimuli

We decided to let participants make indoor/outdoor decisions in the priming task, since it was possible to equally often assign the single components of the 264 picture pairings of Experiment 2 to either the indoor or outdoor category. The single components were further assigned to either the prime or the target category (see Figure 17 for an example of prime and target stimuli).

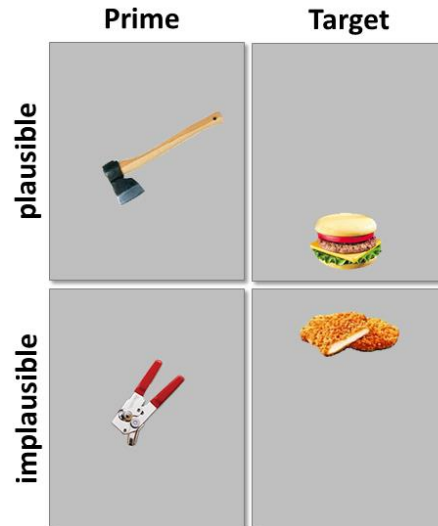


Figure 17 - *Examples of Stimuli and the spatial arrangement of primes and targets in the plausible and the implausible condition.*

These assignments were performed by three independent raters. Categorized as indoor were those objects that were more likely to be encountered in the majority of households rather than in the environment. A prime was defined as the object that is more informative about where on screen a second item would appear in order to depict a plausible configuration (e.g., an axe is more informative than a hamburger about the location of the second object, since an axe is usually placed above things in order to cut them, whilst a hamburger can be placed below, e.g. a hand, or above an object, e.g. a plate). We chose those stimuli (a) that had received a selective plausibility judgment (mean plausible rating above 4.23 and implausible rating below 2.34, for each pairings) at the study phase of Experiment 2 (b) for which a prime/target assignment was clear (c) for which we were able to counterbalance whether the item was an indoor or outdoor object and whether this category differed across prime and target (d) for which we were able to counterbalance whether the target was more likely to appear above or below the prime. These constraints were used to make sure that items within and across participants did not differ in plausibility and that items between conditions did not differ in relations known to influence semantic priming: spatial relations (target above/below) and categorical relations (indoor/outdoor).

With these constraints, 144 item pairings remained for the current experiment. These pairings were distributed to four sub-lists à 36 item pairs of similar mean plausible/implausible ratings. The sub-lists were paired with each other in a way to form two different lists à 144 items within which the assignment of plausibility and above mentioned spatial and categorical relations

was counterbalanced. Finally, within these lists the plausibility category was mirrored yielding four main lists that were randomly assigned to participants.

7.2.3 Procedure

As in Experiment 2, object stimuli were presented on a gray background on a 17"- display monitor with a viewing distance of approximately 65 cm. Prime and target stimulus size varied from 1 to 5 cm in height and 1 to 6 cm in length dimension (approximate visual angle of 0.9°-4.4° and 0.9°-5.3° respectively). Prime stimuli were presented centrally and target stimuli appeared with a 1 cm distance above/below the prime.

Participants saw a series of pictures on screen and were instructed that each trial consisted of two pictures of which the first one would appear at the center of the screen and the second one in the upper or lower part of the screen. Participants were required to attend each picture and to make an indoor/outdoor decision on the second picture of each trial by pressing 'c' or 'm' on a standard keyboard with the left or right hand. Assignment of indoor/outdoor to response buttons was counterbalanced across participants. Each sequence of a priming trial was composed of a 1000 ms fixation cross, a 400 ms prime presentation followed by a 200 ms blank screen and a 400 ms target presentation that was followed by 1100 ms blank screen during which a response could be made. Trials appeared in a continuous fashion with a SOA of 600 ms and participants were given 1500 ms for making an indoor/outdoor decision on the target. No shorter SOA was used because we wanted participants to integrally register these complex picture pairings and it has been shown that object-cueing effects are established relatively slowly (≥ 400 ms-SOA; Roberts & Humphreys, 2011). Four self-paced breaks were provided during the task. After the priming task, participants completed the same psychometric test as in Experiment 2 to ensure that participants of the current experiment did not differ from the former sample.

7.2.4 EEG recording

EEG recording and data processing was completely the same as in Experiment 1 (see section 5.2.3). Impedance of electrodes was kept below 7 k Ω .

Target items that did not receive a response did not enter analysis. The mean number of target trials for subsequent analysis was 43 (23-57) in the plausible and 45 (23-55) in the implausible condition.

7.2.5 Data Analysis

Usually faster mean RTs for primed compared to unprimed conditions are taken as evidence of successful priming (Gronau, Neta, & Bar, 2008; McPherson & Holcomb, 1999). However, mean RT differences across conditions are ambiguous and can reflect skewed or shifted RT distributions (Balota, Yap, Cortese, & Watson, 2008). Therefore, individual RTs were corrected for outliers to avoid a bias. We excluded all trials with more than ± 2 standard deviations away from mean RTs (collapsed across conditions). Nevertheless, mean RTs can be insensitive to subtle changes in semantic processing across conditions (Kutas & Federmeier, 2011) when the individual response pattern differs between conditions, i.e. when the trial-to-trial variation of fast and slow responses is different across conditions (Whelan, 2008). In this study we additionally afforded vincentized RTs and the intra-individual standard deviation of RTs (ISDRTs) – that are indeed correlated with mean RT, but associated with qualitatively different behavioral aspects (Jensen, 1992) - to discover underlying characteristics of behavioral priming effects that could potentially be obscured by mean RT analysis. Vincentized RTs allows the investigation of the distribution of response times across the trial course in each condition (Balota et al., 2008) and ISDRTs are usually understood as a measure of processing efficiency (MacDonald, Nyberg, Sandblom, Fischer, & Bäckman, 2008; Phillips, Segalowitz, O'Brien, & Yamasaki, 2004). For vincentizing RTs, each participant's data was rank-ordered from fastest to slowest within each condition. For each participant, mean RTs for every 10% quantiles of responses were averaged, such that ten quantiles (bins) were obtained. These individual quantiles were then averaged across participants for each condition resulting in vincentized distribution curves (Balota et al., 2008; Roelofs, 2012). As for mean RT latencies, we expected that ISDRTs were smaller and vincentized RTs were shifted for targets appearing in a plausible location compared to implausible prime-target pairings.

Behavioral data analysis then comprised repeated measurement analysis of variance (ANOVA) on mean RTs and ISDRTs with the factor Encoding Condition (plausible, implausible). We further conducted an Encoding Condition \times Quantile ANOVA on vincentized RTs (Balota et al., 2008; Roelofs, 2012).

