

Event-related Potentials Reveal Age Differences in the Encoding and Recognition of Scenes

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Abstract

■ The present study used event-related potentials (ERPs) to investigate how the encoding and recognition of complex scenes change with normal aging. Although functional magnetic resonance imaging (fMRI) studies have identified more drastic age impairments at encoding than at recognition, ERP studies accumulate more evidence for age differences at retrieval. However, stimulus type and paradigm differences across the two literatures have made direct comparisons difficult. Here, we collected young and elderly adults' encoding- and recognition-phase ERPs using the same materials and paradigm as a previous fMRI study [Gutchess, A. H., Welsh, R. C., Hedden, T., Bangert, A., Minear, M., Liu, L., et al. Aging and the neural correlates of successful picture encoding: Frontal activations compensate for decreased medial temporal activity. *Journal of Cognitive Neuroscience*, 17, 84–96, 2005]. Twenty young and 20 elderly adults incidentally encoded and then recognized photographs

of outdoor scenes. During encoding, young adults showed a frontocentral subsequent memory effect, with high-confidence hits exhibiting greater positivity than misses. Elderly adults showed a similar subsequent memory effect, which, however, did not differ as a function of confidence. During recognition, young adults elicited a widespread old/new effect, and high-confidence hits were distinct from both low-confidence hits and false alarms. Elderly adults elicited a smaller and later old/new effect, which was unaffected by confidence, and hits and false alarms were indistinguishable in the waveforms. Consistent with prior ERP work, these results point to important age-related changes in recognition-phase brain activity, even when behavioral measures of memory and confidence pattern similarly across groups. We speculate that memory processes with different time signatures contribute to the apparent differences across encoding and retrieval stages, and across methods. ■

INTRODUCTION

There is a long-standing debate regarding the extent to which the long-term memory impairments associated with normal aging are driven by difficulties at the level of encoding, retrieval, or both. Such distinctions can be difficult to draw from behavioral measures, although studies using divided attention paradigms have revealed greater evidence for age-related differences when encoding, rather than retrieval, is disrupted (Anderson, Craik, & Naveh-Benjamin, 1998; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Park, Smith, Dudley, & Lafronza, 1989), suggesting a larger encoding deficit with age. Cognitive neuroscience methods are uniquely positioned to address this debate because the neural correlates of both stages of memory can be investigated relatively independently. However, thus far, differences across the paradigms and methods employed in such studies have limited the degree to which cognitive neuroscience data contribute to the resolution of this debate. Whereas functional magnetic resonance imaging (fMRI) studies have identified more drastic age differ-

ences at encoding than at recognition (as reviewed by Park & Gutchess, 2004), event-related potential (ERP) studies have accumulated substantial evidence for age differences at retrieval (as reviewed by Friedman, 2000; although see Mark & Rugg, 1998; Friedman, 2003). In the present study, we seek to evaluate age-related changes in encoding and retrieval processes using ERPs and to compare these findings with prior fMRI data obtained using the same paradigm (Gutchess et al., 2005).

Reports of the neural correlates of encoding deficits with age began with the first neuroimaging study of encoding and aging (Grady et al., 1995), and widespread observations of reduced prefrontal and medial temporal activations with age pervade the fMRI literature (reviewed by Park & Gutchess, 2004). Although age-related changes in ERP responses believed to arise from medial temporal lobe structures are not prominent in the literature (Friedman, 2000), purported left inferior frontal negativity is diminished in older adults for early (e.g., 400–600 msec) and late (e.g., 1200–1400 msec) time windows during semantic retrieval and episodic encoding processes that contribute to later recognition (Nessler, Johnson, Bersick, & Friedman, 2006). A particularly useful measure of encoding is the subsequent memory (or “Dm,” difference in subsequent memory) effect

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because it allows comparison of the encoding activity associated with later successful and unsuccessful memory performance. Although the approach originated in the ERP literature (Paller, Kutas, & Mayes, 1987) before extending into fMRI literature (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998), the technique has been used little with ERPs to study aging. The two extant ERP studies of aging and subsequent memory examined encoding of verbal stimuli. These studies found that elderly adults do not exhibit a Dm effect under incidental conditions (Friedman, Ritter, & Snodgrass, 1996), but do under intentional conditions, although they lack the graded response across remember-know-miss trials that young exhibit (Friedman & Trott, 2000). Friedman and Trott (2000) suggest that Dm effects may emerge in elderly only under intentional, semantic encoding conditions because older adults do not spontaneously engage in elaborative encoding under incidental conditions. Functional MRI work supports this explanation in part, but also reveals more widespread changes with age. Deep semantic encoding equalizes left frontal activation for young and elderly, but intentional encoding makes underrecruitment of this frontal region more pronounced for the elderly (Logan, Sanders, Snyder, Morris, & Buckner, 2002). Furthermore, fMRI subsequent memory studies identify Dm effects, albeit somewhat reduced, for elderly under incidental conditions (Gutchess et al., 2005; Daselaar, Veltman, Rombouts, Lazeron, et al., 2003; Morcom, Good, Frackowiak, & Rugg, 2003). Taken together, the literature suggests that small encoding deficits may occur with age for verbal stimuli, but that these may be limited to poorer performing elderly (Daselaar, Veltman, Rombouts, Lazeron, et al., 2003) or shallow encoding conditions (Logan et al., 2002; Friedman et al., 1996). However, deficits may be magnified for encoding visually rich picture stimuli, as a result of decreased parahippocampal engagement by older adults (Gutchess et al., 2005).

During recognition, the distinctions between different item classes are attenuated for the elderly relative to the young. Old/new effects are present in both posterior regions (e.g., Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Mark & Rugg, 1998; Wilding & Rugg, 1996), thought to reflect outputs of the medial temporal lobe (Wilding & Rugg, 1996), and anterior regions (e.g., Trott et al., 1999; Wilding & Rugg, 1996), thought to reflect prefrontally guided source retrieval (Wilding & Rugg, 1996). Age primarily affects the anterior old/new effect, reducing or obliterating the distinction in elderly, whereas the posterior old/new effect is similar for both age groups (Wegesin, Friedman, Varughese, & Stern, 2002; Trott et al., 1999; Trott, Friedman, Ritter, & Fabiani, 1997), although there are slight delays for the elderly (Wegesin et al., 2002; Mark & Rugg, 1998). Furthermore, compared to elderly adults, young show more differentiated waveforms for “remember” judgments, posited to reflect retrieval of rich contextual details from the

encoding experience (Gardiner & Java, 1990; Tulving, 1985), and “know” judgments, thought to reflect familiarity (Friedman & Trott, 2000; Trott et al., 1999).

The ERP memory and aging literature has focused largely on source memory for verbal materials, and these retrieval demands may be key to understanding the pattern of results thus far. The reduced anterior old/new effect likely reflects the source memory element of the task because this component begins roughly after the subject’s old/new response (Trott et al., 1999). The relatively intact posterior response has been interpreted as showing that medial temporal memory functions are immune to normal aging (Trott et al., 1999). The fMRI literature contradicts this claim, with several studies revealing age differences in medial temporal response (Gutchess et al., 2005; Daselaar, Veltman, Rombouts, Raaijmakers, & Jonker, 2003; Park et al., 2003; Grady, McIntosh, Rajeh, Beig, & Craik, 1999; Grady et al., 1995). Notably, the age effects in medial temporal regions appear to be largest when rich visual stimuli, such as photographs of scenes or faces, are used (as discussed in Park & Gutchess, 2004). It could be the case, therefore, that previous ERP recognition studies (Trott et al., 1999; Mark & Rugg, 1998) find similar posterior old/new effects in younger and older adults due to their reliance on verbal stimuli. The few ERP studies to use pictorial stimuli support this notion. In source recognition tasks using pictures of objects, Li, Morcom, and Rugg (2004) noted an attenuated left-hemisphere posterior old/new effect, and Duarte, Ranganath, Trujillo, and Knight (2006) identified disrupted familiarity traces in high-performing elderly and disrupted recollection and familiarity traces in low-performing elderly. These two studies suggest that using visually complex stimuli could possibly reconcile the fMRI literature, which identifies age impairments for medial temporal activation, with the ERP literature, which has not.

