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Age differences in the neural correlates of the specificity of recollection: An event-related potential study

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ABSTRACT

In young adults, the neural correlates of successful recollection vary with the specificity (or amount) of information retrieved. We examined whether the neural correlates of recollection are modulated in a similar fashion in older adults. We compared event-related potential (ERP) correlates of recollection in samples of healthy young and older adults (N = 20 per age group). At study, participants were cued to make one of two judgments about each of a series of words. Subsequently, participants completed a memory test for studied and unstudied words in which they first made a Remember/Know/New (RKN) judgment, followed by a source memory judgment when a word attracted a 'Remember' (R) response. In young adults, the 'left parietal effect' – a putative ERP correlate of successful recollection – was largest for test items endorsed as recollected (R judgment) and attracting a correct source judgment, intermediate for items endorsed as recollected but attracting an incorrect or uncertain source judgment, and, relative to correct rejections, absent for items endorsed as familiar only (K judgment). In marked contrast, the left parietal effect was not detectable in older adults. Rather, regardless of source accuracy, studied items attracting an R response elicited a sustained, centrally maximum negative-going deflection relative to both correct rejections and studied items where recollection failed (K judgment). A similar retrieval-related negativity has been described previously in older adults, but the present findings are among the few to link this effect specifically to recollection. Finally, relative to correct rejections, all classes of correctly recognized old items elicited an age-invariant, late-onsetting positive deflection that was maximal over the right frontal scalp. This finding, which replicates several prior results, suggests that post-retrieval monitoring operations were engaged to an equivalent extent in the two age groups. Together, the present results suggest that there are circumstances where young and older adults engage qualitatively distinct retrieval-related processes during successful recollection.

1. Introduction

Episodic memory – memory for personally experienced unique events – declines with advancing age (Craik, 1983, 1986; Drag and Bieliauskas, 2010; Koen and Yonelinas, 2014; Light, 1991; Naveh-Benjamin, 2000; Old and Naveh-Benjamin, 2008; Park et al., 2002; Schoemaker et al., 2014; Spencer and Raz, 1995). Importantly, the different cognitive processes that support episodic memory do not all decline with age at the same rate. Notably, a substantial fraction of age-related variance in episodic memory performance appears to be attributable to a decline in the efficacy of encoding processes (e.g., Craik, 1983; Craik and Rose, 2012; Friedman and Johnson, 2014; Luo and Craik, 2008). The impact of age on processes supporting episodic retrieval (henceforth, 'recollection') is less clear, although there is behavioral and event-related potential (ERP) evidence that goal-appropriate processing of retrieval cues ('retrieval orientation') is negatively impacted by increasing age (Duverne et al., 2008; Jacoby et al., 2005; Keating et al., 2017; Morcom and Rugg, 2004). In the present study, we used ERPs to examine the effects of age on the neural correlates of successful episodic retrieval. We build on the findings of numerous prior studies in which ERP correlates of successful recollection were contrasted across age groups. Below, we lay out the rationale for the study.

Dual-process models of recognition memory (e.g., Jacoby, 1991; Wixted and Mickes, 2010; Yonelinas, 2002; Yonelinas et al., 2010) posit that recognition can be supported by two distinct processes: retrieval of qualitative information about a study episode (recollection), and an

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acontextual sense that a retrieval cue has been previously encountered (familiarity). One way to operationalize this distinction is with the Remember/Know/New (RKN) procedure (Tulving, 1985). In this procedure, participants are instructed to endorse a studied item as 'Remembered' (R) if one or more specific details about the study context are retrieved, and to give the item a 'Know' (K) response if no contextual details of the study episode are retrieved (e.g., Gardiner, 1988; McCabe and Geraci, 2009). A second method commonly used to operationalize recollection is the source memory procedure (for review, see Johnson et al., 1993; Mitchell and Johnson, 2009), in which memory for a contextual detail from the study episode is tested (e.g., the spatial location or the font color of a study item). These procedures have been combined in some studies (for behavioral studies, e.g., Perfect, 1996; Wais et al., 2008; for neuroimaging studies, e.g., Duarte et al., 2004; Duarte et al., 2006; Vilberg et al., 2006; Vilberg and Rugg, 2007, 2009b; Yu et al., 2012b). One rationale for combining the RKN and source memory procedures is that the amount and specificity of recollected information signaled by an R judgment varies across trials (for similar proposals, see Harlow and Donaldson, 2013; Harlow and Yonelinas, 2016; Murray et al., 2019). We consider the amount and specificity of retrieved information to be related factors (Boywitt et al., 2012), but for the sake of simplicity, we will refer to this combined concept as 'specificity' throughout the present report. By segregating items given an R judgment according to the accuracy of an associated source memory judgment, it is possible to distinguish between items that elicited a recollection signal that was sufficiently differentiated to permit identification of a specific, experimentally defined contextual feature about the study episode from items associated with recollection of details that were not diagnostic of the source feature (i.e., 'non-criterial' recollection; cf. Parks, 2007; Toth and Parks, 2006; Yonelinas and Jacoby, 1996).