Figure 18 illustrate averaged ERPs at three representative electrodes. For ERP data analysis repeated measurement ANOVAs were conducted on mean amplitudes in a 300-500 ms time window from frontal (F3/Fz/F4), central (C3/Cz/C4) and parietal (P3/Pz/P4) locations with the within-subject factors Encoding Condition (plausible, implausible) \times Location (frontal, central, parietal) \times Laterality (left, midline, right). We report only main effects and interactions including the factor Encoding Condition. For subsequent contrasts one-way ANOVAs or t-tests

were performed. Whenever sphericity was violated, the corrected p -values (according to Greenhouse-Geisser method; Greenhouse & Geisser, 1959) were reported together with uncorrected degrees of freedom.

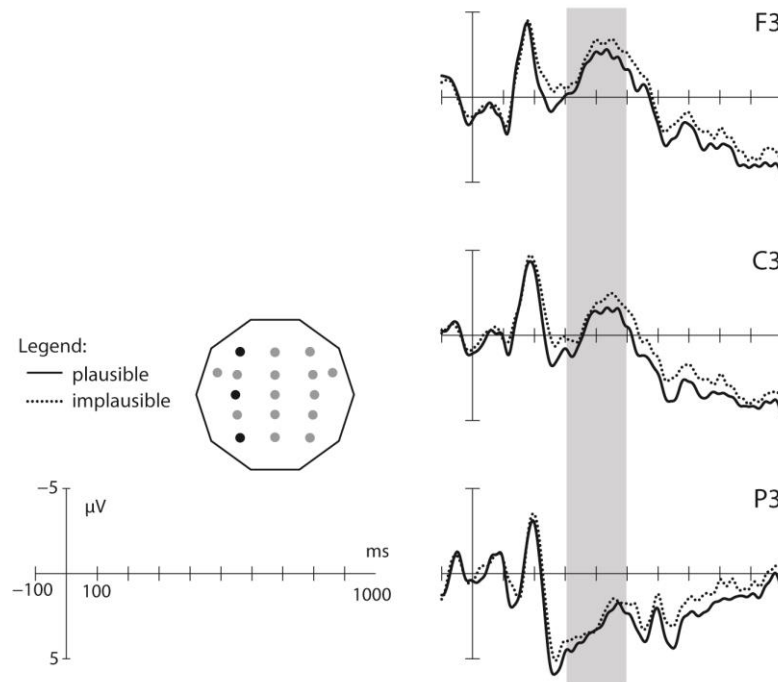


Figure 18 - Grand average ERPs of plausible-new and implausible-new pairs. Grey shading denotes the 300-500 ms time-window.

7.3 Results

7.3.1 Behavioral Results

For mean RTs, an ANOVA on levels of Encoding Condition revealed no main effect of Encoding Condition ($p = .19$). For vincentized RT data an Encoding Condition \times Quantile ANOVA did not show a main effect or interaction including the factor Encoding Condition ($p \geq .40$). An ANOVA on the levels of Encoding Condition for ISDRTs revealed a main effect Encoding Condition ($F(1,20) = 8.50, p < .05$), that unexpectedly followed a plausible $>$ implausible pattern.

7.3.2 ERP Results

An Encoding Condition \times Location \times Laterality ANOVA on ERP mean amplitudes revealed no main effect of Encoding Condition ($p = .40$), but a marginal significant interaction of Encoding Condition \times Laterality ($F(2,40) = 2.98, p = .06$). Even though visual inspection suggests a left-lateralization of the effect, the decomposition of the Encoding Condition \times Laterality interaction revealed no significant ERP effect at any level of Laterality (left: $p = .17$, midline: $p = .49$, right: $p = .75$).

7.4 Discussion

The primary goal of this study was to investigate what triggered the attenuated N400 effect for plausible pairings in young adults in Experiment 2, when objects were presented corporately. We assumed that location-based or functional priming, due to the configuration of objects being directed towards or away from each other, could inherently have facilitated semantic guidance and attenuated the N400. Thus, the stimulus material of Experiment 2 was presented in the current study consecutively as prime-target pairs, requiring an indoor/outdoor decision on target items. Behavioral as well as ERP results do not give evidence for priming of plausible object relations.

ERP analysis did not reveal N400 modulations by the plausibility of the prime target pairing. This was unexpected given that we observed an attenuated N400 following plausible pairings in Experiment 2. It is unlikely that the current null-finding can be attributed to sample differences between Experiment 2 and 3, since the same number of young adults participated in these studies and groups were matched on neuropsychological tests across experiments. Probably, plausible prime-target pairings are not inherently powerful enough to generate bottom-up semantic priming effects. Experiment 3 differed from Experiment 2 in two main manipulations, the first one is the sequential versus simultaneous presentation of stimuli and the second one refers to the encoding instruction. Since modulations of the N400 have been observed in paradigms with simultaneous (Ganis & Kutas, 2003; Mudrik et al., 2010) as well as sequential stimulus presentation (McPherson & Holcomb, 1999; Philips et al., 2004; Bach et al., 2009; Kutas & Federmeier, 2011; Bridger et al., 2012), it is tempting to assume that it was the encoding instruction rather than the presentation type that facilitated semantic integration of plausible pairings in Experiment 2. Encoding instructions in Experiment 2 guided attention towards the interactive object-to-object relation, thus creating a context in which participants attempted to find meaning in semantically unrelated item pairings, whereas encoding in

Experiment 3 required an indoor/outdoor decision and was thus more shallow with respect to the location-related prime-target association. Since the indoor/outdoor decision was required only on the target object, it is possible that prime information was less well encoded. Importantly, another ERP study showed that semantic violations during scene processing (e.g., observing a soap at the expected location of a computer mouse in front of the computer) produced a larger N400 compared to semantic consistencies (e.g., observing a computer mouse at its expected location in front of the computer) and compared to syntactic violations (e.g., observing the computer mouse at an unexpected location) (Võ & Wolfe, 2013a). However, since we only used semantically unrelated stimuli and manipulated the location-based (or syntactic) information between pairings, the observed attenuation of the N400 for plausible pairings in Experiment 2 might have been the result of the (semantic) context provided during encoding, that allowed participants to meaningfully integrate semantically unrelated objects that were presented in proper syntactic locations and that attenuated the N400 for plausible pairings at test.