Another gap in the literature concerns the impact of aging on event-related potential activity corresponding to true and false recognition. Studies with young adults have revealed that accurate recognition of old items (hits) differs from false recognition of new items (false alarms). These differences take the form of amplitude modulations, with some studies showing more positive ERPs to false alarms (Goldmann et al., 2003) and others showing more positive ERPs to hits (Curran, 2000; Gonsalves & Paller, 2000; Rubin, Van Petten, Glisky, & Newberg, 1999). The difference is more pronounced in late time windows (Goldmann et al., 2003; Gonsalves & Paller, 2000; Rubin et al., 1999), and is particularly marked for highly confident decisions (Rubin et al., 1999). Both the parietal old/new effect (Curran, Schacter, Johnson, & Spinks, 2001; Nessler, Mecklinger, & Penney, 2001; Curran, 2000; Rubin et al., 1999) and the frontal source recollection effect (Goldmann et al., 2003) reflect differences in true compared to false recognition. Differentiation of true from false memory

is of interest in elderly populations because false alarm rates increase with age, particularly for lure items closely related to studied items (Koutstaal & Schacter, 1997; Norman & Schacter, 1997). Neuropsychological studies of healthy elderly and patient populations point to impaired frontal function as underlying increased false alarms and difficulty distinguishing old from new items with age (Rubin et al., 1999; Swick & Knight, 1999).

In the present study, then, we aim to address some of the gaps in the literature by using ERPs to investigate the influence of aging on the incidental encoding and subsequent recognition of complex visual scenes. Functional MRI studies suggest that age differences in medial temporal and frontal responses during encoding are magnified for this class of stimuli. To date, ERP aging studies have not used visual scenes, and the reliance on primarily verbal materials could explain why the ERP literature reports only slight encoding differences with age. Using the same materials and paradigms as a prior fMRI study will allow us to examine whether the inconsistencies in the literature remain when stimulus and task factors are controlled and to thereby gain a more complete understanding of the nature and magnitude of the impact of aging on encoding as compared with retrieval processes. Furthermore, by using lures at retrieval that are visually and semantically similar to the studied pictures, we can look for age-related differences in the brain activity associated with false, as compared with true, recognition.

METHODS

Participants

Data were obtained from a final set of 20 undergraduates (ages 18–26 years) from the University of Illinois at Urbana-Champaign (UIUC) and 20 community-dwelling elderly (ages 61–74 years) from the Champaign area, all of whom participated in the experiment for monetary compensation. Demographic characteristics of the participants are presented in Table 1. All were native English speakers, free from neurological and psychiatric disorders, and reported right-hand dominance (based on the Edinburgh inventory; Oldfield, 1971). The study was approved by the UIUC Institutional Review Board, and the participants provided written informed consent upon arrival at the laboratory.

Neuropsychological Assessment

Participants completed a battery of neuropsychological tests to compare cognitive ability across age groups. Samples were characterized with demographic and health questionnaires and screened for dementia using the Mini-Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975). Cognitive function was assessed by a variety of measures: for speed of processing, Digit Com-

Table 1. Demographics, Neuropsychological Measures, and *p* Values Corresponding to the *t* Test for Age Differences on These Measures

	Young	Elderly	<i>p</i>
<i>n</i>	20	20	
Sex	11 M, 9 F	10 M, 10 F	
Age (years)	20.45 (1.67)	68.50 (4.49)	<.001
Years of education	14.45 (1.39)	15.85 (2.01)	.014
Mini-mental score ^a	29.80 (.52)	28.65 (1.23)	.001
Digit Comparison	81.35 (17.26)	62.35 (11.73)	<.001
Dot Comparison	53.55 (11.29)	38.45 (7.76)	<.001
Trails A (sec)	28.50 (11.78)	41.60 (12.65)	.002
Trails B (sec)	53.40 (19.39)	82.10 (20.66)	<.001
Digit–Symbol	68.65 (9.99)	52.90 (9.58)	<.001
Letter–Number Sequencing	13.95 (2.33)	10.60 (2.37)	<.001
Forward Digit Span ^b	11.80 (2.19)	10.15 (2.54)	.034
Backward Digit Span ^b	8.65 (2.35)	6.65 (2.08)	.007
Verbal Fluency (“A”)	15.95 (4.98)	15.75 (5.95)	.909
Verbal Fluency (“round”)	14.40 (3.47)	13.75 (3.61)	.565
Paired Associates memory	28.60 (4.92)	20.90 (7.40)	<.001
Verbal Recall memory	7.70 (.73)	6.05 (2.11)	.002
Shipley Vocabulary	34.25 (1.94)	35.70 (3.33)	.101

Scores are presented as means and standard deviations.

^aMMSEs were scored using the 7 subtraction task rather than WORLD backward. The minimum score was 27.

^bAverage denotes number of correct trials (out of 18), not span length. The task is terminated when the participant misses both trials for a given span length.

parison (Hedden et al., 2002), Dot Comparison, Trail-Making tests A and B (Reitan & Wolfson, 1993), and Digit–Symbol coding (Wechsler, 1997a); for working memory/executive function, Letter–Number Sequencing (Wechsler, 1997b), Forward and Backward Digit Span (Wechsler, 1997a), and Verbal Fluency (Ekstrom, French, Harmon, & Derman, 1976; Benton, 1968); for long-term memory, Paired Associates memory (Wechsler, 1997b) and Verbal Recall (Wechsler, 1997b); and for crystallized knowledge, Shipley Vocabulary (Shipley, 1986). Performance on each measure is displayed in Table 1. Although elderly adults had significantly more years of education and marginally higher vocabulary scores than young adults, they performed significantly more poorly on all other speeded and memory measures, with the exception of verbal fluency.

Materials

Stimulus materials consisted of 388 full-color photographs of outdoor scenes, identical to those used in a previous fMRI study (Gutchess et al., 2005). The images subtended 10.85° of visual angle horizontally and 8.01° vertically. Each of the 194 encoding pictures was paired with a recognition lure matched on the basis of perceptual similarity and semantic content (see Figure 1). Participants received one of four pseudorandomized orderings of stimuli, with counterbalanced assignment of response hands.

Experimental Procedure

Each volunteer participated in a single experimental session. There were three phases for the experimental task: encoding, an intermediate filler task, and recognition. Each phase began with a short practice trial designed to familiarize the participants with the experimental condition and task. At times the practice trial was repeated upon participants' request to ensure they understood the tasks. Participants were asked not to blink or move their eyes from the center of the screen during the first second of picture presentation, and advised to blink after responding. Each phase contained several short breaks to prevent fatigue.

During the encoding phase, the participants were instructed to make a perceptual judgment for each of the 194 photos (namely, whether or not water was present), and to respond by pressing the "yes" or "no" button. They were not informed of a subsequent recognition task in advance. Each photo was presented for a duration of 4000 msec with an interstimulus interval (ISI) of 3000 msec.

After a 10-min intermediate filler task (living/nonliving judgments to verbal stimuli), a surprise recognition test

was administered. Participants determined whether they had seen each photograph during the encoding phase and responded with a yes or no button press for all 194 encoded photographs plus 194 perceptually similar lures. In addition, for the photos they thought they had seen previously, participants were instructed to decide how certain they were. If they were highly confident that they saw the picture before, they were to press the yes button twice. If they were less confident, they were instructed to press the yes button once. Each photo was presented for a duration of 5000 msec with an ISI of 2000 msec.

