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Is faster better? Effects of response deadline on ERP correlates of recognition memory in younger and older adults.

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Contributor's statement page

All persons designated as authors qualify for authorship according to following criteria:

- 1) Substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data.
- 2) Drafting the article or revising it critically for important intellectual content; and
- 3) Final approval of the version to be published.

ABSTRACT

Aging studies generally suggest that recollection is impaired whereas familiarity-based recognition remains relatively preserved in healthy older adults. The present event-related potential (ERP) study explores whether age-related impairments in recognition memory can be reduced under conditions in which recognition decisions are primarily driven by familiarity. Old and young adults performed an item recognition task with perceptually rich visual stimuli. A response deadline procedure was employed following previous studies which have shown that limiting response times attenuates recollection but leaves familiarity relatively unaffected. Age effects on memory performance were large in the non-speeded response condition in which recollection contributes to performance. When response time was limited, performance differences between groups were negligible. In the nonspeeded condition the ERP correlate of recollection was not detectable in old adults. Conversely, in the speeded condition ERP correlates of familiarity were obtained in both age groups, though attenuated for old adults. For old adults in the speeded condition a temporally extended, posterior negativity was obtained which was more pronounced for low performing participants. The results suggest that even though the neural generators of the familiarity signal degrade with age, familiarity is an important contributor to recognition memory in older adults and can lead to a disproportional benefit in memory in conditions designed to specifically enhance familiarity-based responding.

Keywords: aging; episodic memory; recognition; familiarity; recollection; event-related potentials.

1. Introduction

Binding different features of an event into a cohesive memory representation and retrieving bound information of previous experiences are core functions of episodic memory. According to the dual-process perspective, retrieving information about 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 fast and strength-based process that supports recognition memory, whereas recollection is described as a slow-acting more strategic process that allows for the retrieval of qualitative information from a prior study event as required not only in recognition memory but also in associative recognition and recall tasks (Yonelinas et al., 2010).

A large number of studies examining the effects of aging on recognition memory, associative memory and recall suggest that normal aging impairs recollection but leaves familiarity relatively intact. For example, recognition of single items is less affected by aging than is associative recognition (Old and Naveh-Benjamin, 2008). Age-related associative memory deficits have been observed for an ample amount of stimuli, comprising word-word (Naveh-Benjamin, 2000), face-face (Jäger et al., 2012) or word-color associations (Bastin et al., 2013). Studies using more direct behavioral measures of familiarity and recollection, such as receiver operating characteristics (ROCs) (Yonelinas, 2002) or the remember-know procedure (Gardiner and Richardson-Klavehn, 2000) also support the view that aging leads to a decrease in recollection but leaves familiarity intact (Angel et al., 2013; Kilb and Naveh-Benjamin, 2011; Prull et al., 2006), although this pattern is less consistently reported when performance levels are very high (Yonelinas, 2002). Studies that have combined process dissociation methods with response deadline procedures have also shown that older adults are less able than young adults to use recollection to oppose increases in familiarity which are represented in high false alarm rates to rearranged word pairs (Light et al., 2004).

It has been argued that the recollection deficit in old age reflects a failure to spontaneously implement elaborative encoding and retrieval strategies. In support of this view, Naveh-Benjamin et al. (2007) have shown that the associative memory deficit for word pairs in older adults can be eliminated when appropriate associative strategies (i.e. to create sentences to bind the two words) are provided at encoding and retrieval. In addition, age differences in associative memory in another study were larger after intentional than after incidental encoding (Chalfonte and Johnson, 1996), suggesting that younger adults self-initiate elaborative encoding strategies during intentional tasks to a larger extent than older adults.

The recollection deficit in older adults has been related to frontal lobe dysfunction. Elderly individuals with poor frontal lobe functions perform poorly on associative recognition tasks, for example, but show no impairments in item recognition tasks (Glisky et al., 1995). Age deficits in associative

memory are also reduced in situations that make low demands on self-initiated effortful processing mediated by the prefrontal cortex (PFC), such as in situations in which preexisting semantic knowledge supports learning and retrieval of associations (Naveh-Benjamin et al., 2003) or when unitization strategies can be used at encoding to form new associations that in turn can be remembered on the basis of familiarity (Bastin et al., 2013).