Turning to the behavioral analyses, results did also not exhibit reaction time differences between conditions for mean RTs and vincentized RTs, but differences between ISDRTs revealed an unexpected pattern, namely larger latencies in the plausible than implausible condition. Does this mean that processing of implausible prime-target relations is facilitated? Interestingly, Green and Hummel (2005, 2006), observed a similar response pattern: They investigated whether object identification is influenced by the functional relationships between objects in a priming paradigm. Participants were given a word label (e.g., glass), followed by a sequential brief presentation of line drawings of the distractor (e.g., pitcher) and of the target (glass) and they had to indicate whether word label and target picture were matching or non-matching. The critical manipulation concerned the distractors identity and its spatial presentation, creating different functional distractor-target relations: the distractor was either semantically related or unrelated to the target and arranged as to work or not to work with the target picture. Green and Hummel (2005, 2006) observed that a functionally plausible distractor-target configuration benefited target identification when distractor and target were semantically related, whereas it impaired identification for semantically unrelated targets. Gronau et al. (2008) conducted an fMRI experiment on a similar priming paradigm with colored photographs of objects to investigate whether semantic and spatial relations between objects are processed separately or conjointly in memory. Semantic relations contained information about which objects are likely to co-occur (e.g., an office desk and a computer) and spatial relations contained information about where in scene objects are likely to occur (e.g., “a phone is typically placed above, and not below desks” Gronau et al., 2008, p. 371). In this priming paradigm, also a semantic by spatial relation interaction effect was observed that was reflected in larger reaction

times and neural response enhancement for semantically unrelated but spatially plausible compared to semantically unrelated but spatially implausible prime-target pairings. These results support the assumption that semantic features and meaningful relations between objects are functionally grouped and represented within a unified schema (Green & Hummel, 2004; Gronau et al., 2008). Semantic and spatial object knowledge interacts and can either benefit or impair object identification, depending on object semantics (Green & Hummel, 2006). Thus, when objects are semantically and functionally related, object-to-object associations can be rapidly and efficiently processed (Gronau & Shachar, 2015). However, when objects are semantically unrelated, but are arranged as to work together (Green & Hummel, 2005) “greater neural resources [are] required to process an unexpected object identity appearing in an expected location” (Gronau et al., 2008, p. 380). Importantly, it was suggested that this inhibitory effect of semantically unrelated pairs being presented in spatially plausible locations was due to the inclusion of semantically related pairs at encoding (Gronau et al., 2008). By this it was argued that participants formed specific expectations about the semantics of a target that could have counteracted the spatial relation between objects. Our current findings however suggest that the formation of semantic expectations reflect a general tendency and occurs even in the absence of semantic information. The observed implausible < plausible pattern of ISDRTs – that are associated with processing efficiency and smaller ISDRTs reflect more efficient processing (McDonald, 2008; Philipps et al., 2004) - in the current study are thus in line with the abovementioned findings from Green and Hummel (2005, 2006) and Gronau et al. (2008) and suggest that implicit processing of plausible target locations is less efficient when prime and target are unrelated.

Since ERP and behavioral results did not reveal the expected priming effect, we tested whether variance in reaction times across conditions can account for ERP differences, i.e. whether some participants that show the behavioral plausible < implausible priming effect, also show the N400 attenuation following plausible targets. There was indeed a correlation between the N400 effect (ERP difference plausible – implausible, collapsed across all levels of Location and Laterality) and mean RT differences (plausible – implausible) ($r(21) = .44, p < .05$). Interestingly, this correlation was not driven by a relation between RTs and the N400 in the plausible condition ($p = .12$), but rather by a relation between RTs and the negativity of the ERP deflection to implausible targets ($r(21) = .45, p < .05$). This depicts that faster reaction times on implausible targets co-vary with a more negative going deflection of the N400 to implausible targets, suggesting that when expectations are highly violated by improper semantic and spatial relations, implausible targets can be processed more efficiently causing faster response latencies.

In line with the behavioral findings from Gronau and Shachar (2015) and Green and Hummel (2005, 2006), the current results suggest that the prime inherently generated expectations about semantics of the target (i.e., object identity) and its location (i.e., appearing above or below) and these expectations might have been violated whenever the target-location was plausible (violation on semantics) or implausible (violation on semantics and object location). When location-based information was plausible, participants might have focused on the semantic relationship between objects and experienced a conflict. However, when expectancies were violated by semantics and object locations – as is the case in the implausible condition – location violation might have off-set the pronounced impact of semantic knowledge that was activated by the cue allowing faster decisions performed on the target.

To summarize, the current priming experiment adds evidence to those studies suggesting a joint influence of semantic and spatial factors on the efficiency of associative processing (Green and Hummel, 2005, 2006; Gronau and Shachar, 2015; Gronau et al., 2008). It shows that solely the orientation of objects towards each other does not suffice to generate bottom-up semantic priming effects. It is probable that unrelated stimuli only benefit from plausible spatial configuration when they can be encoded within a context that promotes giving a meaning to the configuration (i.e., when encoding instructions focus on location-based object relation) allowing participants to actively link these objects to one integrated percept/representation.

VIII GENERAL DISCUSSION

The global purpose of this thesis was the exploration of age-related changes in episodic memory retrieval with a particular focus on the process of familiarity and its putative role in counteracting age-related memory differences. This was based on findings showing that experimental manipulations that particularly support familiarity-based remembering can decrease age-related memory deficits (Bastin & Van der Linden, 2003; Bastin et al., 2013). Despite the general assumption that recollection is impaired while familiarity remains rather intact with age (Koen & Yonelinas, 2014a, 2014b), previous reports on age effects on the ERP correlate of familiarity instead depict a more ambiguous picture (Ally et al., 2008; Duarte et al., 2006; Morcom & Rugg, 2004; Wang et al., 2012). Thus, another aim of this thesis was to investigate whether changes in the early frontal old/new effect occur under conditions which best foster familiarity-based recognition.

For this purpose, we created experimental task settings that were supposed to facilitate recognition of item and associative information based on familiarity and by this reduce memory impairments in older adults. In all experiments conducted within this thesis, perceptually rich colored object pictures were used that were expected to disproportionately support recognition memory strength in old adults and ERPs were recorded. In Experiment 1, we added a response deadline manipulation to foster the contribution of familiarity to item recognition. In Experiment 2, we manipulated the unitizability of two arbitrary objects by its spatial locations and expected a spatially plausible arrangement to promote unitization at encoding and hence facilitate familiarity-based memory at retrieval. Experiment 3 was performed as a follow-up of Experiment 2 to more thoroughly explore what has triggered the N400 fluency signal in young adults for semantically unrelated object pictures that were presented in a spatially plausible arrangement.

In the following sections the main findings of all three experiments will be summarized and its theoretical implications will be discussed with respect to the initially formulated research questions. Then conceptual limitations of these experiments and an outlook of possible directions for future research will be provided, before a general conclusion is drawn.

8.1 Summary of main findings

In Experiment 1, we have shown that age-related impairments in recognition memory are reduced under conditions in which the dependence on recollection is attenuated and recognition judgments are primarily driven by familiarity. Young and old adults performed a recognition

memory task with colored object stimuli under speeded and non-speeded response conditions. Supporting the view that limiting the time to respond attenuates recollection but leaves familiarity largely unaffected, age effects on memory performance were substantial in the non-speeded condition and negligible in the speeded condition. Additionally, the ERP correlate of familiarity was present in both conditions in both groups, though smaller in amplitude in old adults, while the ERP correlate of recollection was completely absent in older adults in both conditions. At the same time, in the speeded condition, a posterior negativity that varied with memory performance emerged for elderly and was interpreted as an adaptive strategy to account for the increasing task demands in the more difficult condition.