Electroencephalogram Recording Parameters

The electroencephalogram (EEG) was recorded from 26 geodesically arranged silver/silver chloride electrodes (see icon in Figure 2). These sites included midline prefrontal (MiPf), left and right medial prefrontal (LMPf and RMPf), left and right lateral prefrontal (LLPf and RLPf), left and right medial frontal (LMFr and RMPf), left and right mediolateral frontal (LDFr and RDFr), left and right lateral frontal (LLFr and RLFr), midline central (MiCe), left and right medial central (LMCe and RMCe), left and right mediolateral central (LDCe and RDCe), midline parietal (MiPa), left and right mediolateral parietal (LDPa and RDPa), left and right lateral temporal (LLTe and RLTe), midline occipital (MiOc), left and right medial occipital (LMOc and RMOc), and left and right lateral occipital (LLOc and RLOc). These sites were referenced online to the left mastoid, and then re-referenced offline to the average of the left and right mastoids. Blinks and eye movements were monitored via electrodes placed on the outer canthus of each eye and the infraorbital ridge of the left eye. Electrode impedances were kept below 5 kΩ. EEG was processed through Sensorium (Charlotte, VT) amplifiers set at a

Figure 1. Example stimuli. Recognition of the pictures presented at encoding was tested for the original pictures (left) as well as matched lures (right).

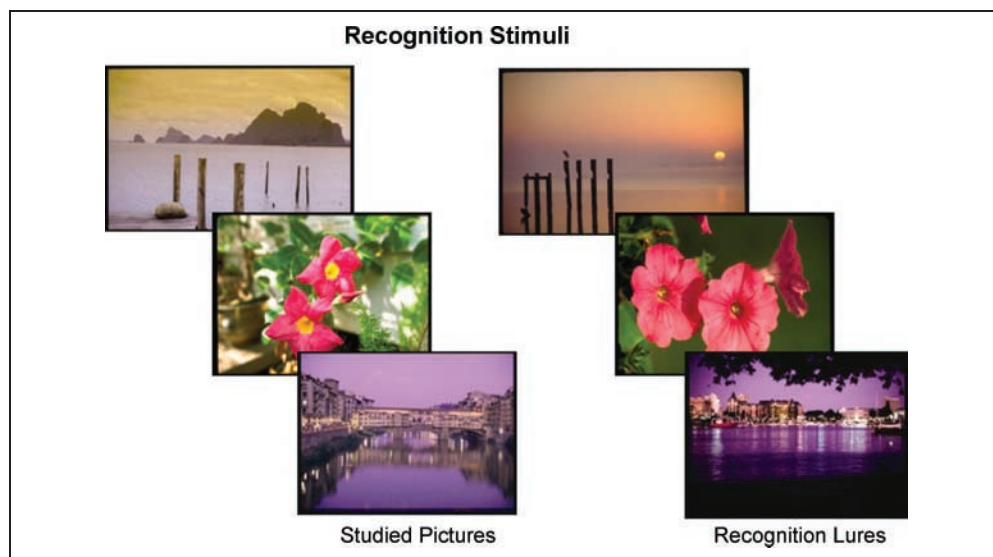
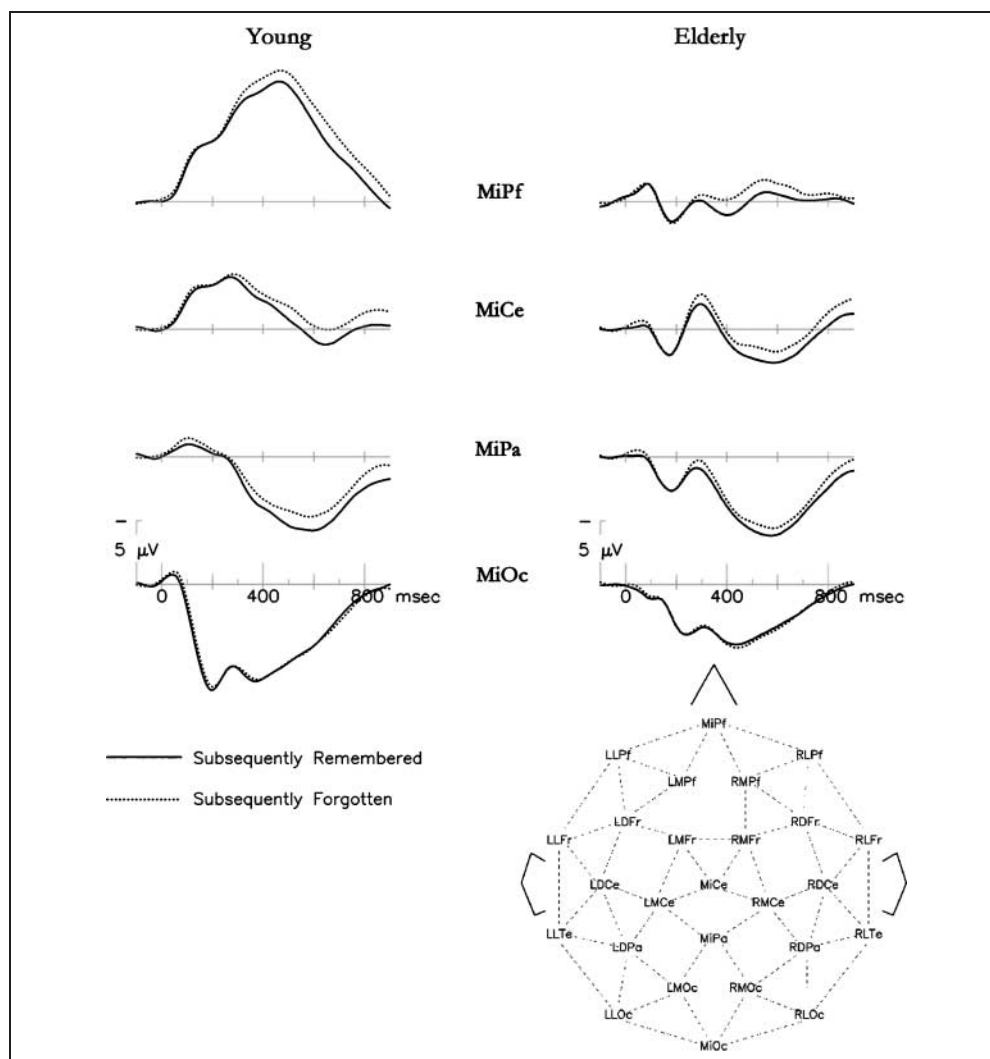


Figure 2. Encoding: subsequent memory comparison. ERPs at encoding for subsequent hits (successful encoding) and subsequent misses (unsuccessful encoding) are plotted at the four midline channels for young (left) and elderly (right). The head icon (bottom right) shows the full electrode arrangement. Negative is plotted up in this and all subsequent figures. Both groups exhibit a subsequent memory effect, with more positivity to the remembered items. See text for abbreviations.



bandpass of 0.02–100 Hz. EEG was continuously digitized at 250 Hz and stored on hard disk for later analysis.

Data Analysis

ERPs were computed from 100 msec prior to picture onset to 920 msec after. The entire picture presentation duration could not be examined because the complex scenes introduced the potential for greater contamination from eye movements; participants were asked to refrain from eye movements during the first second of picture presentation and were largely successful at doing so. Epochs containing artifacts from amplifier blocking, signal drift, excessive eye movements, or muscle activity were rejected offline before averaging, and those contaminated by eye blinks were corrected (Dale, 1994) for those participants (10 young and 14 elderly) with sufficient numbers of blinks to obtain a stable blink filter. Data were re-referenced to the algebraic mean of the left and right mastoids, and, after subtraction of the 100-msec prestimulus baseline, averages of artifact-free

ERPs were calculated for each picture classification for both encoding (back-sorted based on recognition response) and recognition. Prior to measurement, ERPs were digitally filtered with a bandpass of 0.2–20 Hz.

