

Intact Recollection Memory in High-performing Older Adults: ERP and Behavioral Evidence

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Abstract

■ Numerous behavioral studies have suggested that normal aging has deleterious effects on episodic memory and that recollection is disproportionately impaired relative to familiarity-based recognition. However, there is a wide degree of variability in memory performance within the aging population and this generalization may not apply to all elderly adults. Here we investigated these issues by using event-related potentials (ERPs) to measure the effects of aging on the neural correlates of recollection and familiarity in older adults with recognition memory performance that was equivalent to (old-high) or lower than (old-low) that of young adults. Results showed that, behaviorally, old-high subjects exhibited intact recollection but reduced familiarity, whereas old-low subjects had impairments

in both recollection and familiarity, relative to the young. Consistent with behavioral results, old-high subjects exhibited ERP correlates of recollection that were topographically similar to those observed in young subjects. However, unlike the young adults, old-high subjects did not demonstrate any neural correlates of familiarity-based recognition. In contrast to the old-high group, the old-low group exhibited neural correlates of recollection that were topographically distinct from those of the young. Our results suggest that the effects of aging on the underlying brain processes related to recollection and familiarity are dependent on individual memory performance and highlight the importance of examining performance variability in normal aging. ■

INTRODUCTION

Many healthy people experience memory problems as they age (reviewed in Light, 1991). Such reports might reflect aging effects on at least two types of memory processes: the assessment of an item's *familiarity* and the *recollection* of specific details of the episode during which an item was initially encountered (Aggleton & Brown, 1999; Aggleton & Shaw, 1996; Mandler, 1980). Because older adults tend to be less impaired in tests of item recognition than for the recovery of source or contextual information (see Spencer & Raz, 1995, for a review), it is generally believed that age-related memory loss is primarily observed for recollection. Nonetheless, results from some studies suggest that, for some adults, recollection may not be affected by aging (Cabeza, Anderson, Locantore, & McIntosh, 2002; Davidson & Glisky, 2002), whereas for others, both familiarity and recollection may be impaired (Davidson & Glisky, 2002).

Most studies that have examined aging effects on memory have not examined intersubject variability, leaving open the possibility that different subgroups of elderly individuals might exhibit different patterns of memory changes. Indeed, results from both lesion (Yonelinas et al., 2002; Aggleton & Shaw, 1996) and neuro-

imaging (Ranganath et al., 2004; Davachi, Mitchell, & Wagner, 2003; Henson, Rugg, Shallice, Josephs, & Dolan, 1999) studies suggest that recollection and familiarity depend on different neural substrates. Furthermore, aging is associated with neuronal loss in several brain regions (Rodrigue & Raz, 2004; Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998). Thus, age-related changes in recollection and familiarity may vary, perhaps due to heterogeneity in underlying age-related neuropathology.

One way to more precisely characterize age-related memory changes is to separately examine effects in high- and low-performing elderly individuals (Cabeza et al., 2002; Davidson & Glisky, 2002; Rypma & D'Esposito, 2000). Initial evidence suggests that high-functioning elderly subjects (as determined by neuropsychological tests) can exhibit intact recollection (Cabeza et al., 2002; Davidson & Glisky, 2002). Accordingly, high- and low-performing elderly subjects might exhibit different patterns of memory performance and related neural activity.

Event-related potentials (ERPs) provide a way to assess neural activity associated with recollection and familiarity processes. Studies of young adults have identified several ERPs that dissociate recently encountered items from new items ("old–new effects"). One such effect, termed the "parietal old–new effect," occurs between 400 and 800 msec and is maximal at parietal scalp sites (see Johnson, 1995, and Rugg, 1995, for reviews). Because the

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parietal old–new effect is sensitive to the depth of processing (Gonsalves & Paller, 2000; Rugg, Allan, & Birch, 2000; Rugg, Walla, et al., 1998) and is largest for items that elicit correct source (Ranganath & Paller, 2000; Trott, Friedman, Ritter, & Fabiani, 1997; Wilding & Rugg, 1996, 1997) or “remember” judgments (Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Smith, 1993), it is believed to reflect recollection-based memory. Other ERP studies have reported late-onsetting, frontally distributed, old–new effects related to recollection (Paller, Bozic, Ranganath, Grabowecky, & Yamada, 1999; Trott et al., 1999; Wilding, 1999; Senkfor & Van Petten, 1998; Wilding & Rugg, 1996).

Previous studies investigating the effects of aging on ERP correlates of recognition memory have yielded conflicting behavioral and ERP results. One study showed that elderly adults, relative to young adults, exhibited impaired source recollection as well as attenuated ERP old–new effects over frontal and parietal scalp sites (Wegesen, Friedman, Varughese, & Stern, 2002). However, two other studies from this group reported that source recollection and frontal old–new effects were reduced in the elderly but that the parietal old–new effect was equivalent between young and old adults (Trott et al., 1997, 1999). Another study reported impaired source memory in the elderly but equivalent parietal and frontal ERP effects in young and old adults (Mark & Rugg, 1998). Finally, one recent study reported that when source memory performance was equated between young and old adults, parietal and frontal old–new effects were unaffected by age (Li, Morcom, & Rugg, 2004).

Previous ERP studies of aging have not emphasized differences between neural correlates of recollection and familiarity (Li et al., 2004; Wegesen et al., 2002; Mark & Rugg, 1998) so it is unclear to what extent familiarity contributed to the ERP effects described above. Furthermore, these previous studies have not examined performance variability in older adults. In light of the remarkable variability in elderly memory performance (see Friedman, 2003, for a review), more insight might be gained by examining changes in memory-related brain activity separately for high- and low-performing elderly subjects (Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Cabeza et al., 2002).

In the present study, schematically depicted in Figure 1, we aimed to determine the extent to which behavioral differences in memory performance are related to age-related changes in brain activity during retrieval. To this end, we separately examined recollection and/or familiarity impairments in groups of elderly adults with high (old-high) or low (old-low) memory performance. During each study phase, subjects were presented with a series of laterally presented objects and performed one of two orienting tasks. During each test phase, ERPs were recorded in response to a series of centrally presented studied and unstudied objects. For each test object, subjects were to decide whether they

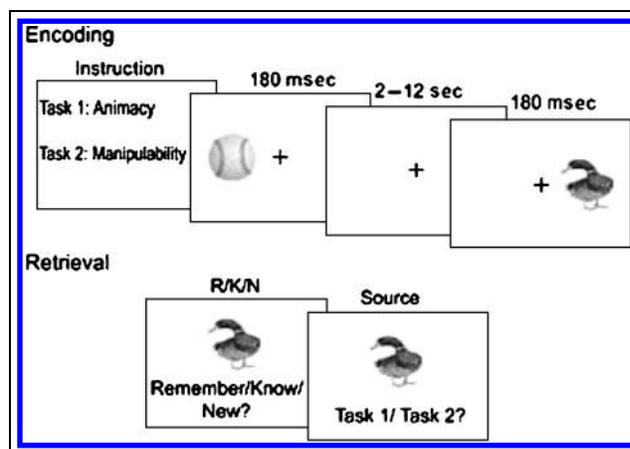


Figure 1. Example stimuli and task requirements during study and test blocks.

recalled something specific about studying the object (remember), confidently recognized the item based on familiarity (“know”), or believed the object was not previously encountered (“new”). For objects judged to be old (remember or know), subjects were additionally required to identify which study task was performed for that object. With these data, we were able to estimate behavioral indices of recollection and familiarity (Yonelinas, 2002) and the neural correlates of these processes (Duarte, Ranganath, Winward, Hayward, & Knight, 2004).