In Experiment 2, we have shown that spatial coherence of arbitrary object pairings can facilitate associative memory in young and older adults, but does so to a smaller extent in the latter group. ERP results indicated that the early old/new effect was attenuated and only evoked in the plausible condition in old adults, while the ERP correlate of recollection was completely absent in this group. Further, as in Experiment 1, older adults showed a posterior negativity in the more demanding implausible condition. In young adults, the early old/new effect was larger and topographically more widespread distributed for plausible than implausible pairings and the ERP correlate of recollection was similarly observable in both conditions. Additionally, we observed an early plausible/implausible effect for old items in both age groups that was dissociable from a plausible/implausible effect for new items (N400). We suggest that these findings demonstrate that spatial object information even in the absence of a semantic relationship enhances familiarity-based associative recognition.

In Experiment 3, plausible and implausible object pairings were presented consecutively as prime-target pairs to test whether the spatial coherence between objects produced the N400. Neither ERPs nor behavioral results revealed the expected priming effect, but one RT measure showed an unexpected plausible > implausible effect, suggesting that merely location-based information is not sufficient to produce effects of fluency.

8.2 Can older adults overcome age-related deficits in episodic memory under conditions that facilitate familiarity-based remembering?

The results of Experiment 1 and 2 clearly show that older adults benefit from manipulations that facilitate familiarity-based recognition. In the non-speeded response condition where both familiarity and effortful recollection can contribute to recognition decisions, older adults perform worse than young adults. However, when response time was limited and

recognition performance relied mainly on familiarity, age-related memory differences were largely reduced in comparison to a condition with unlimited response time, and elderly participants showed equal performance to young adults. This strongly suggests that a response-deadline procedure is a powerful manipulation that can reliably reduce age-related memory differences by enhancing familiarity-based recognition. This further supports the assumption that impaired recollection is the main contributor to the age-related episodic memory impairments and that reduced retrieval control requirements can elevate this age deficit.

In Experiment 2, we expected unitization encoding to reduce the age-related associative memory deficit and manipulated the spatial plausibility of object pairs. Spatial plausibility benefited both, young and old adults. Importantly, the benefit was actually smaller in older than young adults, leading to larger age-related differences in the plausible condition, which was assumed to promote unitization, compared to the implausible condition. This finding is in contrast to other studies that reported unitization encoding to effectively reduce the associative memory deficit in older adults (Ahmad et al., 2014; Bastin et al., 2013; Zheng, et al. 2015a). These studies provided either appropriate encoding instructions that fostered the creation of intra-item associations (between a word and its background color) or pre-experimentally associated compound words to manipulate unitization encoding. Such manipulations seem to effectively reduce the need for self-initiating encoding strategies. The finding of larger age-related associative differences in the putative supportive condition suggests that the provided schematic support inherent in a spatially plausible object arrangement was not sufficient to reduce older adults' difficulty in creating and retrieving associations between arbitrarily paired items and older adults were required to self-initiate appropriate encoding and retrieval strategies. That plausible pairs do not inherently provide schematic support can be concluded from results of Experiment 3. In this study, plausible and implausible object pairings were presented to young adults sequentially in an implicit priming task and a plausible prime-target relationship did neither elicit a behavioral priming effect nor an N400 effect, indicating that a plausible configuration per se does not facilitate processing. As such, what might have facilitated unitization encoding in young and old adults was the encoding instruction that emphasized the evaluation of the relationship between the paired objects. Importantly, as discussed in section 3.3, when encoding is intentional and does not explicitly state how to process arbitrary item pairings, then participants must self-initiate the appropriate processing and thus older adults are at a disadvantage compared to younger adults (Naveh-Benjamin et al., 2009).

In cases when information is arbitrary and incongruent with existing schemata, binding depends largely on the HC and prefrontal mediated strategic processes (Brod et al., 2013; Opitz, 2010; Van Kesteren et al., 2012, see section 1.3.3) whose function is largely affected by aging

(Daselaar et al., 2006a; Raz et al., 2005, see section 1.3.4 and 1.3.5). Additionally, processing location-based information was especially critical to build unitized representations, which is also vulnerable in old age (Moffat et al., 2001). As a consequence, older adults potential to bind multiple information might largely depend on its congruency with pre-existing schemata (Ofen & Shing, 2013; Van Kesteren et al., 2012). Since we used only semantically unrelated pairs whose co-occurrence is incongruent with pre-existing semantic knowledge, binding mechanism in older adults might have been largely reduced.

Also, previous studies have shown that the age-related associative memory deficit can be reduced when older adults are trained in using strategies such as interactive imagery or meaningful sentence generation during encoding of word pairs (Naveh-Benjamin et al., 2007; Shing & Lindenberger, 2011; Shing et al., 2010). Since the current unitization manipulation can be regarded as an externalized instantiation of visual imagery, it is likely that a strategy training of participants would have particularly facilitated associative recognition in older adults, by reducing demands on self-initiating such effortful mental operations. Further, since Experiment 1 has impressively demonstrated that speeded responding can reliably reduce age-related recognition performance differences, applying a response-deadline in Experiment 2 either at study or test, might have enhanced unitization of plausible object pairs in older adults.

Similarly to the current findings, another study from our lab reported larger age-related memory deficits for highly similar face stimuli that were expected to encourage the formation of unitized face representations as compared to arbitrarily paired faces (Jäger et al., 2006). This may suggest that participants were able to compensate their associative memory deficit for arbitrarily paired faces but less so in the unusual situation of highly similar face pairs. Hence, the unexpected results regarding age effects on unitization in Experiment 2 suggest that unitization is very sensitive to specific conditions and whether associations are processed as separate items or as a unit may depend on individual differences in the use of encoding and retrieval strategies and the prior experience with the materials (see also Parks & Yonelinas, 2015, for similar arguments).

Taken together, we were able to show that a response-deadline manipulation that strongly fosters the use of familiarity during recognition can effectively support older adults to counteract reduced recollective processing. The findings of Experiment 2 support the view that unitization engendered by spatial coherence can enhance associative memory for older and young adults by promoting familiarity-based processing, but does so more effectively for the latter group. Thus, the observation of greater age-related associative differences in the unitization encoding condition strongly suggests that the beneficial effect of unitization manipulations in elderly is sensitive to subtle changes in task demands and may largely vary with the type of stimuli and the

type of encoding instructions that was used. Nevertheless, our results suggest that older adults can also benefit from facilitated unitizability by the spatial plausibility of objects at encoding even when there is no semantic relationship between them.