RESULTS

Behavioral Performance

The signal detection measure A' , which combines hit and false alarm rates into a single nonparametric measure (Stanislaw & Todorov, 1999), was calculated for each confidence level across participants. The maximum possible score is a 1, signifying perfect discrimination, and a score of .5 corresponds to chance performance. Using independent t tests to compare young and elderly, we found no age differences in A' scores when considering high confidence, $t(38) = .88, p > .38$; low confidence,¹ $t(37) = .92, p > .36$; or all responses, $t(38) = 1.17, p > .24$. Older adults' performance was better here than seen previously for this paradigm in the Gutches

et al. (2005) study, possibly because the removal of fMRI baseline trials yielded a shorter retention interval, although the noisy scanning environment could also have impaired performance (Gutchess & Park, 2006).

Response bias (tendency to say yes or no) was measured with c ; negative values indicate a yes bias, and positive values a no bias. No age differences were noted for high confidence, $t(38) = .02, p > .99$; low confidence, $t(37) = 1.10, p > .28$; or all responses, $t(38) = 1.63, p > .11$. See Table 2 for A' and c averages for each age group and Table 3 for the hit and false alarm rates used to calculate these measures.

ERPs at Encoding (Dm Effects)

Figure 2 shows the ERPs elicited at encoding by pictures that were subsequently remembered (subsequent hits) or forgotten (subsequent misses) for young (left) and elderly (right) at a set of representative midline channels. Figure 3 shows the responses to subsequent high- and low-confidence hits. There are notable group differences in the morphology of the ERP response to complex scenes, with young adults showing a prominent frontal negativity that appears to be largely absent in the responses of elderly adults. This group difference has been observed previously for retrieval of visually rich materials (Duarte et al., 2006; Senkfor & Kutas, 2000) and was speculated to reflect differences in the use of source information (Senkfor & Kutas, 2000). Here, however, we see the same morphological differences at encoding and under incidental encoding conditions, suggesting it may be a more pervasive age-related difference in the response to complex visual stimuli.

Given the baseline morphological differences, we analyzed effects on the ERP averages within each group separately and then conducted direct comparisons across groups using difference waves (hits minus misses). We adopted a subsequent memory (Dm) approach, compar-

Table 2. A' and Response Criterion Measures for the Recognition Task

	Young	Elderly
A'		
High confidence	.75 (.05)	.73 (.06)
Low confidence	.57 (.08)	.55 (.11)
Across high and low	.73 (.06)	.70 (.08)
c		
High confidence	1.13 (.45)	1.13 (.48)
Low confidence	.69 (.28)	.54 (.53)
Across high and low	.23 (.41)	.09 (.43)

Means and standard deviations are shown for each age group.

Table 3. Raw Hit and False Alarm Scores for the Recognition Task

	Young	Elderly
Hit		
High confidence	.29 (.13)	.27 (.13)
Low confidence	.27 (.11)	.35 (.16)
All	.56 (.15)	.62 (.15)
False alarm		
High confidence	.07 (.07)	.08 (.08)
Low confidence	.21 (.11)	.30 (.16)
All	.29 (.15)	.38 (.18)

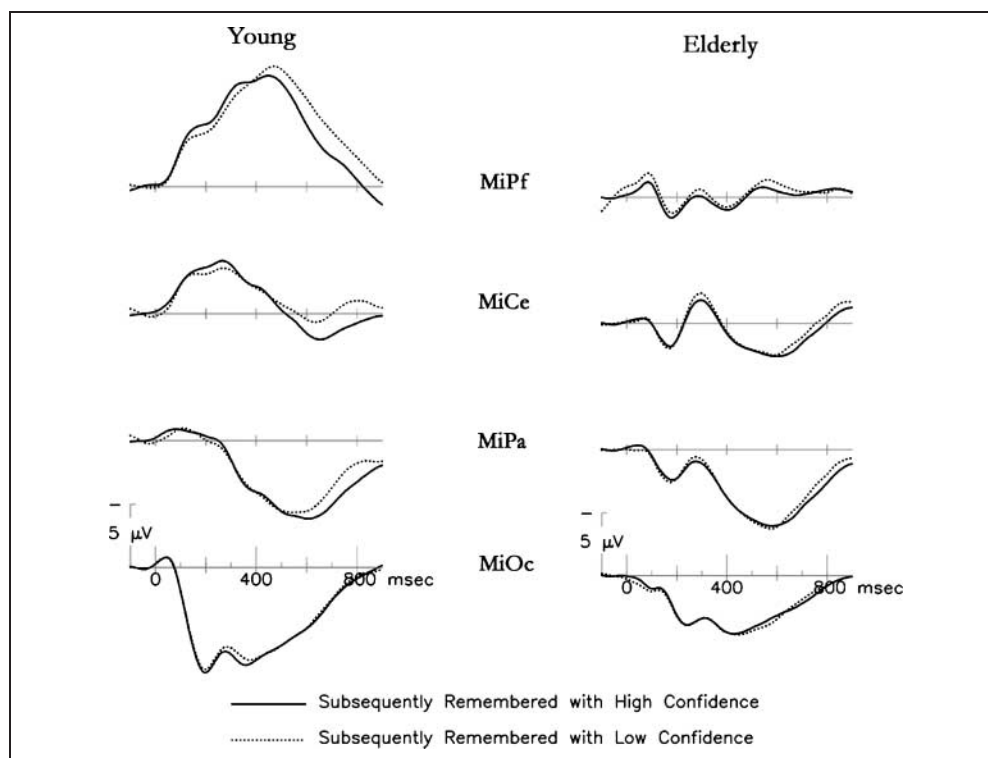
Means and standard deviations are shown for each age group.

ing the ERPs elicited at encoding for items that were later remembered (hits) or forgotten (misses), and further broke the analyses down by confidence. The average numbers of trials included as subsequently remembered was 95 for young and 105 for elderly. Of these, young had 49 high-confidence trials and 46 low-confidence trials, and elderly had 46 and 58, respectively. There were 71 subsequently missed trials for young and 63 for elderly. Across all trial types, 87% were available for young and 89% for elderly after artifact rejection. Encoding data were analyzed in two time windows: from 300 to 600 msec ("early Dm effect") and from 600 to 900 msec ("late Dm effect"). Initial analyses within each age group were conducted on mean amplitudes in the time window of interest and assessed with repeated measures analyses of variance (ANOVAs) with two levels of Condition and 26 levels of Electrode Site (i.e., all scalp sites); p values are Huynh-Feldt corrected for repeated measures with more than one degree of freedom. Interactions of experimental factors with electrode site will only be reported when of theoretical significance. These were followed by across-group comparisons on the difference waves in these same two time windows.

Young Adults: Encoding

As can be seen in Figure 2, young showed a small overall Dm effect with a predominantly frontocentral distribution. A trend for this effect (subsequent hits more positive than subsequent misses) is present in the early time window, $F(1,19) = 2.91, p = .10$,² and the difference increases with time, reaching significance by the later time window, $F(1,19) = 8.80, p < .01$. There is also a main effect of confidence, such that the Dm effect in the later window is largely driven by the greater positivity to high- than to low-confidence items, $F(1,19) = 4.68, p < .05$ (Figure 3). In that late window, items later remembered with high confidence are more positive

Figure 3. Encoding: subsequently remembered with high and low confidence. ERPs at encoding for subsequent high- and low-confidence remember responses are displayed for young (left) and elderly (right). Confidence modulates the subsequent memory effect for young, but not elderly.



than items later missed, $F(1,19) = 12.94$, $p < .003$, unlike items later remembered with low confidence, $F(1,19) = 1.02$, $p > .30$.