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. The primary focus of these studies are the putative ERP correlates of familiarity and recollection which are temporally and topographically dissociable (for reviews Friedman and Johnson, 2000; Mecklinger, 2006; Rugg and Curran, 2007). Familiarity is associated with an early (approximately 300-500 milliseconds) frontally-distributed positivity for correctly judged old (hits) compared to new items (correct rejections), an effect which is often termed the early mid-frontal old/new effect. An ERP effect associated with recollection, the late parietal old/new effect can reliably be observed at posterior electrodes in a later time window between 500 and 700 ms. Behavioral conditions that modulate recollection also lead to modulations of the late parietal old/new effect (see Friedman and Johnson, 2000, for a review; Rugg et al., 1998). The effects have distinct topographies and are differentially sensitive to experimental conditions that affect familiarity and recollection. A large number of ERP studies employing old/new recognition memory paradigms, source memory and remember/know paradigms, have shown that the late parietal old/new effect, the ERP correlate of recollection, is diminished in older adults (Eppinger et al., 2010; Friedman et al., 2010; Walhovd et al., 2006; Wegesin et al., 2002). Moreover, a recent ERP study observed that the magnitude of the parietal old/new effect was modulated by aging and executive-control functions, in that the ERP correlate of recollection was generally smaller in old adults, but especially diminished for elderly with low executive functioning (Angel et al., 2010). Alongside an age-related reduction in magnitude, some studies have also reported delayed onset of the parietal old/new effect in older adults (Duarte et al., 2006; Mark and Rugg, 1998; Wegesin et al., 2002).

While these ERP studies support the view that aging is associated with an impairment in recollection, 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 mid-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) 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 et al., 2012) was matched with groups of younger participants. These findings conflict with the aforementioned reports of behaviorally preserved familiarity in old age 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 mid-frontal old/new effect has been observed in a selection of other ERP studies with older adults and in these studies was similar in amplitude to the corresponding effect in younger adults (Ally et al., 2008; Dulas and Duarte, 2013; Eppinger et al., 2010; Friedman et al., 2010; Morcom and 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 et al., 2012; Wolk et al., 2009). One possibility is that the use of color 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 and Schloerscheidt, 2011) and indicates the importance of material selection when studying the effects of healthy aging on episodic memory.

To summarize, aging is associated with impairments in episodic memory and a growing number of studies suggest that this age-related decline is not a general and inevitable process. Using different methods to operationalize familiarity and recollection, a considerable number of studies have shown that recollection is disproportionally more attenuated in older adults than familiarity. The aforementioned 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. Conversely, there is some inconsistency in the presence of the ERP correlate of familiarity in older adults, with some studies showing that aging is associated with a decrease in amplitude which is similar for the early mid-frontal and late parietal old/new effects.

One goal of the present study was to more systematically explore how the ERP correlate of familiarity is affected by age, under conditions which best foster familiarity-based recognition. Alongside the use of a response deadline (see below), 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). 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). 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 the current conditions, which were chosen to particularly support familiarity-based processing.

As a corollary to this, the present study was also able to test 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 a 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).

The use of ERP measures in combination with a response deadline procedure to explore ageassociated 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 and 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). 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.

2. Results

2.1 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).

2.2 Behavioral results

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

---- Insert Table 2 about here ----

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).

A Response Condition x 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 Group x Response Condition 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 time-outs 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 ms + 111 ms = 861 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 x 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 time out 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.

2.3 ERP results

The grand mean ERP waveforms of the mean amplitude measures are illustrated in Figure 1 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 Type in each time window and the outcomes of these ANOVAs are reported below.