Here, we employ the event-related potential (ERP) technique to examine the neural correlates of recollection at differing levels of specificity and as a function of age. A much-studied ERP correlate of recollection in young adults is the so-called 'left parietal effect'. As its name suggests, the effect has a left posterior maximum. It is evident between approximately 400 to 800 ms post-stimulus onset, and takes the form of a positive-going deflection for trials associated with recollection relative to both correct rejections of new items and items judged old on the basis of familiarity alone (e.g., Curran, 2000; Rugg et al., 1998a; Wang et al., 2012; Wilding and Rugg, 1996; Woodruff et al., 2006; Yu and Rugg, 2010; for reviews see Friedman, 2013; Rugg and Curran, 2007). Notably, the left parietal effect is seemingly invariant to whether recollection is operationalized by the RKN or source memory procedures (e.g., Rugg et al., 1998b; for review see Rugg and Curran, 2007).

Although the left parietal effect has also been identified in healthy older adults, the findings for this age group are mixed. A number of studies reported that the left parietal effect was detectable and either fully preserved in older adults (Ally et al., 2008b; Duarte et al., 2006; Friedman et al., 1993; Mark and Rugg, 1998; Trott et al., 1997, 1999) or attenuated relative to young adults (Ally et al., 2008a; Dulas and Duarte, 2013; Guillaume et al., 2009; Wang et al., 2012; Wolk et al., 2009). However, other studies failed to find clear evidence of a recollection-related left parietal effect in older adults. Instead, these studies reported a sustained, centrally maximal negative-going ERP effect that overlapped and, in some cases, seemingly eclipsed the left parietal effect (James et al., 2016; Kamp and Zimmer, 2015; Li et al., 2004; Scheuplein et al., 2014; see Mecklinger et al., 2016 for review). Superficially, this negativity resembles the 'late posterior negativity' (LPN) previously identified in young adults (Cycowicz et al., 2001) and linked to the reconstruction of contextual details of a studied episode (Johansson and Mecklinger, 2003; Mecklinger et al., 2016; Rosburg et al., 2013). However, the retrieval-related negativity observed in older adults demonstrates a central, rather than a posterior, scalp distribution. The conditions necessary for the emergence of this negativity, and its functional significance, are currently unclear. To our knowledge, the only prior study speaking directly to this issue is that of Trott and colleagues (1997; also see Trott et al., 1999). These investigators required participants to make sequential RKN and source memory judgments to recognition memory test items. Relative to correct rejections, correctly recognized studied items elicited a sustained late negativity in older adults regardless of whether the items attracted an R or a K judgment, and regardless of the accuracy of the source memory judgment. These findings suggest that the retrieval-related late negativity in older adults is insensitive to whether recognition is familiarity- or recollection-driven.

Another sustained retrieval effect, temporally overlapping with the sustained negative effects reported in young and older adults discussed above, has been termed the 'right frontal effect'. This effect takes the form of a sustained positive deflection for correctly endorsed old items, and has been linked with 'post-retrieval monitoring' processes that operate on the products of a retrieval attempt (Cruse and Wilding, 2009; Hayama et al., 2008; Wilding and Rugg, 1996; Woodruff et al., 2006; for reviews see Friedman and Johnson, 2000; Rugg, 2004; Rugg et al., 2002). Echoing the findings for the left parietal effect, some aging studies have identified right frontal effects of equivalent magnitudes in young and older adults (Dulas and Duarte, 2013; Li et al., 2004; Mark and Rugg, 1998), whereas others have reported attenuated effects in older adults (Friedman, 2013; Trott et al., 1997; Wegesin et al., 2002).