In a previous study implementing the same paradigm, we found that young subjects exhibited distinct neural correlates related to recollection and familiarity (Duarte et al., 2004). Specifically, we observed an early-onsetting (~100 msec) positive modulation of ERPs at frontopolar sites for all correctly recognized items relative to previously studied items that were judged to be new. Because this effect did not distinguish between items that were judged as “remembered” or “known,” we and others (Friedman, 2004) have suggested that this effect may be a neural correlate of familiarity-based recognition. Furthermore, we identified widely distributed positive-going activity, including the parietal old–new effect, specifically related to recollection (i.e., greater for remembered than known items) between 450 and 800 msec. These results from young subjects gave us a starting point for assessing ERP correlates of recollection and familiarity in older subjects. We predicted that if recollection, familiarity performance, or both are affected differently in older adults with overall high or low memory performance, then the ERP correlates of these processes should be affected accordingly.

RESULTS

Behavioral Results

No differences in behavioral performance were observed as a function of visual field of presentation (left vs. right)

for any of the three groups, all $F_s < 1$. Thus, all behavioral data were collapsed across visual field for subsequent analyses.

The mean proportions of remember (R), know (K), and new judgments to studied and new items presented at test are shown for all three groups in Table 1 and were used to calculate recollection and familiarity process estimates (see Methods). These probability estimates for recollection and familiarity are shown in Figure 2A. Results from analysis of variance (ANOVA) showed that both recollection, $F(2,41) = 8.1, p = .001$, and familiarity, $F(2,41) = 7.2, p = .002$, differed across the three groups. Follow-up contrasts determined that recollection estimates were significantly lower for the old-low group than for the young and old-high groups (all $F_s > 8.12, p_s < .009$). No significant differences in recollection were observed between young and old-high subjects, $F(1,28) < 1$. In contrast, familiarity did not significantly differ between the two older groups, $F(1,23) = 2.3, p = .14$, but was lower for both of these groups in comparison to young subjects (all $F_s > 3.47, p_s < .05$).

Mean reaction times (RTs) for memory judgments are shown in Table 1. An ANOVA employing the factors of Judgment Type (R, K, missed old [M], correctly rejected new [CR]) and Group (young, old-high, old-low) yielded main effects for Judgment, $F(3,117) = 68.0, p < .0001$, and for Group, $F(2,39) = 5.3, p = .01$. As shown in Table 1, the main effect of Group indicates that both groups of older subjects were slower to respond to test items than young adults. In addition, follow-up analyses confirmed that RTs were longer for K than for all other judgments (all $t_s > 3.5, p_s < .004$) for all groups, but no significant differences were observed between RTs for R and CR judgments (all $t_s < 1.3, p_s > .19$).

Our next analyses concerned source memory accuracy. Before proceeding, it should be noted that source memory decisions in this study required subjects to

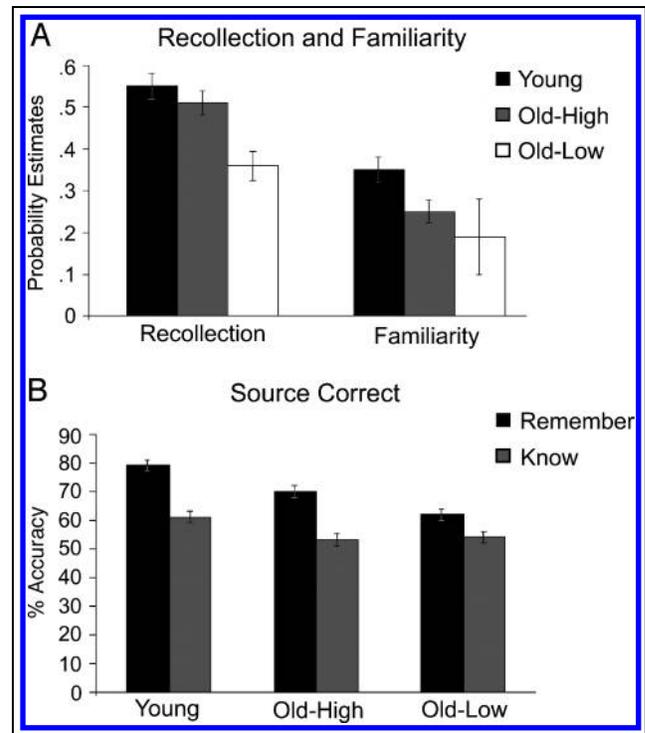


Figure 2. Behavioral results for each group. (A) Recollection and familiarity estimates for young, old-high, and old-low groups. (B) Proportions of correct source judgments for studied items that elicited R and K responses for young, old-high, and old-low groups. Error bars depict the standard error of the mean across subjects.

remember which orienting task was used to encode each object. Such decisions are typically assumed to reflect recollective memory, but it is conceivable that familiarity could have contributed to source memory performance in this study. This is because the two orienting tasks were presented in separate study blocks,

Table 1. Proportions of Remember, Know, and New Judgments Made to Studied and New Items at Retrieval and Corresponding RTs for Each Group

Judgment		Young		Old-High		Old-Low
<i>Studied Items</i>						
Remember	.59 (.14)	2002 (456)	.56 (.17)	2426 (708)	.50 (.19)	2228 (772)
Know	.21 (.09)	2844 (468)	.17 (.12)	4075 (941)	.23 (.12)	3566 (1018)
New (M)	.20 (.08)	2153 (536)	.27 (.10)	2634 (650)	.27 (.13)	2671 (969)
<i>New Items</i>						
Remember	.04 (.03)	2617 (948)	.05 (.04)	3655 (2572)	.14 (.13)	2555 (611)
Know	.15 (.11)	3061 (783)	.11 (.07)	3939 (1015)	.23 (.13)	3788 (1207)
New (CR)	.81 (.13)	1811 (597)	.84 (.07)	2203 (608)	.63 (.18)	2445 (776)

Standard deviations in parentheses.

CR = correct rejection; M = miss.

and thus test items may have differed in recency. If, as some studies suggest, familiarity decays in a lag-sensitive manner (Yonelinas & Levy, 2002), then it is conceivable that subjects used familiarity strength to make source memory judgments. If so, we would expect to see high levels of source memory accuracy even for items that were associated with K judgments.

Source memory accuracy for both R and K judgments are shown for all three groups in Figure 2B. Planned *t* tests confirmed that source accuracy for R judgments was well above chance (50%) for each group (all *t*s > 5.7, *p*s < .001). However, source accuracy was above chance for K judgments only in the young group, *t*(17) = 5.14, *p* < .001. As can be seen in the figure, source memory accuracy was significantly higher for R than K judgments across all three groups, *F*(1,39) = 75.1, *p* < .0001. In addition, a main effect of Group, *F*(2,39) = 12.4, *p* < .001, and a Group × Judgment Type (R vs. K) interaction, *F*(2,39) = 4.3, *p* = .02, was observed. Follow-up contrasts indicated that young adults' R judgments were associated with higher source accuracy than those of both older groups (all *F*s > 10.6, *p*s < .003) and that R responses of the old-high group contained greater source accuracy than those of the old-low, *F*(1,23) = 5.6, *p* = .02. In contrast, source accuracy was greater for young adults' K judgments than those of both older groups (all *F*s > 3.3, *p*s < .05), which did not differ from one another. These results suggest that recollection strongly contributed to accurate source memory in young subjects and that familiarity also made a slight but significant contribution. However, in older subjects, source memory was specifically supported by recollection.

ERP Results

Lateralization Effects

ANOVAs for mean amplitude and peak latency of P1 and N1 potentials during encoding (data not shown) revealed significant interactions between Hemisphere (left vs. right) and Visual Field (left vs. right) at extrastriate locations (PO3, PO4) in each case for both latency and amplitude for each subject group (all *p*s < .001). This confirmed that both P1 and N1 potentials were enhanced and had shorter latencies to contralaterally presented stimuli.

Despite reliable lateralization of visual processing during study, as evidenced by the above analyses, ERPs sorted first as a function of visual field of presentation during study and then by behavioral performance (R, K, M) were similar for left- and right-field stimuli (data not shown). In addition, preliminary omnibus ANOVAs of all electrodes revealed no interaction between the factors Visual Field (left vs. right) and Condition (R, K, and M) during any time window at test for any of the three groups. Thus, all data were collapsed across visual field for subsequent analyses.