Elderly Adults: Encoding

Elderly also show a small overall Dm effect with a frontocentral distribution (Figure 2). In this group, the effect was significant in both the early, $F(1,19) = 6.20$, $p < .03$, and late, $F(1,19) = 6.79$, $p < .02$, time windows. However, confidence did not modulate the results for the elderly (Figure 3), as the high-confidence hits did not differ from low-confidence hits in either time window ($F_s < 1$).

Age Differences: Encoding (Dm Effects)

In a direct comparison of the Dm difference wave (hits minus misses) across young and elderly, age differences do not reach significance (overlapped difference waves can be seen in the left half of Figure 7). When collapsing across confidence levels in an ANOVA with Age (young/elderly) and Electrode Site as factors, there is no main effect of age for the early or late time windows (young Dm effects, 0.49 and 0.79 μV ; elderly Dm effects, 0.56 and 0.52 μV ; $F_s < 1$). Likewise, there are no interactions involving age in either time window (early: $F = 1.25$, $p > .27$; late: $F < 1$) when confidence levels are included in an Age \times Confidence (high-confidence hit minus miss/low-confidence hit minus miss) \times Electrode Site ANOVA. When only the high-confidence Dm effect is considered

(the condition that showed prominent age-related differences in the fMRI study using these materials; Gutchess et al., 2005), a marginal effect of age emerges in the late time window, $F(1,38) = 3.57$, $p < .07$, such that the Dm effect is larger for young ($M = 1.43 \mu\text{V}$) than elderly ($M = 0.55 \mu\text{V}$). No age differences were seen for the low-confidence Dm effect ($F_s < 1$).

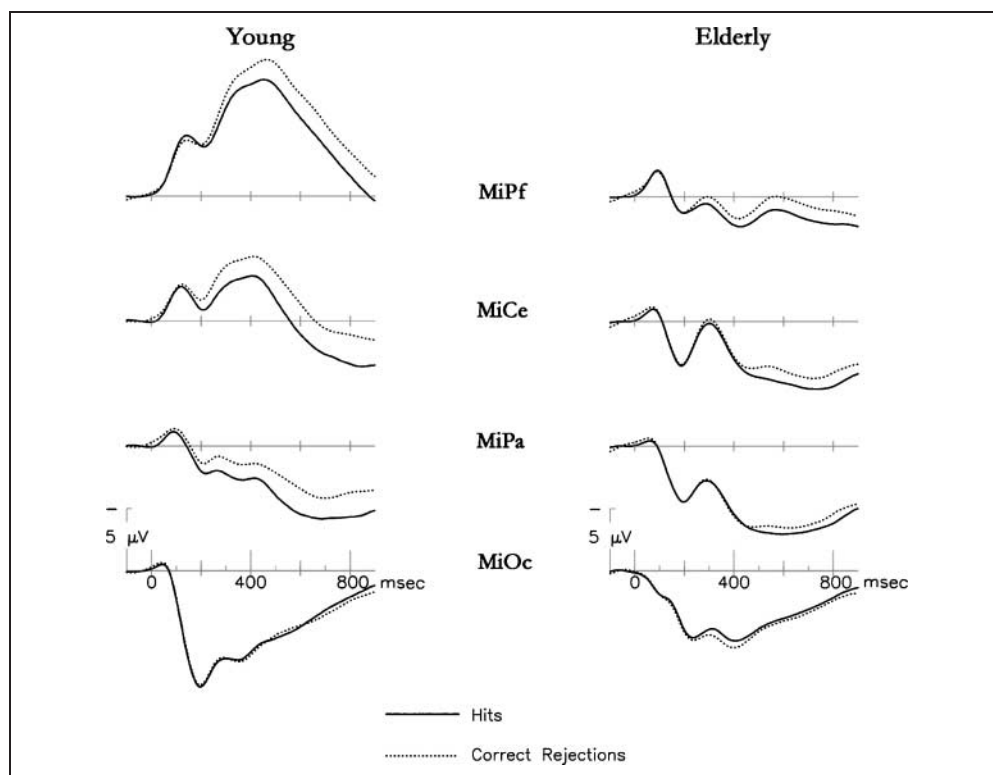
Overall, robust age differences did not occur at the time of encoding. The appearance of an earlier-occurring Dm effect for the elderly was not borne out statistically in the difference wave comparison. Young adults show a marginally larger effect in the later time window for the comparison of misses with items later remembered with high confidence.

ERPs at Recognition (Old/New Effects)

Figure 4 shows the ERPs elicited at retrieval by old pictures and new pictures that were correctly identified as such (hits and correct rejections) for young (left) and elderly (right) at a set of representative midline channels. Figure 5 shows the responses to high- and low-confidence hits. The group differences in waveform morphology noted at encoding are also present at retrieval. Again, therefore, we analyzed effects on the ERP averages within each group separately and then conducted direct comparisons across groups using difference waves.

Based on prior literature identifying discrete parts of the broader old/new effect (Rugg et al., 1998), ERP

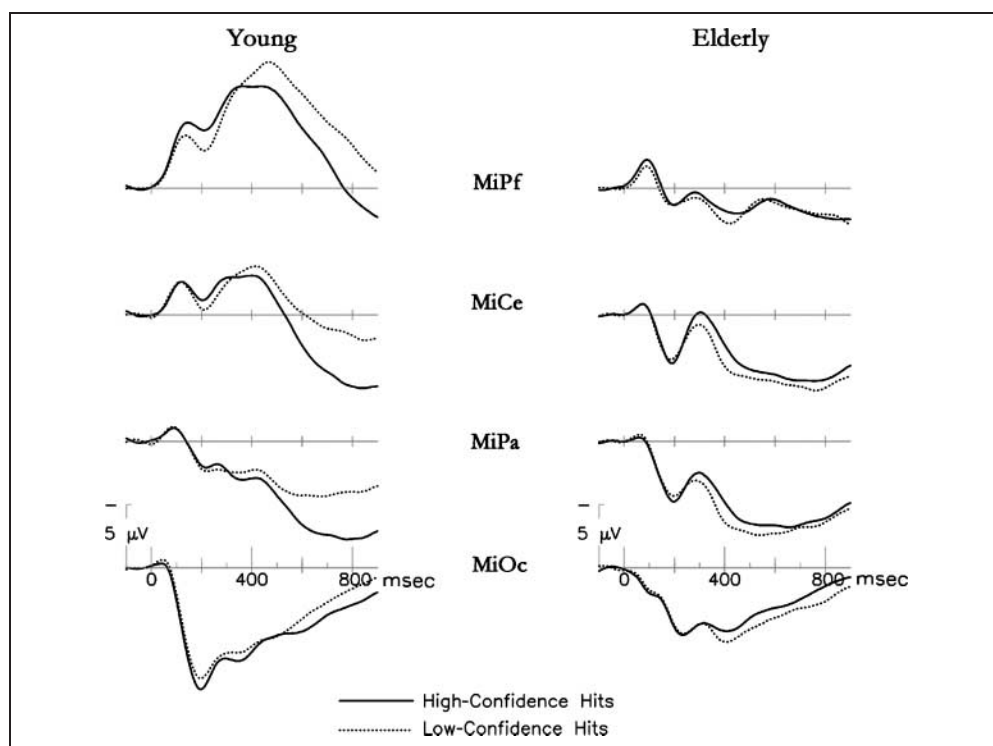
Figure 4. Recognition: old/new comparison. ERPs for hits (old items) and correct rejections (new items) are shown for young (left) and elderly (right). Between 300 and 700 msec, young adults' ERP responses differentiate old from new trials much more than do those of elderly adults.



measures were made separately within an early (300–500 msec; N400) time window thought to capture implicit aspects of memory that are preserved in amnesiacs (Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001) and within two later time windows (500–700 and 700–

900 msec; late positive complex [LPC]) that have been linked to explicit aspects of memory that are impaired in amnesiacs. Hits were compared with correct rejections, and the effects of confidence on hits were assessed. In addition, accurate versus inaccurate recognition was ex-

Figure 5. Recognition: high- and low-confidence hits. ERPs for high- and low-confidence hits are displayed for young (left) and elderly (right). Confidence modulates the old/new effect for young, but not elderly.



amined based on a comparison of hits and false alarms. For young and elderly, respectively, 94 and 103 hit trials were available for young and elderly, and of these, 49 and 46 were high confidence and 45 and 57 were low confidence. The groups averaged 70 (young) and 61 (elderly) miss trials and 115 and 101 correct rejection trials. Because there were few high-confidence false alarms in either group, false alarms were summed across confidence for all analyses, giving young 48 and elderly 71 trials. Across trial types, 85% of trials for young and 87% of trials for elderly remained after artifact rejection.