The present study builds on both this prior aging literature and prior findings in young adults demonstrating that the principal ERP correlate of successful recollection – the left parietal effect – is sensitive to the specificity of recollected information (Murray et al., 2015; Vilberg et al., 2006; Vilberg and Rugg, 2009a; Wilding, 2000; Woroch and Gonsalves, 2010). For example, Vilberg et al. (2006) reported that the effect was greater when participants reported recollecting multiple items belonging to a study episode rather than a single item. Similarly, Murray et al. (2015) reported that the left parietal effect covaried with how precisely a single specific contextual detail about a study episode was retrieved. Thus, at least in young adults, ERP correlates of recollection appear to track both the occurrence of recollection and the specificity of the recollected information (for convergent fMRI data, see Leiker and Johnson, 2014; Richter et al., 2016; Thakral et al., 2015; Vilberg and Rugg, 2009a, 2009b; Yu et al., 2012a, 2012b).

To our knowledge, only one prior study has examined the neural correlates of the specificity of recollection in older adults. Murray et al. (2019) employed a task in which words were paired with arbitrary locations on a circle, and the accuracy of source memory was measured as the difference in angle between the studied location and participants' judgment as to the location. ERPs corrected for latency variability across trials revealed a recollection effect over bilateral parietal scalp that scaled with the degree of source accuracy. This finding suggests that recollection-related ERPs in older adults vary with the specificity of retrieved information in a manner similar to young adults. However, Murray and colleagues did not include a young adult comparison sample. Thus, replication of these results is needed to more firmly establish whether recollection-related activity co-varies with the 'quality' of the recollection signal in older adults in the same way that it does in young individuals, as well as to permit direct comparison of the data with those from young adults.

Here, we used a modified RKN procedure to address this question. We operationalized recollection as the contrast between ERPs elicited by items accorded accurate K (familiar only) and R judgments, and segregated the ERPs elicited by items attracting accurate R judgments according to the accuracy of a subsequent source memory judgment. As in prior studies that have adopted similar approaches (Vilberg et al., 2006; Vilberg and Rugg, 2009a; Yu et al., 2012a, 2012b), we assume that, on average, items given R responses that also attract an accurate source judgment are associated with recollection of more specific contextual information than are items where the subsequent source judgment is uncertain or incorrect. At issue is the nature of the ERP effects revealed by these contrasts in older adults. The prior literature offers little basis for prediction. According to one possible scenario, as in some prior ERP studies (e.g., Ally et al., 2008a, 2008b; Dulas and Duarte, 2013; Duarte et al., 2006; Friedman et al., 1993; Guillaume et al., 2009; Mark and Rugg, 1998; Trott et al., 1997, 1999; Wang et al., 2012; Wolk et al., 2009), the neural correlates of recollection will be qualitatively, if not quantitatively, closely similar in young and older participants, with both groups demonstrating left parietal effects that scale with the specificity of retrieved information (cf. Murray et al., 2019). Another scenario (cf. Li et al., 2004; Scheuplein et al., 2014; Swick et al., 2006), however, is that the ERP correlates of recollection, and their sensitivity to amount of information retrieved, would be expected to differ qualitatively according to age. Arbitrating between these and other possibilities will help to clarify the extent to which age impacts the neural correlates of episodic retrieval. Notably, the finding that ERP correlates of recollection are less sensitive to the accuracy of a source memory judgment in older than younger adults would be consistent with proposals that aging compromises the ability to retrieve highly differentiated information about prior episodes (Folville et al., 2019; McDonough et al., 2014).

2. Methods

The experimental procedures described below were approved by the Institutional Review Board of The University of Texas at Dallas. All participants provided written informed consent prior to participation in the experiment. The participants included in the analyses reported here largely overlap the sample whose ERP data from the encoding phase of this study were reported in Koen et al. (2018). Specifically, 19 young and 18 older adults were included in both the prior encoding and the present retrieval analyses, and 1 young and 2 older adults were included only in the analyses of the retrieval data reported below. Of note, an additional 5 young and 6 older adults were included only in the encoding analyses reported by Koen et al. (2018). The discrepancy between the samples analyzed for the prior report of the encoding data and the present report of the retrieval data reflects the availability of sufficient numbers of artifact-free trials. The ERP data reported below have not been reported previously. However, given the substantial overlap between the participants employed in the present analyses and those reported by Koen et al. (2018), the neuropsychological test data and the behavioral data pertaining to the experimental memory test described below are essentially a re-reporting of previously published findings.