Correct Rejections versus Misses at Retrieval

Consistent with previous observations (Duarte et al., 2004; Tsivilis, Otten, & Rugg, 2001; Wilding & Rugg, 1996), ERPs to missed old (M) items did not qualitatively differ from correctly rejected (CR) new item ERPs, across all subject groups (data not shown). In light of the fact that omnibus ANOVAs at all electrodes did not reveal any significant effects of Condition (CR vs. M) in any time window for any of the three groups, ERPs were restricted to comparisons between R, K, and M items.

Test ERPs to Remembered, Known, and Missed Studied Items

Within-group analyses. YOUNG. ERPs to studied items given remember, know, and new (i.e., miss) judgments are shown for the young in Figure 3. Mean ERP amplitudes to studied items were computed at left and right electrodes and analyzed by region (frontopolar [FP1/FP2], frontal [AF3/AF4/F3/F4], centroparietal [C3/C4/P3/

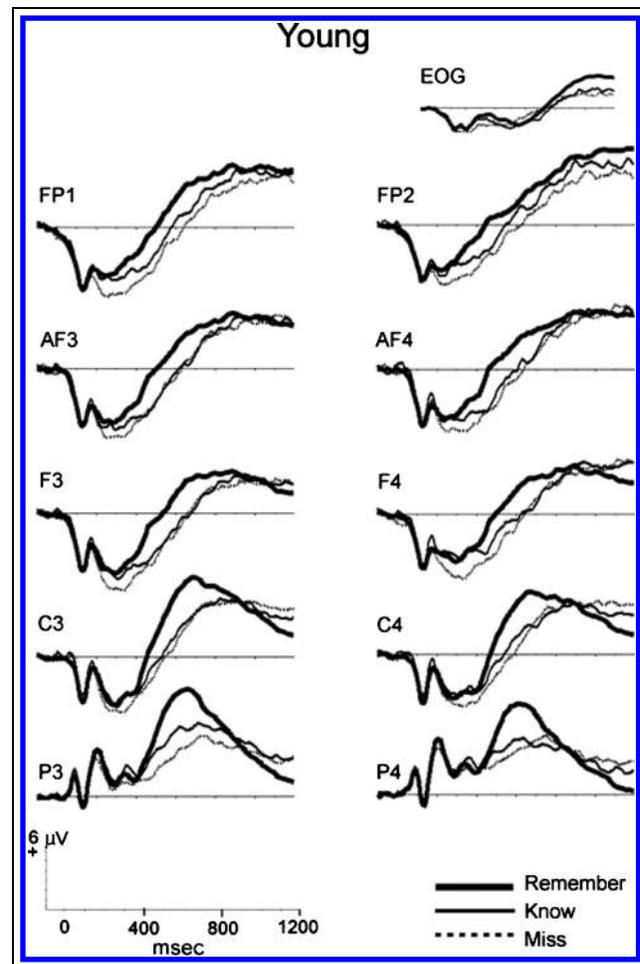


Figure 3. Young subjects. Grand average ERPs for objects recognized and given “remember” or “know” judgments, or unrecognized and given “new” (i.e., miss) judgments. Left and right columns correspond to left and right scalp locations, respectively.

P4]) over successive 200-msec time windows from 100 to 900 msec and in the time window from 900 to 1200 msec, separately for recollection (R vs. K) and familiarity (K vs. M). Between 100–300 and 300–500 msec, significant main effects of Condition (K vs. M) were found at frontopolar sites, all $F_s(1, 17) > 7.0$, $p_s < .01$. For the 300- to 500-msec epoch, significant Condition (R vs. K) effects were identified at both frontopolar and frontal regions, all $F_s(1, 17) > 7.6$, $p_s < .01$. Finally, analysis of the 500- to 700-msec latency revealed Condition (R vs. K) effects for all regions, all $F_s(1, 17) > 4.6$, $p_s < .04$. No familiarity or recollection effects were found for the 700- to 900- or 900- to 1200-msec epochs.

The difference scores for the familiarity (K–M) and recollection (R–K) effects were rescaled by the vector length method across all electrodes (McCarthy & Wood, 1985) and subjected to across latency ANOVAs to determine whether the topographies of these effects changed over time. A Latency (100–300 msec vs. 300–500 msec) \times Location (frontopolar, anterior-frontal, frontal, central and parietal) \times Hemisphere (left vs. right) ANOVA for familiarity revealed no effects involving Latency, so the familiarity effect was collapsed across these epochs for the subsequent analysis. In contrast, the same analysis of the recollection effect across the 300- to 500- and 500- to 700-msec windows did yield reliable Latency \times Location, $F(4,68) = 14.1$, $p < .001$, as well as Latency \times Location \times Hemisphere, $F(4,68) = 3.2$, $p = .03$, interactions. Consequently, distinct early (300–500 msec) and late (500–700 msec) recollection effects were submitted to the following analysis.

The scalp distributions for the familiarity (K–M) and recollection (R–K) effects are shown in Figures 4 and 5, respectively. Each of these difference waves was rescaled and entered into a Memory Effect (familiarity vs. recollection) \times Location (frontopolar, anterior-frontal, frontal, central, and parietal) \times Hemisphere (left vs. right) ANOVA. Familiarity was contrasted with both the early and late recollection effects. The comparison between familiarity and early recollection (300–500 msec) revealed no reliable differences in scalp distribution. As can be seen in Figures 4 and 5, these effects overlapped at frontopolar sites. In contrast, the familiarity vs. late recollection ANOVA gave rise to a Memory Effect \times Location interaction, $F(4,68) = 3.1$, $p = .04$, reflecting the frontopolar distribution for familiarity and the more posterior distribution for recollection in the late time period.

In summary, the above analyses revealed an early-onsetting familiarity effect with a frontopolar focus between 100 and 500 msec. In addition, topographically distinct early (300–500 msec) frontally focused and widespread, posterior-maximal late (500–700 msec) recollection effects were identified. Finally, although the familiarity effect and early recollection effect had similar topographies, familiarity and the late recollection effect could be functionally, temporally, and topographically differentiated. These data suggest that recollection and