8.3 Is the ERP correlate of familiarity affected by aging?

In Experiment 1 and 2 the early frontal old/new effect, the putative ERP correlate of familiarity, was reliably present in older adults, while the late parietal old/new effect, the putative ERP correlate of recollection, was absent in old adults in both experiments. This is in line with previous findings showing that recollection is more affected by aging than familiarity and consequently that the late parietal old/new effect is particularly reduced or absent in older adults (Eppinger et al., 2010; Friedman et al., 2010; Morcom & Rugg, 2004).

One factor which is thought to contribute to attenuations in recollection for older adults is the fact that this group processes retrieval cues differently or less efficiently than young adults. In support of this view, Morcom and Rugg (2004) reported that an ERP measure of retrieval cue processing, differences between ERPs elicited by new words in retrieval phases which required participants to target the recovery of either verbal or pictorial memory contents, was smaller and shorter in its temporal extension in old adults. Although correlates of retrieval cue processing were not assessed in the current experiments because participants were required to target the recovery of similar classes of information in each test block, it is conceivable that processes set in train upon the presentation of a retrieval cue which may influence the likelihood of recollection are engaged to a lesser extent in the elderly.

Moreover, impaired recollection in old adults might also be a consequence of structural changes in recollection-related brain regions. Evidence for this latter view comes from a combined MRI and ERP study with old adults (Schiltz et al., 2006, already described in section 1.3.4) in which a positive correlation between hippocampal diffusion, a measure of hippocampal integrity, and the late parietal old/new effect was reported. The higher reliance of older adults on familiarity may thus either be a consequence of a general impairment in cognitive control processes required for the adoption of cue processing strategies, structural modification in recollection-relevant brain regions or a combination of both factors (Duverne, Motamedinia, & Rugg, 2009).

However, the finding of an ERP correlate of familiarity in Experiment 1 and 2 adds evidence to those studies showing that the use of colored pictures as stimuli (Ally et al., 2008; Eppinger et al., 2010; Morcom & Rugg, 2004), which allow the formation of highly detailed and

distinctive memory representations (Gallo et al., 2004; Paivio & Csapo, 1973), produces an early frontal old/new effect in older adults (Ally et al., 2008; Eppinger et al., 2010; Morcom & Rugg, 2004). Ally et al. (2008) for example reported that, whereas words elicited a reduced early frontal old/new effect in old adults, a larger effect was obtained when colored pictures of nameable objects were used as stimulus materials (see also Eppinger et al., 2010), suggesting that familiarity is sensitive to the perceptual richness of these stimuli (Wang et al., 2012).

In both experiments however, the size of the early frontal old/new effect was attenuated compared to young adults, even though task requirements were supposed to facilitate familiarity-based recognition. Importantly, the attenuated early frontal old/new effect in old adults was accompanied by reduced recognition performance in Experiment 2, but not in Experiment 1. How could this disconnection between performance and the size of the early frontal old/new effect come about? One possibility is that despite a weaker overall memory signal, elderly individuals are better practiced at using familiarity to make old/new judgments. Another possibility is that the physiological sequelae of aging make it more difficult to record familiarity-based electrophysiological signals in the elderly. Similarly, given the view that familiarity is multiply-determined (Bridger et al., 2014; Mecklinger et al., 2012; Rugg & Curran, 2007, see section 1.3.8), it is possible that only some of the component processes associated with familiarity - and which elicit the early frontal old/new effect - degrade with age (Wang et al., 2012). The suggestions put forward here do not necessarily oppose one another, and it is possible that a combination of all three factors is at play. Furthermore, it is reasonable to assume that the emergence of a familiarity signal is highly reliable when recognition memory requires merely decisions about single items, particularly when these decisions have to be made that fast that the contribution of additional recollective processing is reduced, allowing older adults to perform similar to young adults. In contrast, familiarity might be a less reliable source for recognizing the previous encounter of arbitrarily paired items, especially when these pairings produced lower levels of unitization at encoding.

In Experiment 2, we observed that only plausible but not implausible pairings evoked an ERP correlate of familiarity in older adults. As discussed in detail in section 6.6.2, the absence of an early frontal old/new effect in the implausible condition might be due to opposing effects of the negativity to the early frontal effect in the implausible condition and additionally or alternatively due to a weaker familiarity strength signal for single items, because encoding conditions did not encourage unitization and hence later familiarity-based retrieval. Notably, a recent ERP study on unitization in older adults (Zheng, et al. 2015a) that used compound word pairs representing pre-existing unitized associations, reported an early old/new effect in older adults also only in the unitization but not in the non-unitization encoding condition. Since

already unitized word pairs provide powerful schematic support, the age-related associative memory deficit was reduced for compounds compared to arbitrary word pairs. It was suggested, in accordance with the behaviorally reduced associative memory impairment in old adults, that unitization encoding enhanced the contribution of familiarity to recognition of associated items and alleviated age-related memory differences. This suggests that the emergence of the early frontal old/new effects in older adults is highly dependent on task manipulations and that it can be observed when task requirements encourage the contribution of familiarity to recognition.

Taken together, in line with behavioral results, the ERP results of Experiment 1 and 2 suggest that the ERP correlate of recollection, that was absent in the elderly in both recognition experiments, is more impaired than the ERP correlate of familiarity. Additionally, these findings provide strong evidence that the ERP correlate of familiarity can reliably be recorded using colored pictures as stimuli that allow the formation of perceptually rich and distinctive memory traces and when the task conditions promote recognition based on familiarity. The results further suggest that, despite these manipulations, the familiarity signal is reduced in older adults and this might reflect the neural degradation of its generator or a qualitative change in the nature of the signal.

8.4 Did older adults use unitization in Experiment 2?

In case of the young adults, the results show a larger and topographically more widespread distributed early old/new effect for plausible compared to implausible pairs and a widespread plausible-old/implausible-old ERP effect. Importantly, the observed plausible-old/implausible-old effect is topographically dissociable from an attenuated N400 effect for plausible compared to implausible new pairings, suggesting that it depicts a memory effect rather than facilitated semantic processing of functional object knowledge. Hence, these early ERP findings suggest that young adults differentially process plausible and implausible pairings, most likely by engaging in higher levels of unitization for plausible object pairs. This is in line with the behavioral results, showing a large benefit for plausible compared to implausible pairings in young adults.

In Experiment 2, the early old/new effect in the plausible condition in old adults was not only diminished in amplitude, but also less topographically distributed than the early old/new effect in young adults and only present at frontal and central sites. Additionally, the observed plausible-old/implausible-old ERP effect in old adults cannot unequivocally be linked to familiarity-based processing in this group, due to the pronounced negativity in the implausible

condition. As such, the more negative-going deflection of implausible-old pairs could have accounted for this ERP effect rather than greater familiarity for plausible-old pairs.