2.1. Participants

As noted above, twenty young adults (mean age 23.8 years, 11 female) and twenty older adults (mean age 69.3 years, 8 female) were included in the analyses reported here. Participants were compensated at the rate of $30 per hour for the experimental session and were reimbursed for travel. The participants were recruited from The University of Texas at Dallas and surrounding metropolitan Dallas communities. All participants were right-handed, learned English from birth or in early childhood, reported normal or corrected-to-normal vision, and scored a minimum of 27 on the Mini-Mental State Examination (MMSE). Exclusion criteria included a history of cardiovascular disorder (except for treated hypertension), psychiatric disorder, disorder of the central nervous system, substance abuse, current or recent use of psychotropic medications or sleeping aids, and inadequate standardized test performance.

An additional 15 participants were tested but excluded from the present analyses for the following reasons: 1 older male was excluded for incorrect use of RK judgments, and 7 young adults (3 male, 4 female) and 7 older adults (2 male, 5 female) were excluded because of too few artifact-free trials for one or more critical trial types.

2.2. Neuropsychological testing

A standard battery of neuropsychological tests was administered to participants on a separate day prior to the EEG recording session. We used the same test battery as in previous work by our group (e.g., de Chastelaine et al., 2016), with the addition of a test of visual acuity (Bailey and Lovie-Kitchin, 2013). Participants who underwent the neuropsychological test battery did not proceed to the EEG experiment if: 1) they scored >1.5 standard deviations below age- and education-adjusted norms for any long-term memory measure, 2) their standard score on the Wechsler Test of Adult Reading was <100, or 3) they scored >1.5 standard deviations below age- and education-adjusted norms on two or more non-memory tests.

2.3. Materials

2.3.1. Critical stimuli

Twenty experimental stimulus lists were created using 384 concrete nouns selected from the MRC Psycholinguistic Database (Coltheart, 1981). Words ranged from 4 to 8 letters in length (M = 5.32, SD = 1.21), from 1 to 40 occurrences per million in Kucera-Francis frequency (M = 13.33, SD = 10.25; Maverick, 1969), and between 500 and 662 in concreteness ratings (M = 584, SD = 32, on a scale of 100–700 from least to most concrete).

A study list consisted of 256 words, randomly divided into 4 sets of 64 words each. Words were assigned to each of 4 conditions formed by crossing encoding duration (Short vs. Long) and the semantic judgment task performed during the study phase (Manmade vs. Shoebox). Assignment of word sets to these 4 conditions was counterbalanced across lists, such that each set of 64 words appeared in each condition equally frequently across participants. Test lists consisted of the 256 words from the study list, along with 128 unstudied words. Each stimulus list created was assigned to a yoked young-older adult pair.

Words were presented in black upper-case 32-point Helvetica font against a white square (subtending a visual angle of 6.5° × 6.5°) centered on a black background. The longest word subtended a 3.6° horizontal and 0.57° vertical visual angle.

2.3.2. Practice items

Practice lists were created using 24 additional words with similar characteristics to the experimental stimuli. For study, three practice lists (self-paced, speeded, 'real') of eight words each were used, and for test, two practice lists (feedback, 'real') of twelve words each (eight items from practice study lists, four new items) were used. Practice lists were identical for all participants; practice phases were completed immediately prior to the study and test phases.

2.4. Experimental procedure

2.4.1. Study phase

The duration of the study phase (including breaks and electrode checking/adjustment) ranged from 34 to 48 min, (mean = 38 min, SD = 3 min), except for one outlying young participant for whom the duration was 68 min because of the need for an additional break. The phase was divided into four blocks, two of which were assigned to the 'short' encoding condition, and two to the 'long' encoding condition. Note that since memory performance did not differ according to encoding condition (section 3.2.1), the retrieval data reported here were collapsed across this encoding duration variable for all analyses. The short and long encoding durations were intended to manipulate the likelihood of participants' engaging in preparatory processing during the pre-stimulus period (cf. Koen et al., 2018). Each study block consisted of 64 words ('studied' items on the later recognition memory test). A short break was given at the halfway point of each block. Each study trial began with a green fixation cross for 500 ms, followed by a red task cue for 500 ms, then a black fixation cross for 1500 ms (Fig. 1, left). A study word was then presented for 300 ms in the short condition or for 1000 ms in the long condition, followed by a black fixation cross for 2700 ms or 2000 ms, respectively, holding the duration of the trials and the