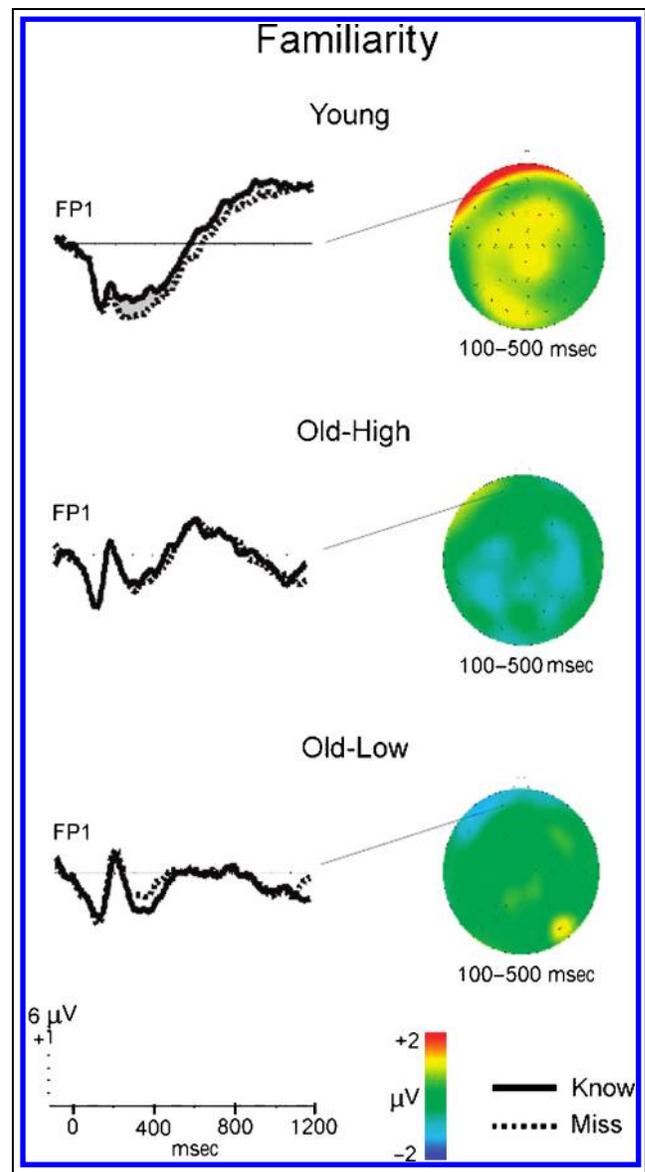
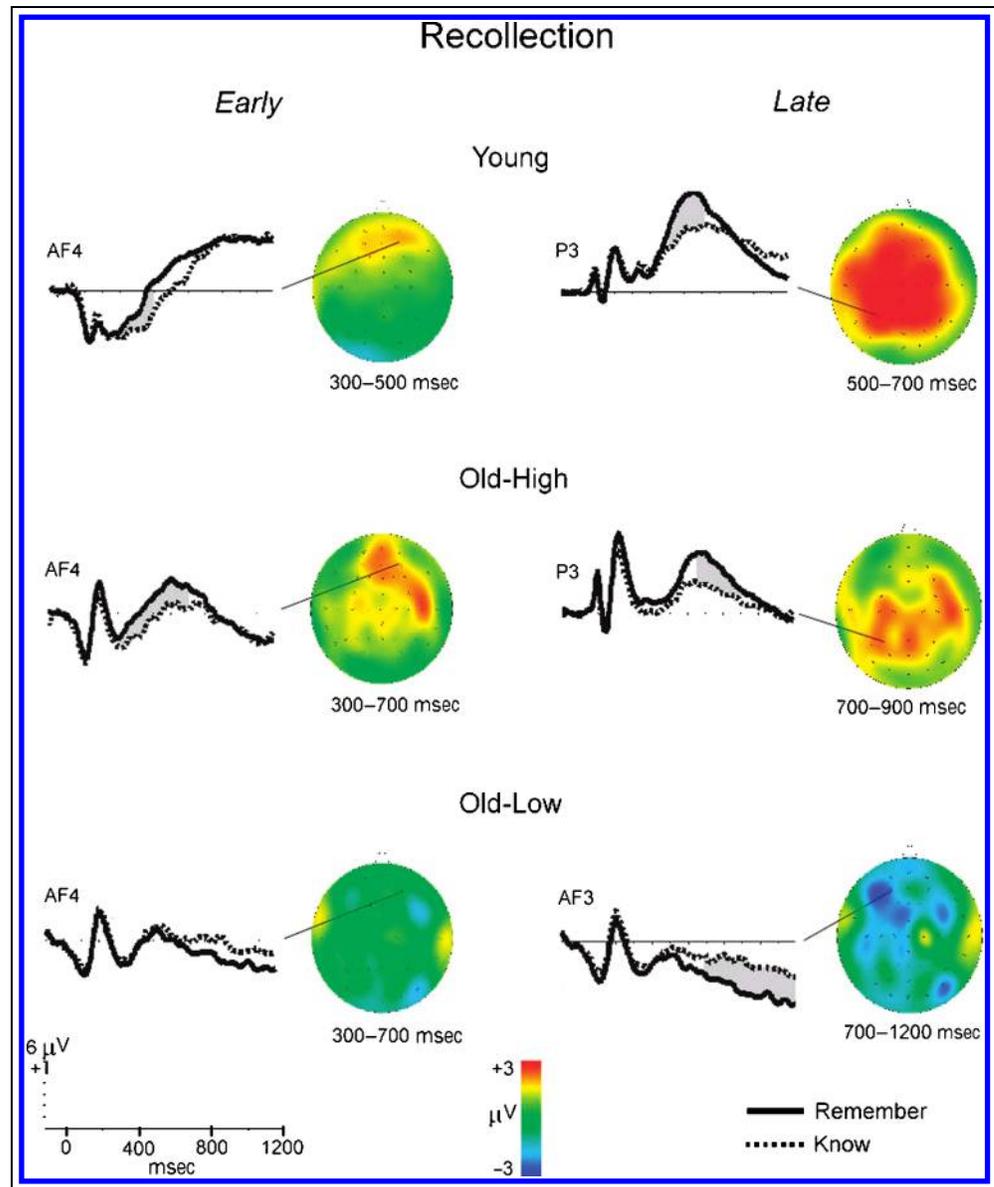


Figure 4. Scalp topography of ERP familiarity (K–M) effect for young adults. Small circles represent electrode locations as viewed from above. ERP plots are shown for the FP1 electrode, where the familiarity effect was largest in the young. ERP plots and topographic maps are additionally shown for the old-high and old-low groups for comparison. Shaded areas indicate the time window when the effect was statistically significant.

familiarity were associated with distinct neural correlates in the young.

OLD-HIGH. ERPs elicited by studied items associated with remember, know, and new (i.e., miss) judgments are shown for the old-high group in Figure 6. Between 300–500 and 500–700 msec, significant main effects of Condition (R vs. K) were found for frontal and centroparietal regions, all $F_s(1, 10) > 4.3$, $p_s < .05$. For the 700- to 900-msec epoch, a main effect of Condition (R vs. K) was reliable at centroparietal sites only, $F(1,10) =$

Figure 5. Scalp topography of ERP recollection (R-K) effects for young, high-performing adults, and low-performing adults. Small circles represent electrode locations as viewed from above. ERP plots and topographic maps are shown for each group at the electrode location where recollection effects were largest. Shaded areas indicate the time window when the effect was statistically significant.



10.8, $p = .008$. No other effects were observed in this group.

The difference score for the recollection effect (R-K) was rescaled and subjected to an across latency ANOVA. A Latency (300–500 vs. 500–700 vs. 700–900 msec) \times Location (frontopolar, anterior-frontal, frontal, central, and parietal) \times Hemisphere (left vs. right) ANOVA gave rise to a Latency \times Location interaction, $F(8,80) = 4.6$, $p = .01$. Subsidiary ANOVAs showed that recollection did not differ between 300–500 and 500–700 msec, whereas each epoch differed topographically from the effect in the latest interval (700–900 msec), as evidenced by reliable Latency \times Location interactions, all $F_s(4, 40) > 3.9$, $p_s < .03$. Thus, recollection was collapsed across the first two intervals to form an early recollection (300–700 msec) and a dissociable late recollection (700–900 msec) effect. The scalp distributions

for the early and late recollection (R-K) effects are shown in Figure 5.

In summary, the above analyses demonstrated the existence of an early-onsetting frontocentral recollection effect between 300 and 700 msec that was temporally and topographically dissociable from a late latency centroparietal maximal recollection effect (700–900 msec). There were no reliable familiarity effects in this group.

OLD-LOW. ERPs elicited by studied items associated with remember, know, and new (i.e., miss) judgments are shown for the old-low group in Figure 7. Between 700–900 and 900–1200 msec, significant main effects of Condition (R vs. K) were found for the frontal region only, all $F_s(1, 12) > 5.6$, $p_s < .03$. No other effects were observed for this group.

The difference score for the recollection effect (R-K) was rescaled and subjected to an across latency ANOVA.