Young Adults: Recognition

As can be seen in Figure 4, young show a widespread old/new effect (comparison of Hits and Correct Rejections), which is largest over central sites. The effect begins in the early (300–500 msec) time window, $F(1,19) = 31.75, p < .0001$, and is sustained through later epochs: 500–700 msec, $F(1,19) = 27.22, p < .0001$; 700–900 msec, $F(1,19) = 19.22, p < .0004$. Confidence modulates the LPC (Figure 5), with high-confidence hits distinct from low-confidence hits from 500 to 700 msec, $F(1,19) = 13.18, p < .003$, and 700 to 900 msec, $F(1,19) = 18.39, p < .0005$, but not from 300 to 500 msec, $F(1,19) = 1.26, p > .25$. Similar to the pattern seen in the encoding data, the effects seem to be driven by the high confidence hits. Although both high-, $F(1,19) = 20.54, p < .0003$, and low-confidence hits, $F(1,19) = 7.65, p < .02$, are distinct from correct rejections between 500 and 700 msec, only high-confidence hits continue to differ from correct rejections, $F(1,19) = 20.57, p < .0003$, in the 700- to 900-msec time window ($F < 1$ for low-confidence hits).

The old/new effect discussed above is based on items correctly identified as old or new (Hit or Correct Rejection), but accurate and inaccurate recognition can also be examined by comparing the response to Hits with that to False Alarms (mistaken identification of a new item as

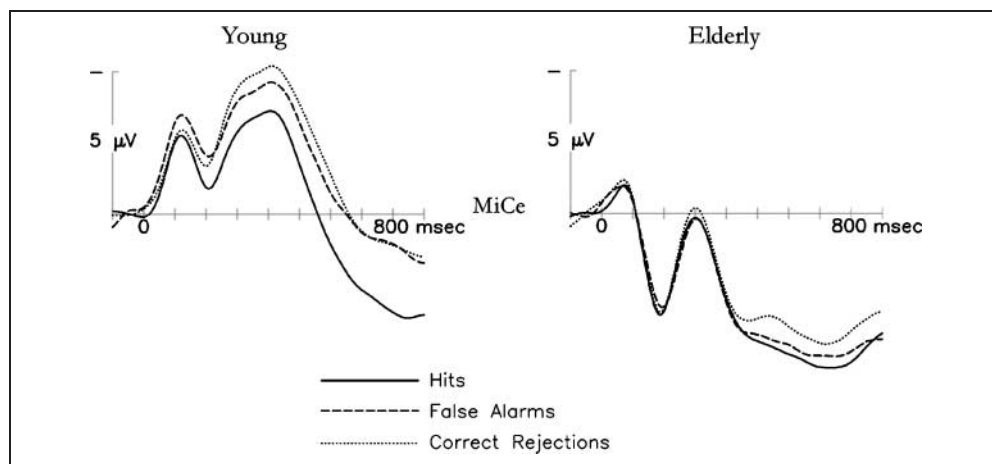
“old”). These can be seen on the left side of Figure 6. Young adults’ waveforms distinguish items correctly called old (Hits) from false alarms across all time windows: $F(1,19) = 6.84, p < .02$ for 300–500 msec; $F(1,19) = 12.11, p < .003$ for 500–700 msec; $F(1,19) = 20.36, p < .0003$ for 700–900 msec. The effect is modulated by confidence during the LPC, with high-confidence hits distinct from false alarms for early, $F(1,19) = 19.66, p < .0004$, and late, $F(1,19) = 23.53, p < .0002$, time windows, but low-confidence hits indistinguishable from false alarms ($F_s < 1$).

To summarize the recognition results for young adults, in the earliest time window (300–500 msec), linked to implicit recognition processes, hits are distinguished from correct rejections and false alarms (which do not differ from each other, $F < 1$). Then, in the early part of the LPC, there is an additional differentiation of high-confidence hits from low-confidence hits. Low-confidence hits were still more positive than correct rejections but did not differ from false alarms in this time window. Finally, between 700 and 900 msec, high-confidence hits were more positive than all other conditions, which did not differ. In other words, it seems that if the brain signal between 500 and 700 msec is positive enough, participants will say yes (to truly old items, and also to some lures). If that signal is particularly large and continues into the 700- to 900-msec window, they will respond with high confidence (which is rarely attributed to lures). Over all channels, misses tended to be more positive than, but were not significantly different from, correct rejections.

Elderly Adults: Recognition

For the elderly, an old/new (Hit/Correct Rejection) effect can be seen in the 500- to 700-msec window, $F(1,19) = 10.02, p < .006$, and the 700- to 900-msec time window, $F(1,19) = 6.23, p < .03$ (LPC), but unlike the pattern for the young, is absent in the earliest (implicit recognition) time window (300–500 msec), $F(1,19) = 1.35, p > .25$

Figure 6. Recognition: true and false memory comparison. ERPs for true recognition (hits), false recognition (false alarms), and correct rejections of new items are plotted for young (left) and elderly (right) at the middle central site, where old/new effects are prominent. Despite identifying both trial types as “old,” young adults’ ERPs reliably differentiate items that are truly old (hits) from those mistakenly called old (false alarms), whereas elderly adults’ ERPs do not.



(see Figure 4). Similar to the pattern seen for this group at encoding, the waveforms for the elderly are not different as a function of confidence ($F_s < 1$ during the LPC) (Figure 5). Strikingly, the responses to hits and false alarms are indistinguishable for the elderly during any time window: 300–500 msec, $F < 1$; 500–700 msec, $F(1,19) = 1.51, p > .20$; 700–900 msec, $F(1,19) = 1.27, p > .25$, (see Figure 6, right). Even the high-confidence hits cannot be discriminated from false alarms during any time window: 300–500 msec, $F(1,19) = 1.14, p > .30$; $F_s < 1$ for 500–900 msec. As was also true for the young, responses to misses and correct rejections do not differ reliably.

In summary, at recognition elderly show no condition-related effects in the earliest time window (300–500 msec). In the LPC time windows (500–700 and 700–900 msec), hits and false alarms—that is, all items that are associated with a yes response—elicit more positive ERPs than do correct rejections (and misses); this old/new effect is not modulated by confidence. However, hits and false alarms do not differ in any window, that is, the brain signal associated with new items that were misidentified as old is, in this group, indistinguishable from that associated with genuinely old items that were recognized as such.