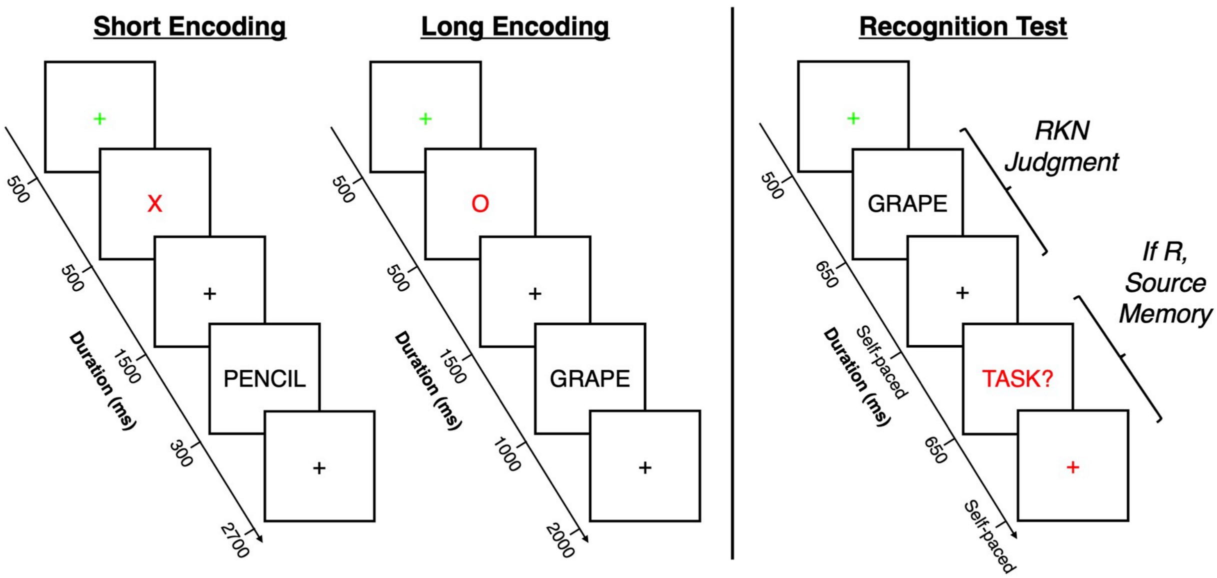

Fig. 1. Experimental procedure for encoding (left) and retrieval (right) phases of the experiment.

inter-trial intervals constant. Participants used a different hand for each question (e.g., Manmade question on right hand, Shoebox question on left), responding Yes/No with the index and middle fingers, respectively. When cued with a red X, participants answered the Manmade question ('Is the item depicted by the word manmade?'), and when cued with a red O, participants answered the Shoebox question ('Would the item depicted by the word fit inside a shoebox?'). Participants were instructed to answer each question according to the first exemplar of the item that came to mind. The mapping of hand to question type remained constant throughout the study phase and was counterbalanced across participants. The manmade and shoebox tasks were pseudorandomly intermixed throughout each study block such that no more than 3 trials with the same judgment occurred sequentially. Participants were instructed to respond as quickly as possible without sacrificing accuracy.

2.4.2. Test phase

Approximately 15 min after completing the study phase, participants received instructions for the test phase. The total duration of the test phase ranged from 39 to 65 min (mean = 51 min, SD = 7 min), other than for one older adult outlier for whom the duration was 76 min due to a technical problem. The average duration of the study/test delay was 38 min for young adults (SD = 4 min) and 44 min for older adults (SD = 7 min). The test phase was divided into 12 blocks of 32 trials each, with a short break between each block. Each test trial began with a green fixation cross for 500 ms, followed by presentation of a studied or new word for 650 ms (Fig. 1, right). The word was then replaced by a black fixation cross, which remained on the screen until a response was given. Participants were instructed to first make an RKN judgment for each test word. They were to respond R if they recognized the word and were able to recollect one or more specific details from the study episode (e.g., which question they answered for the word at study, a thought that came to mind as they studied the word, or an association made with the word). The instructions emphasized that an R response should only be given if the participant could explain to the experimenter what specific detail(s) they had recollected about the study episode. Participants were to respond K when they were confident that they had seen the word at study but were unable to recollect any specific detail from the study episode. The K response was labeled as Familiar in instructions to participants. A New (N) response was to be given when participants did not believe the word had been studied, or if they were uncertain about the word's study status.