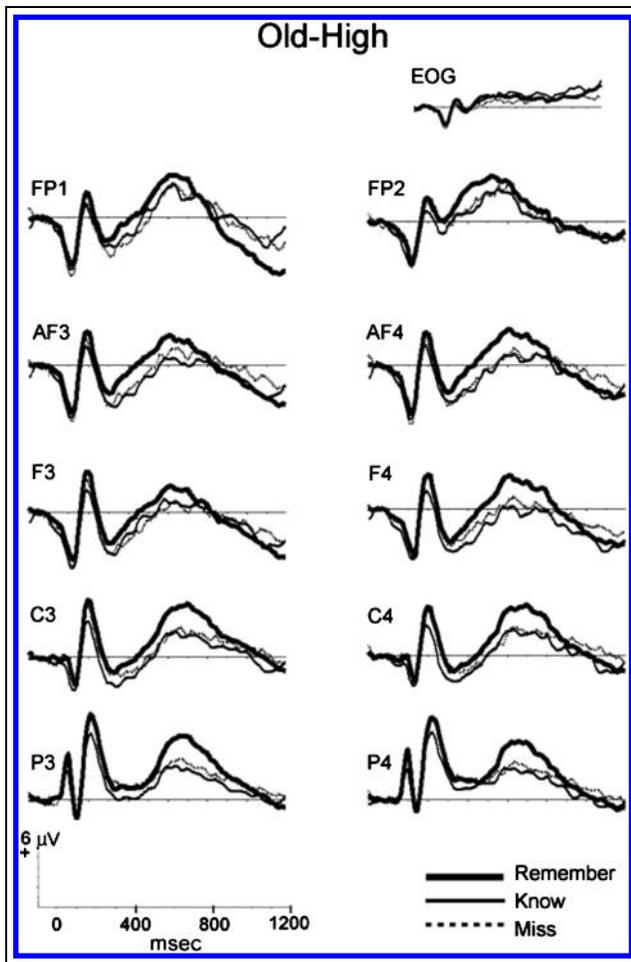


Figure 6. Old-high subjects. Grand average ERPs for objects recognized and given remember or know judgments, or unrecognized and given new (i.e., miss) judgments. Left and right columns correspond to left and right scalp locations, respectively.

A Latency (700–900 vs. 900–1200 msec) × Location (frontopolar, anterior-frontal, frontal, central, and parietal) × Hemisphere (left vs. right) ANOVA did not yield any reliable effects involving the factor Latency. Thus, recollection was collapsed across these two intervals to form a late latency recollection effect (700–1200 msec), as shown in Figure 5.

As can be seen in Figure 5, recollection in the old-low group occurred as a frontal maximal long-lasting negativity with R trials eliciting greater negativity than K trials. There were no reliable familiarity effects for this group.

Between-group analyses. **MAGNITUDE.** The early and late recollection effects were compared directly between the young and old-high groups. The frontocentral negativity associated with recollection in the old-low group was not observed in the other two groups and, as such, contrasts were not performed for this component. The ANOVA contrasting the early and late recollection effects for the young and old-high groups did

not reveal any effect involving the factor Group (all $F_s < 1.7$, $p_s > .16$).

TOPOGRAPHY. The scalp distributions for the early and late recollection effects are shown in Figure 5. Again, contrasts were not performed for the frontocentral negative component, as it was observed only in the low performers. ANOVAs of the rescaled early and late recollection data for the young and old-high did not reveal any effects involving the factor Group (all $F_s < 2.2$, $p_s > .11$). As is evident from the figure, this early effect was frontally distributed in both groups, whereas in the later periods, recollection was more posteriorly distributed.

Summary of ERP Results

Consistent with the fact that recollection was intact in the high-performing elderly adults, the ERPs related to recollection in this group were similar to those of the

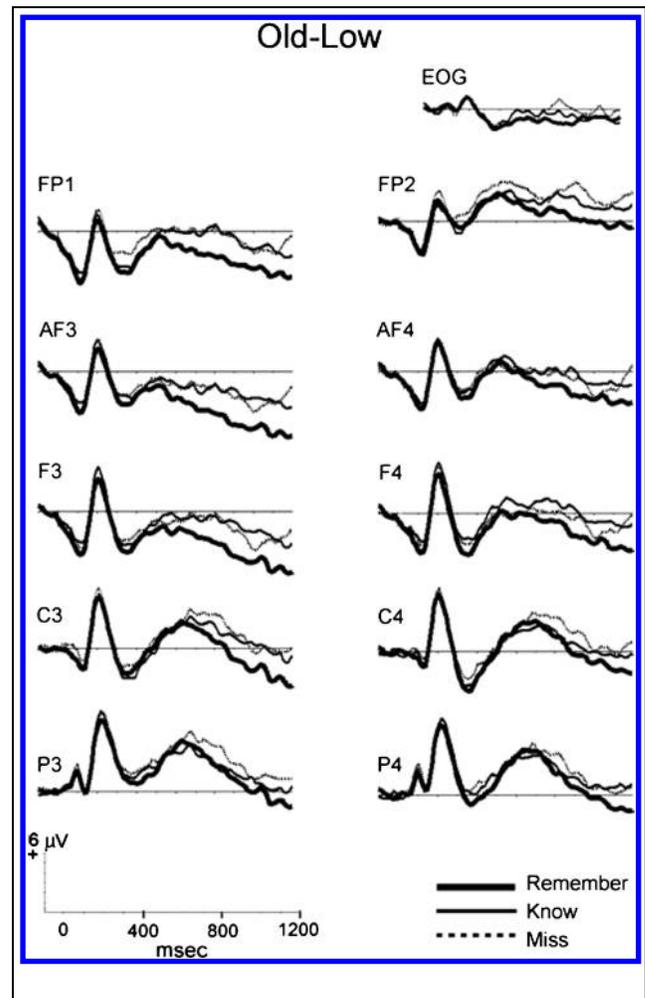


Figure 7. Old-low subjects. Grand average ERPs for objects recognized and given remember or know judgments, or unrecognized and given new (i.e., miss) judgments. Left and right columns correspond to left and right scalp locations, respectively.

young. The old-high group, like the young, showed topographically dissociable, early frontally focused (300–500 msec in young; 300–700 msec in old-high) and late posterior maximal recollection (500–700 msec in young; 700–900 msec in old-high) effects. These effects were topographically indistinguishable between groups, suggesting that the young and old-high-performing elderly groups recruited much of the same neural circuitry to support recollection. In contrast, recollection in the old-low group was associated with a frontally distributed negativity between 700 and 1200 msec that was not observed in either of the other two groups.

Whereas ERP correlates of recollection were intact in old-high subjects, neither older adult group showed ERP correlates related to familiarity that were evident in young adults. In the young, familiarity was associated with an early-onsetting positivity for remember and know trials at frontopolar sites from 100 to 500 msec. This effect was topographically dissociable from the late recollection effect, suggesting that recollection and familiarity were associated with distinct neural correlates.

DISCUSSION

In the present experiment, the effects of aging on the neural correlates of recollection and familiarity were examined in elderly adults with relatively high or low overall recognition memory performance. We found that high-performing elderly subjects exhibited intact recollection but impaired familiarity, whereas low-performing elderly exhibited impairments in both processes. ERP results showed that the old-high group exhibited neural correlates of recollection that were similar to those of the young. In contrast, recollection in the old-low group was characterized by a late-onset negativity that was not observed in either of the other groups. In contrast to the younger subjects, neither of the elderly groups exhibited neural activity related to familiarity. These results and their implications are discussed in more detail below.

Intact Recollection, Impaired Familiarity in Old-High Subjects

Our results showed that elderly subjects with relatively high memory performance exhibited intact behavioral and neural indices of recollection and impaired behavioral and neural indices of familiarity. For both old-high and young groups, two temporally and topographically distinct ERP correlates of recollection were apparent. Although the latencies of these ERP effects were somewhat delayed in the old-high group (consistent with their longer reaction times), the topography and magnitude of these recollection effects were indistinguishable between the two groups.

Our findings of intact recollection and impaired familiarity in old-high subjects were surprising, given work from other studies of normal aging, suggesting that familiarity is spared relative to impaired recollection (see Yonelinas, 2002; Spencer & Raz, 1995, for reviews). Interestingly, one recent study showed that item recognition was impaired despite intact source memory for pictorial stimuli in a group of older adults (Li et al., 2004). These results may also suggest that familiarity may be impaired despite intact recollection in some older adults. Our pictorial memory paradigm and that of Li and colleagues might have been more sensitive than typical verbal learning paradigms to detecting familiarity impairments in older adults. For example, familiarity in our task might have emerged as a consequence of visual perceptual fluency (Yonelinas, 2002), and this fluency might have been impaired in the elderly. Nonetheless, it should be noted that in the current study, no significant age-related differences were seen in performance of the study task discriminations during encoding (data not shown), suggesting that their familiarity deficits are unlikely to simply reflect impaired perceptual processing in older subjects.