---- Insert Figure 1 about here -----

2.3.1 Early time window: Anterior effects (300 - 500 ms)

To investigate the early frontal effect, an ANOVA with the factors Response Condition (non-speeded, speeded), Item Type (hits, crs), Location (frontal, frontocentral), 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 Type (F(1, 54) = 48.77, p <.001) and a marginally significant interaction between Response Condition and Item Type (F(1, 54) =3.85, p = .06) that was followed-up by condition-specific analyses reflecting greater Item Type 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 Type by Group interaction (F(1,54) = 27.44, p < .001) and a marginally significant Item Type, Laterality and Group interaction (F(2, 108) = 3.23, p = .06). These interactions suggest that Item Type 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 Type and Group were conducted for each response condition at each level of the laterality factor. In the non-speeded condition significant Item Type 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 Type 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 Type 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 Type and Group were evident at all levels of Laterality (all *p*-values < .01). At left anterior sites the Item Type effect was significant for young adults (p < .001) and marginally significant for old adults (p = .054). At midline recording sites the Item Type effects were significant for young adults (p < .001) but not for old adults (p = .94), whereas at right anterior sites the Item Type 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 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.

2.3.2 Late time window: Posterior effects (500 - 700 ms)

In the late time window the overall global ANOVA with factors of Response Condition, Item Type, Location, Laterality and Group revealed interactions between Item Type and Group (F(1, 54) = 6.79, p < .05), Response Condition and Item Type (F(1, 54) = 4.04, p = .05), and Response Condition, Item Type, 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 Type 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 Type effects in time windows from 500 to 600 ms and 600 to 700 ms revealed a significant Item Type effect in the former (F(1, 19) = 5.68, p < .05) but not in the latter of these two time windows (p = .17). Item type 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: $\eta_p^2 = .23$). Group-specific analysis for old adults revealed no effect of Item Type in the non-speeded response condition (p = .57). Notably, for older adults in the speeded response condition,

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¹ To explore whether Item Type 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 Type x Location x Laterality) ANOVAs separately for each condition. The resulting pattern did not change (Item Type 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.

the polarity of the Item Type 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 centroparietal 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.

2.3.3 Parietal old/new effect with performance matched age groups

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 and 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 Type x Location x Laterality x 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 Type (F(1,46) = 4,56; p < .05) and an interaction of Item Type and Group (F(1,46) = 4,71; p < .05). A group-specific break-down of the interaction revealed an Item Type effect in young (F(1,20) = 8,49; p < .01) but not in older adults (p = .98)².

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² 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. A performance matched age group analysis for the early frontal effect was not conducted for the speeded condition, because performance differences between age groups were negligible in this response condition and in addition older adults performed slightly better. Hence, in the non-speeded condition, the same selection of older adults (n = 28) as for the parietal analysis entered the Item Type x Location x Laterality x Group ANOVA, for whom performance in the non-speeded condition was equated to performance of the young adults. There was a significant main effect of Item Type (F(1,46) = 31,26; p < .001), an interaction of Item Type and Group (F(1,46) = 11,28; p < .01) and an interaction of Item Type by Laterality (F(2,92) = 12,95; p < .001). Group-specific analysis for each level of laterality revealed significant Item Type effects in young adults at all levels of laterality (left: $\eta_p^2 = .51$, midline: $\eta_p^2 = .50$ and right: $\eta_p^2 = .50$ and right: $\eta_p^2 = .50$. In contrast in old adults Item Type effects were significant at midline ($\eta_p^2 = .22$) and right ($\eta_p^2 = .28$), but not at left frontal recording sites (p = .68). The result pattern of the performance matched analysis resembles the former one with all old adults, suggesting that the smaller early frontal old/new effect in old adults is not modulated by their poorer performance.

2.3.4 Analysis of the posterior negativity

As is apparent in Figure 1, 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 Type, 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 Type (F(1,35) = 20.64, p < .001) and interactions between Response Condition and Item Type (F(1,35) = 7.82, p < .01) and between Item Type, Location and Laterality (F(2,70) = 4.53, p < .05). Separate analyses for each response condition revealed a main effect of Item Type 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 Type (F(1,35) = 7.62, p < .01), a marginally significant interaction between the factors Response Condition and Item Type (F(1,35) = 3.88, p = .06) and a significant interaction between Response Condition, Item Type, Location and Laterality (F(2,70) = 3.63, p < .05). Follow up analyses revealed significant effects of Item Type 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.