Age Differences: Recognition (Old/New Effect)

In a direct age comparison of old/new effects (difference waves; see Figure 7, right) using an Age \times Electrode Site ANOVA, there was a main effect of age in the early, $F(1,38) = 9.78, p < .004$, and middle, $F(1,38) = 5.77, p < .03$, time windows, but the age difference was not reliable by the latest time window, $F(1,38) = 2.79, p = .10$. In both time windows, the old/new effect was larger for young adults (300–500 msec: young = $-1.10 \mu\text{V}$, elderly = $0.23 \mu\text{V}$; 500–700 msec: young = $1.49 \mu\text{V}$, elderly = $0.65 \mu\text{V}$). When confidence (high/low) was considered in the model, interactions of Age \times Confidence were present across all time windows and particularly pronounced in the LPC: early, $F(1,38) = 5.48, p <$

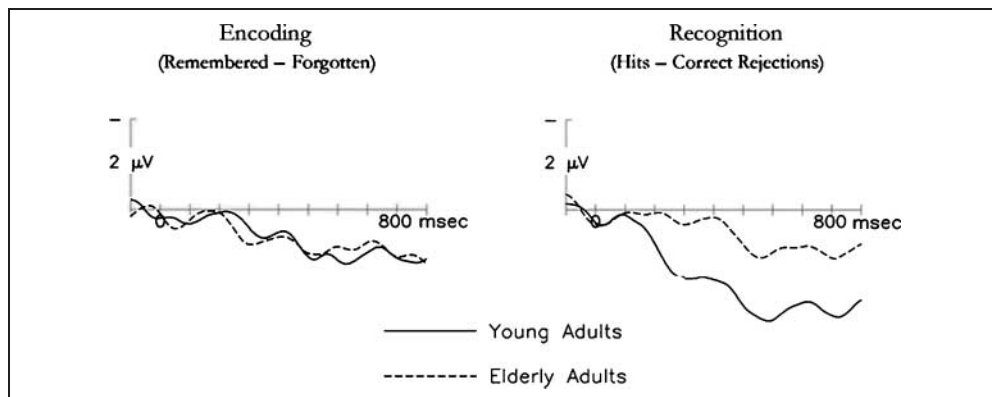
.03; middle, $F(1,38) = 13.13, p < .0009$; late, $F(1,38) = 15.17, p < .0005$. Main effects of age were present in the early and middle windows, and main effects of confidence were present in the middle and late windows. High-confidence responses contributed substantially to age differences in the old/new effect. When only highly confident “old” responses were considered, there was a main effect of age such that young showed a more pronounced old/new effect than elderly for early, young = $1.4 \mu\text{V}$ vs. elderly = $-0.07 \mu\text{V}$; $F(1,38) = 12.54, p < .002$; middle, young = $2.49 \mu\text{V}$ vs. elderly = $0.56 \mu\text{V}$; $F(1,38) = 10.00, p < .004$; and late, young = $3.05 \mu\text{V}$ vs. elderly = $0.70 \mu\text{V}$; $F(1,38) = 10.07, p < .004$, time windows. This pattern did not extend to the low-confidence old/new effect. In the analysis of low-confidence responses, age differences were not significant for early or middle time windows ($F_s < 1$), and the marginal age difference in the late time window, $F(1,38) = 3.25, p = .08$, was driven by a larger old/new effect in the elderly ($.89 \mu\text{V}$) than the young ($0.00 \mu\text{V}$).

In contrast to the relative convergence of the encoding data for young and elderly, old/new effects at recognition show much more pronounced age differences. Young show a larger overall old/new effect, and this is driven by an enhanced response for high-confidence items in all time windows.

Age Differences: Recognition (Hits/False Alarms)

Turning to the direct comparison of the age groups for the Hit/False alarm discrimination, age differences are again significant across the time windows: early, $F(1,38) = 4.16, p < .05$; middle, $F(1,38) = 4.70, p < .04$; and late, $F(1,38) = 7.30, p < .02$. Young adults’ waveforms discriminated hits from false alarms to a greater extent than elderly adults’ did (0.81 vs. $0.05 \mu\text{V}$ for early, 1.22 vs. $0.30 \mu\text{V}$ for middle, 1.55 vs. $0.33 \mu\text{V}$ for late). When confidence is considered, age interacts with confidence across all time windows: early, $F(1,38) = 5.50, p < .03$; middle, $F(1,38) = 13.16, p < .0009$; late, $F(1,38) = 15.18, p < .0005$. In the analyses including confidence,

Figure 7. Age differences at encoding and recognition. Encoding difference wave ERPs for the subtraction of subsequently remembered minus subsequently forgotten trials for young and elderly (left) and recognition difference wave ERPs for the subtraction of Old items minus New items (right). Note the pronounced age differences during recognition, in contrast to the similarity of the difference waves for the young and elderly during encoding.



main effects of age and confidence are present for the middle and late time windows, whereas only a marginal main effect of age exists in the early time window. The age differences were driven by the high-confidence hits, with significant age differences present across all time windows: early, $F(1,38) = 10.10, p < .003$; middle, $F(1,38) = 12.68, p < .002$; late, $F(1,38) = 14.02, p < .0007$. No significant age effects emerged for the comparison of low-confidence hits with false alarms ($F_s < 1$). Because only related lures were included in this study, it is unknown whether these age differences represent a general pattern of age-related changes or are specific to the case when lures are related to studied items.

DISCUSSION

The results of the present ERP study reveal substantial age-related differences during recognition and more circumscribed age-related differences during encoding. In addition, to our knowledge this is the first aging study to identify age-related differences in the neural response to correctly recognized items (hits) as compared with falsely recognized items (false alarms). These findings will be discussed in turn.

At the encoding stage, we observed similar subsequent memory effects for young and elderly adults. In contrast to prior ERP studies looking at incidental encoding of verbal stimuli (Friedman et al., 1996), elderly in the present study did exhibit a Dm effect for the incidental encoding of complex scenes. However, there were some differences across the age groups, with confidence modulating the Dm effect for young but not elderly, consistent with Friedman and Trott's (2000) observation of reduced remember-know differences in older adults for intentional verbal encoding. Young showed a marginally larger Dm effect in the late time window (700–900 msec) for items later recognized with high confidence, which converges with the fMRI finding of reduced medial temporal signal with age for this same comparison (Gutchess et al., 2005). These data leave open, however, the possibility that this is not an encoding deficit as such, but a retrieval deficit that leads to a different distribution of the encoding signal across confidence bins for the old as compared with the young subjects. We note that restrictions on eye movements during the first second of picture presentation make the task less natural and prevent the detection of age-related encoding differences that might be associated with the willful direction of attention via eye movements. However, such instructions were necessary to obtain clean ERPs; different methodological constraints apply to most brain imaging methods and may affect task performance (see Gutchess & Park, 2006, for a discussion of the effects of fMRI environment on performance).

It is important to consider how sorting the waveforms by confidence might contribute to the pattern of results

observed. Wagner, Koutstaal, and Schacter (1999) discuss two ways that binning by confidence can affect Dm effects. Restricting analyses to high-confidence responses may help to remove items that receive correct responses on the basis of guessing and can also serve to distinguish those studied items that have been meaningfully integrated with other episodic memories. These factors might apply differently to the two age groups. For example, if restricting analyses to high-confidence responses reduces guessing-related noise, then the low-confidence responses should pattern like misses (i.e., neither low-confidence hits nor misses were encoded and only guessing separates the two item classes). Although this is the pattern seen for the young adults, it is not the case for the elderly, whose brain waves differentiate both high- and low-confidence hits from misses but do not distinguish the levels of confidence from each other. Thus, low-confidence responses for the elderly may not be guesses in the same sense as for the young. Indeed, had we examined encoding phase data only for the items later given a high-confidence response, we would have been led to conclude that the overall amount of encoding phase activity associated with successful retrieval is reduced for elderly as compared with young participants. Instead, when the brain activity to subsequent hits is combined across confidence category, young and elderly show similar levels of encoding phase activity. These points underscore the possibility that even when behavioral recognition performance is similar for young and elderly groups, there may be important differences in the mapping of that behavior to neurocognitive processes.