Before moving on, it is useful to consider whether the results observed in the old-high group are subject to alternative interpretations. For example, our conclusions regarding intact recollection in old-high subjects are based on the remember–know method (Tulving, 1985), which is thought to index qualitative differences between the subjective experiences of familiarity and recollection. Numerous studies support this assumption (see Yonelinas, 2002, for a review), but one might question whether older subjects treated the remember–know distinction as a confidence judgment. If so, then R judgments in the old-high subjects might have been based on items that were highly familiar instead of, or in addition to, items that were recollected.

However, several considerations suggest that older subjects in the present study did in fact follow the proper procedure for making remember–know judgments. First, we took special care to ensure that all subjects understood the remember–know procedure by instructing them to apply know judgments when items were confidently recognized but without contextual recollection. The high level of source memory accuracy for items associated with remember judgments in old-high subjects provides objective evidence to suggest that their remember judgments were based on recollection. Second, ERP results observed in our study showed that the parietal old–new effect—an ERP modulation that has strongly and specifically been linked to recollection (e.g., Wilding, 2000)—was intact in the high-functioning elderly (see Mark & Rugg, 1998, for similar results). Furthermore, the absence of ERP correlates of familiarity-based recognition—such as the FN400 old–new effect (e.g., Curran & Cleary, 2003; Curran, 2000)—additionally

substantiates our belief that familiarity was specifically impaired in this group.

If, as we have suggested, recollection was intact in old-high subjects, then why was source memory accuracy impaired? One possibility is that old-high subjects recollected approximately as much contextual information as did young subjects but that this information was not necessarily relevant to the source memory judgment (i.e., “noncriterial recollection”). Another possibility is that old-high subjects recollected the same type of information as controls but were impaired at using this information to make source decisions. Indeed, this explanation is consistent with a growing body of evidence suggesting that the elderly may exhibit impairments in source-monitoring processes that allow one to use retrieved information to make specific memory attributions (see Spencer & Raz, 1995, for a review).

The late-onset recollection effect was most robust at parietal locations and specifically related to recollection in both groups. Based on its timing and topography, this latter effect bears strong similarity to the parietal old–new effect purported to be a neural correlate of conscious recollection (Curran & Cleary, 2003; Ranganath & Paller, 2000; Wilding, 2000; Paller et al., 1999; Duzel et al., 1997; see also Friedman & Johnson, 2000, for a review). Our results are generally consistent with previous ERP research (Trott et al., 1999; Mark & Rugg, 1998; Trott et al., 1997) on heterogeneous samples of healthy elderly subjects, which found that the amplitude and topography of the parietal old–new effect did not differ between old and young adults. At the same time, results from the old-high subjects do not agree with one study by Wegesin et al. (2002) showing that this effect was reduced in a sample of older adults. However, Wegesin et al. did not separate subjects on the basis of memory performance, as we did here. Based on the results from the old-low subjects (see below) in our study, one might expect that the reduction in the parietal old–new effect they observed was specific to poor performers in their study.

Consistent with the impaired familiarity estimate of the old-high group, we additionally found that old-high subjects did not exhibit the robust neural correlates of familiarity-based recognition that were apparent in young subjects. Positive-going activity, beginning as early as 100 msec, dissociated all recognized (R and K) studied items from missed studied items at frontopolar sites in young adults only. This effect is similar in latency and topography to frontopolar old–new effects observed in recent ERP studies (Duarte et al., 2004; Tsivilis et al., 2001; Friedman, 2004). Previous results suggest that this effect differentiates between correctly recognized and forgotten items (Duarte et al., 2004) but not between items associated with high or low amounts of contextual retrieval (Tsivilis et al., 2001) or between recognized items associated with R or K judgments (Duarte et al., 2004; Friedman, 2004). These characteristics would sug-

gest that the frontopolar effect is a neural correlate of familiarity.

A second neural correlate of familiarity that was not observed in the old-high performers was a negative-going wave between 300 and 500 msec that differentiated recollected, familiar, and missed items in the young adults only. This too is consistent with the impaired familiarity estimate in this group. This effect was also observed in our previous study (Duarte et al., 2004) and its latency and frontal topography suggest that it may be related to the FN400 old–new effect, which onsets at approximately 400 msec at frontal sites (see Friedman & Johnson, 2000, for a review). Previous studies have shown that this effect is insensitive to recollection, in that it only dissociates items based on whether they were correctly identified as old or new (Trott et al., 1997; Smith, 1993) or by how similar test items were to studied ones (Curran & Cleary, 2003; Tsivilis et al., 2001). However, one recent study, also employing remember–know judgments (Friedman, 2004), showed that this frontal negativity encompassed temporally and topographically overlapping familiarity and recollection effects, similar to what we observed in the young adults here and in Duarte et al. (2004). Importantly, old-high subjects did not demonstrate this FN400-like effect. Because familiarity was impaired in this group, these results are consistent with the view that the FN400 reflects familiarity-based recognition.

One potential explanation for the absence of ERP correlates of familiarity in the old-high group might be that K responses in these subjects were contaminated by “guesses.” To some extent, we agree with this explanation. Specifically, many psychological theories view familiarity-based recognition as a signal detection process (e.g., Yonelinas, 2001). In such models, it is assumed that both studied and unstudied (i.e., new) items elicit some degree of familiarity and that recognition decisions are made by assessing an item’s familiarity relative to a criterion value. In this framework, responses to studied and unstudied items with near-criterion levels of familiarity would likely be subjectively viewed as low-confidence responses or guesses. When discriminability is poor (i.e., familiarity is impaired), a larger proportion of items are likely to exhibit near-criterion levels of familiarity, resulting in more responses that are viewed as guesses. Accordingly, we do believe that K responses by old-high subjects might have included trials that would be classified as guesses, but we view this as a direct consequence of the fact that familiarity is impaired in these subjects.

Although the absence of ERP correlates of familiarity in older subjects is consistent with the idea that familiarity was impaired in the elderly, it should be noted that familiarity was not completely absent in these groups. Thus, ERP correlates of familiarity strength, such as the frontopolar or the FN400 old–new effects, may be best conceived as imperfect measures of familiarity. Indeed,

most memory-retrieval studies have not demonstrated the early frontopolar effect, and others report a lack of any correlates of familiarity-based recognition (e.g., Yovel & Paller, 2004). Therefore, high levels of familiarity may be required in order to elicit reliable ERP correlates of familiarity.

Impaired Recollection and Familiarity in Old-Low Subjects

In contrast to the old-high group, the old-low group demonstrated impaired recollection and familiarity. Consistent with their reduced familiarity estimates, neither the early frontopolar nor the FN400-like effects were observed in the old-low subjects. Furthermore, the old-low group did not demonstrate the distinct early frontally distributed and late parietally distributed ERP correlates of recollection that were observed in the other two groups.

However, in contrast to both the old-high and young subjects, low-performing elderly exhibited an enhanced negative slow wave related to recollection. This late negativity bears resemblance to the “late posterior negative slow wave” (LPN) that has been observed in previous studies that required retrieval of contextual information associated with a previous study episode (Friedman, Cycowicz, & Bersick, 2005; Cycowicz, Friedman, & Snodgrass, 2001; see also Johansson & Mecklinger, 2003, for a review). A similar effect has been observed in some recent aging studies of source memory (Li et al., 2004; Wegesin et al., 2002). As noted in these previous studies, the LPN does not differentiate between items associated with correct or incorrect source information (Friedman et al., 2005; Cycowicz et al., 2001; Wilding, 1999; Senkfor & Van Petten, 1998). Accordingly, some have suggested that this effect may be correlated with the continued evaluation of task-relevant attributes and reconstruction of the study episode, when such attributes are not readily recovered during retrieval (see Johansson & Mecklinger, 2003, for a review). It should be noted that the negative slow wave observed in this study, and in some previous studies of older adults (Li et al., 2004; Wegesin et al., 2002), has a more anterior distribution than the relatively posterior distribution of the LPN in younger adults. It is therefore unclear whether the anteriorly distributed negativity observed in the old-low subjects reflects the same neurocognitive processes associated with the LPN.