Still, the ERP correlate of familiarity in the plausible condition in older adults together with their better memory performance in this compared to the implausible condition indicates that older adults beneficially used the information provided by spatial object coherence for their associative recognition decisions. Following the assumption that unitization operates in a continuous fashion and its memory products can vary between high and low levels of unitization (Parks & Yonelinas, 2015), the current finding might suggest that spatial plausibility engendered lower levels of unitization in old compared to young adults. In contrast to other studies that used different unitization manipulations and that observed a reduced age-related associative memory deficit in the high unitization encoding condition (Ahmad et al., 2014; Bastin et al., 2013; Zheng, et al. 2015a), it seems that the current unitization manipulation was insufficient for older adults to engender high levels of unitization. By this, engaging in lower levels of unitization, older adults cannot efficiently counteract the age-related associative memory deficit, especially when recollection and higher levels of unitization support associative recognition in young adults.

Nevertheless, our results suggest that (unit) familiarity can still support associative recognition in old adults when the contextual layout of an object scene displays a plausible configuration.

8.5 What does the early posterior negativity in older adults reflect?

In Experiment 1 and 2, we observed a posterior negativity in older adults that was elicited by hit responses at around 300 ms and extended for several hundred milliseconds. The negativity was associated with memory performance and larger in low performing older adults. In each case, the negativity was particularly present in the more demanding task condition, that is the speeded response condition in Experiment 1 and the spatially implausible condition in Experiment 2.

In its topographic characteristics, this negativity resembles the so-called late posterior negativity (LPN), a bilateral posterior negativity which is elicited primarily in tasks that require the retrieval of source information (Johansson & Mecklinger, 2003) and is thought to reflect the search for and retrieval of bound information from a prior study episode. The temporal dynamics of the LPN and the here reported posterior negativity are somehow different. While the LPN starts at around 600 ms (Johansson & Mecklinger, 2003), the posterior negativity in the current studies demonstrates an earlier onset (~300 ms). Further, the left-lateralization and the

lack of any explicit source retrieval requirements in Experiment 1 make an LPN interpretation of the current posterior negativity unlikely, however.

In several respects however, the negativity in the present study resembles posterior slow waves reported in other ERP aging studies. Using a source memory task in which subjects had to indicate the study context in which a picture was presented, Li, Morcom, and Rugg, (2004) found a pronounced posterior and left-lateralized negativity for correct source judgments that partly obscured the parietal old/new effect and that was only present in older adults. The authors took this negativity to reflect the over-reliance of old adults on the retrieval of visually-based information as opposed to young adults who relied mainly on the retrieval of conceptual information. The assumption that older adults show a predisposition to retrieve visual rather than more abstract, conceptual knowledge was also discussed by Ally et al. (2008). They observed parieto-occipital slow wave activity during a recognition memory task for verbal stimuli that was present in the old but not young adults. Ally and colleagues speculate that older participants may be aware of their degraded verbal memories and attempt to retrieve more visual perceptual information to compensate for their poor verbal memory.

By this, the observation of the posterior negativity in the more demanding task conditions questions whether this effect can be deemed as compensatory or inefficient processing. For instance in Experiment 2, the posterior negativity was observed merely in the implausible (low unitization) condition, where age-related differences were less pronounced than in the plausible (high unitization) condition. Similarly, Jäger et al. (2010), who tested associative recognition memory for face-pairs, representing either physically different photographs of the same person (high unitization) or different persons (low unitization), also reported age-related differences to be smaller in the low than in the high unitization condition. However, they observed that high performing older adults showed similar performance as young adults in the low unitization condition, suggesting that they could effectively counteract the associative deficit in this condition. It was suggested that older adults effectively engaged in compensational strategic processes to create associations between items in more difficult task conditions that are likely to benefit more from such mnemonic operations. As a consequence, age-related performance differences were particularly pronounced in the unitization condition. However, on the basis of the current relationship between memory performance and the size of the posterior negativity that is larger in low performing older adults, a compensational mechanism may not account for the observed negativity in Experiment 1 and 2.

Thus, the current negativity may reflect inefficient processing. It is worth speculating whether it reflects attempts to recruit alternative retrieval strategies to cope with the high task

demands in the speeded and the implausible condition in Experiment 1 and 2, respectively (see section 5.5.4 and 6.6.2). Low performing older adults may have relied more on assessing sensory features of memory traces, which facilitates familiarity-based remembering. The fact that the negativity onsets at around the time the ERP correlate of familiarity is usually observed and also the observation that the regression analyses in Experiment 1 and the overall ANOVA in Experiment 2 revealed significant results only for the early (300-500 ms) time interval is consistent with this view. Such an explanation would also be consistent with the possibility considered in section 5.5.1 that older adults invested additional effort in the more challenging task condition, and this may especially be the case for the low performing older adults. To what extent the posterior negativity reflects attempts to retrieve more visual perceptual information or more effortful processing in the more demanding task condition or a combination thereof cannot be unambiguously decided with the data at hand.

To summarize, the occurrence of the posterior negativity predominantly in older adults suggests that this effect is age-associated. Additionally, the finding that the negativity is larger in low performing older adults while high performing older adults show a more similar ERP pattern to young adults, is in line with the concept of brain maintenance (see section 1.3.5), that suggests that minimized changes in the aging brain play a key role in successful memory development in aging (Nyberg et al., 2012).

8.6 Limitations and open issues

One limitation of the studies of this thesis is that age-related memory differences are tangled with cohort effects and other factors, such as socio-economic status and experience in performing these types of experimental tasks. However this limitation refers to all cross-sectional developmental investigations. Though we surveyed the educational level (in years) and the neuropsychological status of our participants in all experiments and mainly recruited elderly that were already experienced with participating in aging studies at Saarland University, cohort effects may still play an unknown role.

Further, the present thesis aimed at investigating age differences in episodic memory processing at recognition. Admittedly, differences between young and old adults can already occur at encoding and refer mainly to the ability in using elaborative and effective encoding strategies. Age-related differences at encoding may produce less distinctive memory representations and in turn aggravate later recognition (Grady et al., 1995; Ofen & Shing, 2013, see also section 1.2). However, we recorded the plausibility rating in Experiment 2 at study, a

factor that was expected to influence unitization and later recognition, and did not find an effect of age differences at study to differences at the recognition test. Though, such behavioral judgements are highly subjective and do not directly reflect ongoing processing. As such, future aging studies of recognition would benefit from additionally taking age-associated differences in encoding-related ERP effects into account.

Another caveat of this thesis refers to experimental manipulations in Experiment 1. In this study, we applied age-specific response deadlines that were slightly longer in older adults compared to young adults to account for cognitive slowing. However, the results of the post-hoc analysis, where we excluded slow responses (see section 5.3.2), suggests that we did not advantage our older adults by providing age-specific response deadlines. Nevertheless, the use of an adaptive response deadline would have been the best experimental manipulation, since adaptive deadlines can account for age-related differences in cognitive slowing on an individual level.