3. 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.

3.1 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 et al., 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 Light et al. (2004), 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) to dominate.

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 remember/know 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.

3.2 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 and Rugg, 2004) which are inherently more memorable and more distinctive than verbal stimuli (Gallo et al., 2004; Paivio and Csapo, 1973). Ally et al. (2008) for example reported that, whereas words elicited a reduced early frontal 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).

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 and Rugg, 2004; Wegesin et al., 2002). This suggests that the neural generators of the early frontal old/new effect change with age and that familiarity-related processing does not comprise entirely the same operations across these age groups. 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 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 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 Light et al.'s data (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. How could this disconnect 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 (Rugg and Curran, 2007; Bridger et al., 2014; Mecklinger et al., 2012), it is possible that only some of the component processes associated with familiarity - and which elicit the mid-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. The behavioral data in the speeded response condition, however, nonetheless indicate that although familiarity-based processing in older adults may be qualitatively different from that engaged in younger participants, it is an important contributor to the disproportionally good memory performance of the elderly in the fast response condition.

3.3 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 and Rugg, 2004; Yonelinas, 2002).

Observing a preserved mid-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.

One factor which is thought to contribute to attenuations in recollection for older adults is the fact that this group process 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. Moreover, the ERP correlate of recollection was not observed for the elderly group in that paradigm. In a similar study, Duverne et al. (2009) showed that whilst older adults are capable of retrieval cue processing when the retrieval task explicitly requires episodic recollection, they do not engage in this processing automatically when faced with simple recognition decisions, instead basing recognition decisions on familiarity. Although correlates of retrieval cue processing were not assessed in the current design because participants were required to target the recovery of similar classes of information in each test block, it is nonetheless 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.

It is also possible that impaired recollection in old adults might 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) in which a positive correlation between hippocampal diffusion, a measure of hippocampal integrity, and the 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 et al., 2009).

3.4 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 at around 300 ms that extended for several hundred milliseconds. In its temporal and topographic characteristics, this negativity resembles the so-called late posterior negativity (LPN), a bilateral posterior negativity which is elicited primarily in source memory or associative memory tasks (Johansson and Mecklinger, 2003) and is thought to reflect the search for and retrieval of bound information from a prior study episode. The left lateralization and the lack of any explicit source retrieval requirements make an LPN interpretation of the current posterior negativity unlikely, however.

In several respects, 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 et al. (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 view that older adults show a predisposition to retrieve visual rather than more abstract, conceptual knowledge is also supported by the results of 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. The occurrence of the posterior negativity predominantly in older adults suggests that this effect is age-associated and might reflect qualitatively different retrieval strategies in young and old adults.

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 adults³. As illustrated in Figure 2, 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.

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). 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 in the speeded condition. 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 revealed significant results only for the early (300-500 ms) time interval is consistent with this view. Such an explanation would also

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³ An ANOVA with the factors Item Type (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 Type (F(1,34) = 35.69; p < .001) and a marginally significant interaction of Item Type by Subgroup (F(1,34) = 3.68; p = .06). Subgroup-specific analyses, collapsed across the Laterality factor, showed a greater Item Type 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; $\eta_p^2 = .39$).

be consistent with the possibility considered above, that older adults invested additional effort in the more challenging speeded 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.

3.5 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 nonspeeded 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.

4. Methods and materials

4.1 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 \in 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).

4.2 Neuropsychological screening

All participants underwent a comprehensive neuropsychological test-battery that was conducted separately from the Electroencephalographic (EEG) session and lasted approximately $1\frac{1}{2}$ 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 et al., 2000). An operation span task (adapted from Turner and 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).