In the present data, the negative slow wave was associated with recollection (R vs. K). Furthermore, the fact that this group’s R judgments were associated with greater source memory accuracy than were their K judgments suggests that this negativity may have reflected some degree of successful recollection in the old-low adults. However, it should be noted that the old-low group demonstrated the lowest estimates of subjective recollection and source memory accuracy of all

groups. Thus, the cognitive processes associated with the anterior negativity, even if potentially supportive of successful recollection, may not have been sufficient to overcome the age-related memory impairments in this group, reflected by the absence of the frontally distributed familiarity and parietally distributed recollection effects observed in the young.

Relevance to Cognitive Theories of Aging

Recent neuroimaging studies of aging have shown that, during performance on a given memory task, older adults often recruit different neural networks than young subjects (Madden et al., 1999; Cabeza et al., 1997). One theory suggests that differential recruitment in the elderly reflects compensation for age-related reductions in the efficiency of cortical memory networks (Cabeza, 2002). According to this view, alternative patterns of activity should be exhibited in older adults with the highest memory performance. Alternatively, it has been suggested that recruitment of additional brain regions in the elderly is a negative consequence of aging and represents a failure to elicit neural activity specialized for the task (Logan, Sanders, Snyder, Morris, & Buckner, 2002). In this case, it might be expected that alternative patterns of activity would be present in elderly subjects with reduced memory. The current data are most consistent with the latter hypothesis. Whereas high-performing elderly adults exhibited neural correlates of recollection similar to those of the young, low-performing elderly demonstrated an entirely different pattern of activity associated with recollection. It should be noted that although there were morphological differences between the waveforms of the old-high and young groups, these differences were not directly related to recognition memory performance (i.e., recollection and/or familiarity). It is conceivable that overall differences in ERP morphology between high-performing elderly and young adults might have reflected relevant differences in task-related processing. Future investigations could test this hypothesis by comparing ERPs during our retrieval task with activity during a nonmemory baseline task or a memory task with fewer demands on controlled retrieval processes.

Conclusion

In conclusion, results from the present study suggest that not all elderly adults exhibit similar profiles of memory impairment. The present data emphasize the importance of examining performance variability when investigating the effects of aging on episodic memory. Although it has yet to be determined what brain areas might contribute to the recollection and familiarity effects discussed here, it is noteworthy that single-unit (Brown & Aggleton, 2001) and functional neuroimaging studies have dissociated neural correlates of these pro-

cesses within the medial temporal lobes (Ranganath et al., 2004; Davachi et al., 2003; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000) and frontal cortex (Yonelinas, Otten, Shaw, & Rugg, 2005; Ranganath et al., 2004; Henson et al., 1999). Furthermore, age-related neuronal loss has been shown in both of these brain regions (Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Rodrigue & Raz, 2004; Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998; Haug & Eggers, 1991). Thus, it is plausible that elderly adults in the current study may have exhibited distinct patterns of recollection and familiarity deficits due to dysfunction in one or multiple medial temporal and frontal brain regions, or in the white matter connections between these regions. Future studies would benefit by correlating volumetric changes in different brain regions with individual variability in both behavioral and ERP measures of memory performance (Van Petten et al., 2004).

METHODS

Subjects

Eighteen young adults between the ages of 18 and 25 and 25 older adults between the ages of 60 and 83, recruited from local universities and newspaper advertisements, participated in the experiment. Subjects were paid for participation and signed consent statements approved by the Institutional Review Board of the University of California, Berkeley. Subjects were right-handed and all had normal or corrected-to-normal vision. None of the participants had a history of psychiatric or neurological disorder, psychoactive drug use, diabetes, or hypertension. All subjects were native English speakers.

Older adults were divided into two groups by a median split based on their overall recognition memory performance [(%Remember + %Know) – %False alarms]. This ensured that subjects were divided by a measure relevant to the current study without directly biasing the results toward one or the other measure of interest (i.e., recollection or familiarity). Other studies have divided subjects in a similar manner (Daselaar et al., 2003; Van Petten, Luka, Rubin, & Ryan, 2002). Although not completely independent of these measures, it is unlikely that this procedure would systematically bias the behavioral or ERP results. Neuropsychological tests have also been used for dividing subjects (Cabeza et al., 2002); however, our neuropsychological test battery was not sufficient for this purpose. Older subjects in the top half were classified as high performers (old-high), whereas those in the bottom half were classified as low performers (old-low). Demographic and neuropsychological characteristics of all three groups are shown in Table 2. As can be seen in the table, no significant differences were found between the three groups for years of education, the Mini Mental State test (Folstein,

Table 2. Demographic Characteristics and Neuropsychological Test Scores for Young, Old-High, and Old-Low Subject Groups

<i>Measure</i>	<i>Young (n = 18)</i>	<i>Old-High (n = 11)</i>	<i>Old-Low (n = 13)</i>
Age	21.0 (2.7)	69.3 (5.8)	70.8 (5.3)
Sex	11/18 Female	6/11 Female	8/13 Female
Education	14.8 (1.3)	14.6 (2)	15.3 (2.3)
MMSE	30.0	29.5 (.9)	29.7 (.6)
WAIS-III vocabulary	58.0 (5.5)	56.8 (4.5)	54.3 (4.1)

Standard deviations in parentheses. MMSE = Mini Mental State Exam; WAIS = Wechsler Adult Intelligence Scale.

Folstein, & McHugh, 1975), or the vocabulary subtest of the Wechsler Adult Intelligence Scale-III (Wechsler, 1997). The two older groups did not differ in age but both were older than the young.

Stimuli

Stimuli were presented on a computer monitor against a white background. Stimuli consisted of 450 grayscale photographs of meaningful objects. Stimuli subtended a visual angle of $7.87^\circ \times 10.98^\circ$.

Procedure

All participants were seated comfortably in a dimly lit and sound-attenuated booth facing a computer screen at a distance of 1 m. Subjects were instructed to fixate centrally throughout stimulus presentation and to minimize all unnecessary movements. Subjects responded to stimuli by button press on a joystick held in the right hand and in all cases, accuracy was emphasized over speed. Participants were trained on each task and instructions were repeated verbally throughout the experiment. Subjects were informed that they would be tested on their memory for all studied objects.

Blocks were ordered study–study–test, such that each block of test trials covered the items that were studied in the two preceding study blocks. On each block of study trials, 50 stimuli were presented one at a time 4.15° either to the left or to the right of a central fixation cross for a duration of 180 msec and a randomized stimulus onset asynchrony (SOA) of between 2 and 12 sec (mean 4 sec). The 180-msec presentation time was chosen to prevent subjects from making a saccade into the hemifield of presentation. Preliminary analyses determined that SOA did not interact with subsequent memory performance. Half of the stimuli were randomly presented to the left and half to the right of fixation in a random sequence. In three of the study blocks, subjects were asked to determine the animacy of each object

by pressing 1 for living and 2 for nonliving. In the other three study blocks, subjects were asked to determine the manipulability of each object by pressing 1 if manipulable and 2 if nonmanipulable. Subjects completed one of each type of study block and were allowed a few minutes to relax before proceeding to the corresponding test block.

Stimuli were lateralized during encoding because we were interested in determining whether impaired interhemispheric collaboration may account for impaired memory performance in elderly adults (Cabeza, 2002; Reuter-Lorenz, Stanczak, & Miller, 1999). In order to maximally observe such differences, we chose a task that has been shown to produce intrahemispheric processing (Gratton, Corbalis, & Jain, 1997). However, our preliminary analyses did not reveal any effects of laterality either behaviorally or on memory-related ERPs during encoding or retrieval for any group. Thus, all data were collapsed across visual field of initial presentation.