Although ERP responses during the encoding phase were fairly similar across age groups, ERP responses at retrieval differed markedly with age, with the young showing an earlier old/new difference and a larger effect, particularly for high-confidence items, across all time windows. There is precedent for these findings in the verbal recognition literature, which reports that the old/new effect is reduced in older adults at frontal (Wegesin et al., 2002; Trott et al., 1997, 1999) and, for pictures, parietal sites (Li et al., 2004), with studies also reporting a delay in the appearance of the old/new effect for older adults (Wegesin et al., 2002; Mark & Rugg, 1998). As was seen at the encoding stage, high- and low-confidence responses at retrieval are more distinct for young than elderly, which is consistent with prior findings using the remember-know distinction (Friedman & Trott, 2000; Trott et al., 1999). Indeed, in the present study the brain signal elicited by older adults was indistinguishable for high- and low-confidence responses, which is interesting because in the old (as in the young) behavioral discrimination was better for high-confidence responses.

In addition, young adults' brain responses distinguished truly old items from lures, even those that ultimately yielded a yes response; again, this effect was largely driven by the high-confidence hit responses. For

the young, then, brain responses elicited by the test stimulus differentiate old from new items and, for hits, predict the confidence with which the response will be given. The brain signal in older adults strikingly fails to discriminate between truly old items and some of the new items—those that will then be misidentified as old. Thus, the brain signal for older adults is predictive of whether they will say yes or no (but not of the confidence of their response), but does not differentiate truly old and new items as effectively as that in younger adults. This diminished ability of the elderly brain at retrieval to (at least immediately) distinguish old items from new lures is likely to be an important contributor to the memory difficulties experienced with age. Previous studies of young adults suggest that ERPs to hits and false alarms can be similar when lures are highly related to the targets by gist or general conceptual or thematic information (Cheng & Rugg, 2004; Curran et al., 2001; Nessler et al., 2001). Our results suggest that, relative to elderly, young may acquire more item-specific details during incidental encoding. Encoding of these additional details may create, at retrieval, differentiated brain signals for truly old items. A reliance on gist, shared by target and lure items, could be responsible for the indistinguishable brain responses to hits and false alarms for elderly adults, consistent with their robust tendency to make gist-based memory errors (Koutstaal & Schacter, 1997). Alternatively, it may be that both groups encode detailed information but that the older adults fail to use this information as effectively at retrieval. In some studies, older adults have been found to encode perceptual details as well as young, with gist-based interference then inflating older adults' errors during recognition (Koutstaal, 2003). Our data are largely consistent with these behavioral findings, although we find that subtle neural differences with age are present at encoding. Future studies could explicitly manipulate the degree of gist-based processing to assess whether the convergence of hit and false alarm waveforms in the elderly is specific to gist recognition, or generalizes more broadly to recognition memory. For example, elderly may have distinct waveforms for hits and false alarms when the lures are unrelated to the studied items. Regardless of whether the effect is due to gist-based processing, it is surprising that elderly adults perform as well as young adults on the recognition task, despite the lack of any reliable brain signal difference in the ERPs. This suggests that whereas the present data may capture a signature of gist-based recognition, we do not capture a mechanism involved in overriding the contribution of gist, which informs the ultimate memory decision.

For the elderly, the lack of distinct signatures associated with both the overriding of gist-based recognition and the determination of confidence is puzzling. Elderly show similar levels of behavioral discrimination as young adults in the face of clearly reduced levels of brain dis-

crimination, which suggests that other brain signals not seen here contribute to elderly adults' recognition discrimination. We identified compensatory dorsolateral prefrontal cortex activity in our fMRI study of subsequent scene memory (Gutchess et al., 2005), but it is possible that this activity is not amenable to measurement by ERPs because it has a slow or temporally jittered time course or comes from areas that cannot be seen at the scalp electrophysiologically (although this is relatively unlikely for frontal cortical areas that have previously been suggested to serve a compensatory function based on fMRI evidence; Reuter-Lorenz & Lustig, 2005; Cabeza, 2002; Reuter-Lorenz, 2002; Grady et al., 1994). Frontally based evaluative components in recognition have been identified after 1000 msec that may discriminate true from false recognition (e.g., Nessler & Mecklinger, 2003). However, the use of complex scenes in the present study introduces heightened contamination from eye movements, making it difficult to examine extended periods (although trends for late time window differences in true and false recognition were apparent before 1000 msec in Nessler and Mecklinger's [2003] study). Although it is possible that we were unable to capture some slow effects with our restricted time window, the peak of the old/new effect (as well as the Dm effect) is well within the time epoch for both age groups. Because of this, we believe that older adults' potentially slower information processing is unlikely to impact the conclusions drawn from these measures.

It is also possible that the kind of compensatory effects seen with fMRI are not detectable using ERPs. Other recent studies also fail to find evidence of compensation using ERPs (Nessler et al., 2006), although one study finds evidence of an increased anterior P3 component during an oddball task in high-performing elderly adults (Daffner et al., 2006). If compensatory activity can be identified using ERPs, the method holds much potential to clarify how additional regions contribute to task performance in older adults and to rule out alternative explanations for the recruitment of additional brain areas. For example, one alternative explanation for the correlation between increased prefrontal cortical activity and decreased medial temporal activity in older adults is that the prefrontal regions could be suppressing—rather than compensating for—the activity of medial temporal regions (Gutchess et al., 2005). If medial temporal regions are engaged first and their signal is not dampened by the subsequent recruitment of prefrontal regions, it would suggest that reduced medial temporal activation in older adults does not result from a suppression function of the prefrontal cortex.

More generally, then, we find notable differences in the pattern of aging effects observed using fMRI and ERPs, even when stimulus and task parameters are held relatively constant across the two methods. Whereas the pattern of hemodynamic activity seen in the fMRI version of this task (Gutchess et al., 2005) revealed age-

related encoding deficits and compensatory recruitment of additional brain areas during the encoding stage, ERPs collected in the same paradigm were largely similar at encoding for younger and older adults, with only a change in the distribution of the encoding signal across confidence categories. In contrast, at retrieval, ERPs revealed striking age-related reductions and delays in the old/new effect and a reduced neural differentiation of hits from false alarms. The literature suggests that retrieval-phase fMRI data, in contrast, exhibit modest age-related differences (Park & Gutchess, 2004). We suspect that these method-related differences arise because fMRI and ERPs are biased to tap into memory processes with different temporal signatures. ERPs offer a detailed picture of the first second of stimulus processing, time-locked to the appearance of the study or test item. Whereas subsequent memory effects during this initial phase of encoding of complex scenes appear largely similar for young and elderly, the trend for age differences here could foreshadow later differences in more reflective (and temporally ill-defined) processes, such as elaborative encoding, which fMRI is primed to detect across a broader time window. In contrast to the relative similarity of the first second of encoding, ERPs reveal important age-related differences in neural processing during the first second of response to a test probe. Whereas young adults' brain activity seems to provide a robust and rapid indication of whether a scene is old or new, older adults' brain activity in this time window was much less distinct for hits and correct rejections and failed to differentiate hits from false alarms. fMRI is less likely to be sensitive to these rapid signatures of recognition and, hence, to age differences in these processes. However, fMRI may be able to pick up slower processes that could contribute to older adults' attempts to resolve interference in memory, processes that inform the final memory decision. By combining methods, therefore, we gain a more complete picture of the multiple brain processes involved in laying down and accessing memory traces and, in turn, a fuller understanding of how those processes are affected by normal aging.

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Notes

1. One young participant is excluded from the low-confidence comparisons because he did not make any low confidence responses.
2. Breaking down the early time window suggests that the effect begins around 500 msec [mean amplitude 500–600 msec: $F(1,19) = 6.39, p < .03$].

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