---- Insert Table 1 about here -----

4.3 EEG session

4.3.1 Stimuli

Stimuli consisted of 256 colored pictures of the Snodgrass and Vanderwart object drawings (Rossion and 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; Szekely et al., 2004) and were colored using Adobe® Photoshop® CS6.

4.3.2 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 3.58° x 5.01°. 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).

4.3.3 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 Society, 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 Electrooculogramms (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 kΩ. 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 et al., 1983) while trials containing other artifacts (whenever standard deviation in a 200 ms time interval exceeded 25 µV 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 of hit trials that entered ERP calculation were 45 (range: 28-53) for young and 41 (range: 20-57) for old adults; mean trial numbers for correct rejections were 47 (range 24-58) for young and 42 (range 24-56) for old adults. In the speeded condition, mean trial numbers for hits were 37 (range 24-46) for young and 40 (range 21-56) for old adults; mean trial numbers for correct rejections were 38 (range 22-57) and 40 (range 24-58) for young and old adults, respectively.

4.3.4 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), frontocentral (FC3/FCz/FC4), central (C3/Cz/C4), centroparietal (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 and 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 frontocentral electrodes) in the early time window were used for the quantification of the early frontal effect and only data from posterior recording sites (centroparietal 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 Type (hits, crs), Location (early time window: frontal, frontocentral; late time window: centroparietal, parietal), Laterality (left, midline, right) and the between-group factor Group (YA, OA) was conducted. Interactions involving the factor Response Condition, Group and Item Type 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 (Tabachnick and Fidell, 2007). Violations of homogeneity of variances in ANOVAs were adjusted using the Greenhouse-Geisser correction (Greenhouse and Geisser, 1959) and in t-statistics using Welch's t-test that allows different population standard deviations (Bortz, 2005). Where necessary, corrected p-values are reported alongside uncorrected degrees of freedom.

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Figure Captions

Figure 1 – ERP waveforms associated with hits and correct rejections for young (A) and old adults (B) in the non-speeded condition (upper panel) and for young (C) and old adults (D) in the speeded condition (lower panel). Data are depicted at frontal and parietal electrodes. Gray shading denotes old/new differences in the investigated time window.

Figure 2 – 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 1 gray shading denotes differences between hits and correct rejections in the investigated time windows.

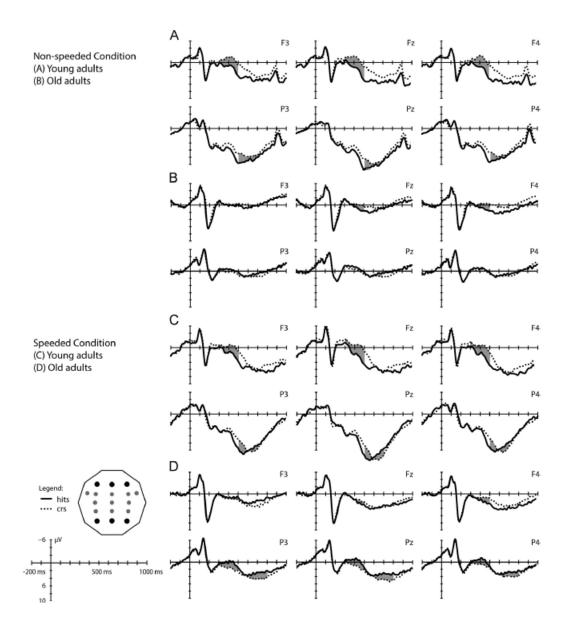


Figure 1

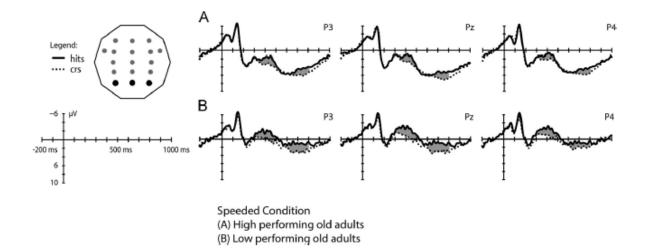


Figure 2