One open issue of this thesis that remains is the question what the posterior negativity may indeed reflect. We suggested that the negativity might reflect memory effort and/or that older and younger adults engage in qualitatively different processing, with the former group relying more on perceptually-based information while the latter group may focus more on abstract, conceptual information. An important task for the future would thus be to explain predisposing factors of the posterior negativity. Future studies could i.e. directly manipulate the perceptual and conceptual characteristics of the stimulus material and investigate its effect on older adults' memory (see Fisher, 2011, for an interesting manipulation of the stimulus material).

Finally, one interesting follow-up on Experiment 2 would be to investigate the effect of unitization, manipulated by spatial plausibility, on the ERP correlate of familiarity for the single components of the object pairs. Following the assumption of Mayes et al. (2007) and Pilgrim et al. (2012) that unitized associations “carry measurable costs” (Mayes et al., 2007, p. 126, see also section 2.1.4), and given the observed plausible-old/implausible-old effect in young and older adults in the plausible condition (though being confounded by the negativity in the latter group), one would expect that the individual components of plausible pairings elicit reduced ERP correlates of familiarity compared to implausible pairings in both age groups. Moreover, given that we suggest that older adults engaged in lower levels of unitization than young adults, this reduction should be particularly observable in young adults.

8.7 General conclusion

Taken together, our results put additional evidence to those studies suggesting that recollection is more affected by aging than familiarity and consequently, that age-related memory differences are particularly pronounced for associative compared to item memory. Moreover, we were able to show that age differences are very sensitive to task manipulations and can be reliably reduced when the task requirements strongly foster the use of familiarity, as in speeded item recognition decisions, but not when the task may still require self-initiated processing, namely when pre-experimentally unrelated stimuli are used in an associative recognition task and when no explicit unitization instruction is applied. Nevertheless, older adults also benefited from such unitization encoding, although to a lesser extent than young adults. The observed early frontal old/new effect together with the plausible-old/implausible-old effect in elderly suggest that familiarity-based recognition can still contribute to associative memory, even when the schematic and strategic support is relatively sparse. These results thus constitute an important contribution to the relatively rare studies that investigate the effects of aging on unitization processing, by showing that the type of stimuli and the type of encoding instructions play an important role when studying the effects of aging on episodic memory. Finally, the coherent finding of the posterior negativity in low performing elderly in the more demanding condition highlights the assumption that aging is not a uniform process but can come along with variability in performance and in memory processing, with some older adults being better able to keep up with their younger counterparts than other older adults.

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Appendix A

Questionnaire used in the pre-experimental rating of materials in Experiment 2

Liebe/r Versuchsteilnehmer/in,

vielen Dank dafür, dass Sie bereit sind an diesem Rating teilzunehmen. Dieser Fragenbogen dient dazu, Stimulus-Material für ein geplantes Experiment zu evaluieren. Ihre Aufgabe besteht nun darin, die folgenden 278 Stimuluspaare nach **PLAUSIBILITÄT** und **SEMANTISCHER RELATIERTHEIT** zu beurteilen.

Die Bearbeitungszeit beträgt ca. 45 Minuten und für Ihre Teilnahme erhalten Sie 1 Versuchspersonenstunde.

1) PLAUSIBILITÄT (P)

Jedes Objektpaar soll dahingehend bewertet werden, ob die räumliche Anordnung der beiden Objekte annehmbar und somit plausibel ist. Ein wichtiger Faktor ist dabei die Orientierung der Objekte: zueinander gerichtete Objekte sind in ihrer Anordnung meistens plausibel, da sie eine Handlung anzeigen (z.B. Känguru fährt Fahrrad und sitzt nicht unter dem Rad, s. Bsp.), voneinander weg gerichtete Objekte sind demnach unplausibel, da sie häufig keine Handlung anzeigen. Die Plausibilitäts-Entscheidung bezieht sich nur auf die räumliche Anordnung und sollte unabhängig davon sein, ob die beiden Objekte related sind oder nicht.





2) SEMANTISCHE RELATIERTHEIT (SR)

Jedes Objektpaar soll dahingehend bewertet werden, wie stark die beiden Objekte aufgrund ihrer Bedeutung zusammenhängen, d.h. wie related sie sind, unabhängig davon, wie plausibel ihre räumliche Anordnung ist. Die Art des Zusammenhanges spielt dabei keine Rolle. Z.B.:

Hund – Katze (hängen zusammen, weil sie sich Eigenschaften teilen: jeweils 4 Beine, beides Tiere)

Stuhl – Tisch (hängen zusammen, weil sie häufig gemeinsam vorkommen)

Für beide Entscheidungen nutzen Sie die folgende Skala:

1 = sehr gering	2 = gering	3 = mittel	4 = hoch	5 = sehr hoch
	<p>P: 5 = sehr hoch</p> <p>Diese räumliche Anordnung wäre plausibel, denn der Sattel ist auf dem Rücken des Pferdes.</p> <p>SR: 5 = sehr hoch</p> <p>Die Objekte sind zudem relatiert, denn Sattel und Pferd treten in der Realität häufig gemeinsam auf.</p>			
	<p>P: 1 = sehr niedrig</p> <p>Diese räumliche Anordnung ist unplausibel, denn der Sattel befindet sich hier unter und dem Pferd.</p> <p>SR: 5 = sehr hoch</p> <p>Die Objekte sind zudem relatiert, denn Sattel und Pferd treten in der Realität häufig gemeinsam auf.</p>			
	<p>P: 5 = sehr hoch</p> <p>Diese räumliche Anordnung wäre plausibel. Das Känguru befindet sich über dem Fahrrad und es scheint, als ob Rad fährt (Handlung möglich).</p> <p>SR: 1 = sehr gering</p> <p>Die Objekte sind wenig relatiert, denn Känguru und Fahrrad treten in der Realität selten gemeinsam auf und teilen sich keine Eigenschaften.</p>			
	<p>P: 1 = sehr gering</p> <p>Diese räumliche Anordnung wäre unplausibel. Das Känguru befindet sich unter dem Fahrrad (keine Handlung möglich).</p> <p>SR: 1 = sehr gering</p> <p>Die Objekte sind wenig relatiert, denn Känguru und Fahrrad treten in der Realität selten gemeinsam auf und teilen sich keine Eigenschaften.</p>			

SOLLTE EINES DER OBJEKTE NICHT ERKENNBAR SEIN, BITTE KENNZEICHNEN SIE DIES, INDEM SIE DAS OBJEKT MIT IHREM STIFT EINKREISEN!

Appendix B

Stimulus material in Experiment 2

Pairings with bold numbers were also used in Experiment 3. Subsequent numbers were recombined (i.e., axe – schnitzel). The first word denotes the upper object in a plausible arrangement.