EEG and behavioral responses were collected during three blocks of test trials. Each of these test blocks included 100 objects that were studied in the preceding two study blocks and 50 new objects in a pseudorandom sequence. Instructions for the test phase included a description of the appropriate use of the remember, know, and new response categories, modeled after previous studies (Rajaram, 1993; Gardiner & Java, 1991). Subjects were instructed to respond, “remember” if they were certain they had seen the object and could recollect specific associations that occurred at study, “know” if they were certain about previously studying the object and could not recollect any specific associations, and “new” if they were certain they had never previously studied the object. Objects were all centrally presented above a response cue (“Press 1” = remember [R], “Press 2” = know [K], “Press 3” = new [N]), both of which remained on the screen until a response was made. If subjects responded new, a centrally presented fixation cross appeared for 500 msec until the next test stimulus was presented. If a remember or know response was made, a new response cue appeared in place of the previous asking the subjects to determine the study task (“Press 1” = animacy, “Press 2” = manipulability). Once subjects made this second response, a centrally presented fixation cross appeared for 500 msec until the next test stimulus was presented. We applied a self-paced design to allow for the variability in responses common in elderly adults, and only trials with RTs less than 200 msec were considered trial failures. On average, this resulted in the rejection of less than 3% of trials.

In order to correct for the underestimation of familiarity inherent in the remember–know design, estimates of recollection and familiarity were calculated according to the independence remember/know procedure (Yonelinas & Jacoby, 1995) and both esti-

mates were corrected for false alarm rates (know false alarms were also corrected by the independence procedure).

ERP Recording

The EEG was recorded from 63 Ag/AgCl electrodes in an elastic cap. Only electrodes in which impedances were reduced below 10 k Ω were examined. All of the electrodes were referenced to a pair of linked electrodes placed on the mastoid processes. The vertical electrooculogram (EOG) was recorded from an electrode placed below the right eye and the horizontal EOG from electrodes placed on the outer canthi of both eyes. All channels were amplified at 20K and online band-pass filtered from 0.1 to 80 Hz. The data were sampled at a rate of 256 Hz and stored for offline analysis. Recording epochs containing amplifier saturating artifacts (± 100 μ V) that occurred between 100 msec prestimulus to 1200 msec poststimulus were excluded prior to averaging. Epochs with correctable eye movements were corrected by a method based on principal component analysis, as is available in Neuroscan version 4.1 (Berg & Scherg, 1994). Extensive analysis of this method determined that there was no reduction in waveform resolution.

ERP Analysis

ERPs were analyzed from 10 electrode sites (FP1, FP2, AF3, AF4, F3, F4, C3, C4, P3, P4), where condition effects were most evident and where we (Duarte et al., 2004) and others who have used similar experimental design (Tsivilis et al., 2001; Trott et al., 1999) have reported such effects. Furthermore, exploratory analyses performed with a larger set of electrodes yielded similar results as those subsequently reported. Therefore, we condensed this large set to the subset listed above in order to simplify the description of the ERP effects. In order to examine whether stimulus presentation during study sufficiently lateralized visual processing and therefore, early extrastriate ERPs, P1 and N1 mean amplitudes and peak latencies were measured at encoding over select extrastriate sites (PO3, PO4) between 90 and 120 msec for the P1 and 125 and 225 msec for the N1 (see Mangun, 1995, for a review). Preliminary analyses indicated that no behavioral or ERP differences in memory-related effects were observed as a function of study task (animacy/manipulability). Thus, all data were collapsed across study task for memory-related analyses.

Specifically, ERPs to objects were averaged first as a function of visual field of presentation during study (left vs. right) and then based on the subject’s behavioral response at test. Thus, ERPs were averaged separately for recognized items that elicited remember (R) or know (K) responses and for missed items that were misidentified as new (M). ERPs were also averaged for correctly rejected (CR) new objects. False alarm rates were too

low to analyze responses to new items that elicited R or K judgments for any subject group.

Based on these considerations, the analyses of ERPs focused on the identification of potentials related to recollection and familiarity. Based on prior characterizations of the remember-know method (Knowlton, 1998; Yonelinas & Jacoby, 1995), we reasoned that K judgments are based solely on familiarity and that the difference in potentials elicited by K versus M items could be interpreted as a neural correlate of familiarity-based recognition. In contrast, we reasoned that because R and K judgments primarily vary in terms of recollection, a difference in brain potentials elicited by R versus K items could be interpreted as a neural correlate of recollection. Additionally, missed items (M) were contrasted with correctly rejected new items (CR) with the statistical procedure described below. In the event that no reliable differences were found in any time window, (M) items would be contrasted with (R) and (K) items because R, K, and M items were likely to have more comparable signal to noise ratios. To quantify these effects, statistical analyses were performed on mean ERP amplitudes for the various conditions over successive 200-msec time windows, with the exception of the last time window, in which amplitudes were analyzed over the last 300 msec of the epoch. Analyses of ERPs began at 100 msec. These data were subjected to the following three within-group and two between-group sets of analyses.

First, the data from the 10 lateral electrodes listed above were subjected to within-group ANOVAs for each of the three groups separately in order to establish the existence of reliable recollection and familiarity effects. In order to examine regional differences in effects, Condition (for recollection [R vs. K] and for familiarity [K vs. M]) \times Hemisphere (left vs. right) ANOVAs were conducted on frontopolar (FP1/FP2), frontal (AF3/AF4, F3/F4), and centroparietal (C3/C4, P3/P4) regions. These groupings had the effect of limiting the total number of analyses performed and were consistent with the topographical characteristics of the effects we observed previously (Duarte et al., 2004). Second, as it was important to determine if the recollection and familiarity effects' topographies changed across the epochs in which they were reliable, these effects' difference scores were rescaled by the vector length method (Ruchkin, Johnson, & Friedman, 1999; McCarthy & Wood, 1985) and subjected to across epoch ANOVAs. In the event that no reliable effect of Epoch was found, recollection and familiarity effects were collapsed across the latency windows in which they were reliable, simplifying the subsequent analyses. Topographic maps of surface potentials, calculated by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989), were used to display the scalp distributions of the recollection and familiarity effects temporally characterized in the previous analysis. Third, in order to determine if recollection

and familiarity were supported by dissociable neural systems, ANOVAs contrasting these topographies were performed after the corresponding difference waves had been rescaled by the vector length method.

Two types of between-group analyses were also performed in order to directly compare recollection and familiarity effects across the groups. First, the raw difference scores for these effects were subjected to ANOVAs that included the factors of Group, Hemisphere (left vs. right), and Location (frontopolar, anterior-frontal, frontal, central, parietal) in order to investigate group differences in effect magnitudes, which would signify different activation strengths. Each group was compared with the other groups for the same effects. Second, these ANOVAs were performed on the rescaled difference scores in order to investigate group differences in scalp topographies for each effect, which would signify differences in underlying neural generators (Rugg, 1995). For all analyses, *p* values reflect the Huynh-Feldt correction where appropriate. Significant interactions at an alpha level of .05 were followed up with subsidiary ANOVAs or paired contrasts restricted to subsets of electrodes to determine the source of the effects when necessary.

ERPs sorted as a function of source memory accuracy were similar to those sorted by R and K judgments, only statistically less robust, as we (Duarte et al., 2004) and others (Rugg, Schloerscheidt, & Mark, 1998) have previously observed. This pattern of results could reflect the fact that ERP correlates of recollection derived from the source memory task were contaminated by correct guesses when items were not actually recollected. Furthermore, ERP correlates of familiarity derived from the source memory task may have been contaminated by items that were recollected, despite the fact that information relevant to the source judgment was not recovered. For these reasons, as well as the fact that we used source memory judgments only to confirm the proper usage of "remember-know," source memory ERPs are not reported here.

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