1	axe - hamburger	30	airplane - telescope
2	can opener - schnitzel	31	cutter - shorts
3	magnifier - ashtray	32	oil - flowers
4	hen - applebowle	33	ajax - salad
5	drill - bagle	34	brush - colors
6	nail - steak	35	soother - bird
7	spatula - red bucket	36	lipstick - cake
8	querl - picnic basket	37	cactus - cabinet
9	dungfork - barrel	38	cafetiera - santa shoe
10	toothpaste - bread	39	bust - violet bowl
11	plier - fruitsalad	40	snow globe - vat
12	syringe - muffin	41	gallon - armchair
13	gateau - pillar	42	color tube - cupboard
14	snake - gametable	43	thermometer - lizard
15	wig - globe	44	mascara - lifebelt
16	headphones - owl	45	zucchini - hammock
17	razor - mushroom	46	melon - backgammon
18	plunger - tennisball	47	spoon - hiking shoe
19	cylinder – hydrant	48	scraper - xylophone
20	ribbon - matrioshka	49	rabbit – trampoline
21	flash - dog basin	50	penguin - slide
22	broom - euro	51	watering can – trunk
23	strawberry - tennisracket	52	statue - baby bed
24	soap - pan	53	beer bottle - basketball net
25	detergent - board	54	shovel - waffle iron
26	teapot - canister	55	mixer - fries
27	shovel - soup	56	baby bottle – bag
28	bottleopener - can	57	can – briefcase
29	dragon - wolve	58	oven glove – hose

59	brush - drum	95	bee - eggcup
60	monitor - commode	96	chess figure - chocolate box
61	saber – pot	97	light bulb - candlestick
62	rasper – quiche	98	flowers - bottle
63	sausage - grater	99	cat - box
64	gingerbread - sink	100	bowling pins - microwave
65	mushroom - cup	101	paint roll - ironing board
66	hazelnut – shelf	102	pizza cutter - music book
67	candle - test glass	103	clamp – eggplant
68	drink umbrella - vase	104	needle – cheese
69	lollipop - cocktail	105	watch - billard table
70	greens – wineglass	106	pillow – bin
71	chopsticks – glass	107	folder – pan
72	chili – coffee	108	smart phone - soap basket
73	muffineer - tissue	109	donut – drum
74	ice – plates	110	table tennis bat - glass table
75	salt cellar - I Pad	111	scissor – shorts
76	sponge – journals	112	barbecue fork - cucumber
77	bird – backpack	113	driving mirror – keyboard
78	butterfly – suitcase	114	traffic light – door
79	paint-brush – sushi	115	ventilator – stairs
80	pen – cookies	116	brush – bench
81	ladle – shoe	117	baseball - wooden bowl
82	tap – teabox	118	soccer ball – tub
83	ketchup – leaves	119	tulip – trophy
84	stapler - 100Euro	120	haw - toilet paper
85	party head - tie	121	caipirinha - camping plate
86	lotion - music stand	122	model aircraft - cooking plate
87	nutcracker - pumpkin	123	mexican hut – popcorn
88	rake – basketball	124	dip net – tomato
89	iron – tent	125	dolphin - bath tub
90	milk – nike shoe	126	guitar – pool
91	compasses – record	127	phone – cage
92	medicine - table	128	papyrus – file
93	newspaper – plank	129	lighted candle – slat
94	pens – tablet	130	wedding figure - skate board

131	fishing rod – squirrel	167	baguette – bucket
132	balloon –ape	168	avocado - squeezer
133	shell - plastic cup	169	toothbrush – eyeshadow
134	trompet – case	170	knife - dart
135	water gun – mouse	171	feather - fondue
136	sauce - witch	172	straw - ice cream
137	cards - beaker	173	saddle – cow
138	apple - baseball glove	174	hot-air balloon – elephant
139	microphone - receptacle	175	ribbon- fridge
140	sunflower - cone	176	flowers – books
141	pizza - record player	177	luster - cloth
142	pralines - shovel	178	pocket bottle – washer
143	ring – cream	179	candy cone - shopping basket
144	cigarette - pan	180	flute - umbrella pod
145	faucet – aquarium	181	present – wagon
146	whisk – jar	182	clock – bowl
147	cake server – beer	183	rubbish bag – log
148	honey spoon - spaghetti	184	printer - bedstand
149	pipette - bread slice	185	mortiser – toaster
150	deodorant - coke	186	button - piggy bank
151	feather - tea	187	swan - trailer
152	wind wheel – umbrella stand	188	pineapple – desk
153	crown - baby loo	189	hanger – curtain
154	pirate hut - token	190	clip – birdcage
155	water bottle – coconut	191	bust –table
156	bottle opener – cake	192	boat - filling cabinet
157	ice cream spoon - billard ball	193	peeler - ladybird
158	broom – ant	194	stamp – chocolate
159	pita - magazine rack	195	chewing gum - milk can
160	cd player - mailbox	196	rugby – bowl
161	carrot - pen sharpener	197	pin - garden pottery
162	leek - ear	198	cutlery – table
163	plastic duck – pot	199	drill – pan
164	fan – bucket	200	shamrock – cosmopolitan
165	brush – tiger	201	branch – jar
166	fork – barrow	202	racket – bell

203	binoculars – coins	234	hat – egg
204	vacuum cleaner – cubes	235	eagle – bed
205	sunglasses - medicine table	236	disco bowl – roadblock
206	binoculars – desk	237	cheese dome – toy
207	knitting - bowl	238	pen - hedgehog
208	bone – grill	239	wool – plate
209	letter – bucket	240	nut - muffin plate
210	chocolate - laundry basket	241	camera – scales
211	rattle – fire	242	towels - cake plate
212	lock – cornflakes	243	goal - street
213	apples – wood	244	pliers - carpet
214	mixer - winner stairs	245	hand – toolbox
215	paprika – piano	246	sauciere – leaf
216	pear – ottoman	247	umbrella – dromedary
217	cork - trophy	248	bavarian hat – horse
218	keys – ring box	249	panda bear – bullock
219	bacon - floating tire	250	duck - slite
220	zorro mask – basket	251	cherry - christmas tree
221	lamp – bench	252	cleaner – palette
222	glasses – plate	253	shaver – nutella
223	bracelets – sieve	254	feather duster – bowl
224	shovel - ice bucket	255	hair-dryer – rabbit
225	key - spectacle case	256	cap – pig
226	cap – pan	257	garlic press - orange juice
227	screw – note board	258	screw - wine bottle
228	scissors - ski boot	259	turtle – nest
229	hammer - computer mouse	260	bananas - chess board
230	lamp - deck-chair	261	pepper – commode
231	fire-drencher – grass	262	tea – etagere
232	shirt – boat	263	color palette – seats
233	nurse hat – frog	264	training jacket - boat