If a K or N response was given, the black fixation cross remained on the screen for an additional 2000 ms, and the next trial began. If an R response was given, the black fixation cross remained on the screen for 500 ms and was then replaced by a red 'Task?' prompt for 650 ms. This was then replaced by a red fixation cross until a response was given, at which point a black fixation cross was displayed for 1000 ms before advancing to the next trial. Participants were asked to provide a source memory judgment with three response options: Manmade, Shoebox, and Don't Know, corresponding to which question had been answered for the word during encoding. Participants were instructed to respond Don't Know if they were unconfident or unable to recollect which question they had answered. Importantly, a Don't Know response following an R response indicated that the participant had recollected one or more details about the word from study but had not recollected the encoding task associated with the word. We did not elicit source memory judgments following K responses under the assumption that most K responses would have elicited Don't Know source judgments, and in order to simplify task instructions and reduce the risk of noncompliance.

2.5. EEG recording

EEG was recorded continuously during the study and test phases (only the test data are presented here; see Koen et al., 2018 for description of the study data). Data were recorded from 64 Ag/Ag–Cl electrodes. Fifty-eight of the electrodes were embedded in an elasticated cap (EasyCap; Herrsching-Breitbrunn, Germany; www.easycap.de; montage 11), while the remaining 6 electrodes were adhered directly to the skin. The electrode sites in the cap covered 6 midline locations (Fpz, Fz, Cz, CPz, PZ, POz) and 26 homotopic lateral locations (Fp1/2, AF3/4, AF7/8, F1/2, F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/7, FT7/8, C1/2, C3/4, C5/6, T7/8, CP1/2, CP3/4, CP5/6, TP7/8, P1/2, P3/4, P5/6, P7/8, PO3/4, PO7/8, and O1/O2). Two additional electrodes were affixed to the left and right mastoid processes. Vertical and horizontal EOG were monitored with bipolar electrode pairs placed above and below the right eye, and on the outer canthi of the left and right eyes, respectively. The ground and reference electrodes were embedded in the cap at sites AFz and FCz, respectively. EEG and EOG channels were digitized at 500 Hz using an amplifier bandpass of .01–70 Hz (3dB points) and the BrainVision Recorder software package (version 1.20.0601, www.brainvision.com). Electrode impedances were adjusted to be ≤ 5 kΩ prior to the start of the study phase and were rechecked during each break throughout the study and test phases, when they were readjusted as necessary.

2.6. EEG/ERP preprocessing

EEG data were processed offline in Matlab R2012b (www.mathworks.com) using EEGLAB version 13.5.4 (Delorme and Makeig, 2004), ERPLAB version 5.0.0.0 (Lopez-Calderon and Luck, 2014), and custom Matlab code (available from the authors on request). The continuous EEG data were digitally filtered between 0.03 and 19.4 Hz with a zero-phase shift Butterworth filter (12 dB/octave rolloff, DC offset removed prior to filtering) using ERPLAB. Epochs with a total duration of 2500 ms (from −500 ms to +2000 ms relative to onset of the test word) were extracted from the raw EEG data. The epoched data were subjected to Independent Components Analysis (ICA; Jung et al., 2000) to identify artifactual EEG components (e.g., blinks, eye movements, muscle artifacts, etc). Prior to ICA, the epochs were baseline corrected to the average voltage across the epoch to improve estimation of ICA components (Groppe et al., 2009), and epochs with non-stereotypical artifacts (e.g., coughs or sneezes) were rejected. When necessary, rejection of an entire electrode channel was conducted prior to ICA. Data from rejected electrodes were replaced using Spline interpolation after removal of artifactual ICA components. The SASICA (Chaumon et al., 2015) and ADJUST (Mognon et al., 2011) software packages were used to aid with the identification of artifactual components. After ICA artifact correction, the epoched EEG data were re-referenced to averaged mastoids (recovering the FCz electrode) and baseline corrected to the average voltage of the 500 ms preceding the time-locked event (onset of the test word). Epochs were rejected for averaging if: (1) voltage in the epoch exceeded ±100 μV, (2) baseline drift exceeded 40 μV (determined as the absolute difference in amplitude between the average amplitude of the first and last 250 ms of each epoch), (3) an artifact was present based on visual inspection, (4) the participant failed to respond to the corresponding trial at study or used the incorrect hand for the encoding judgment, or (5) the participant's response time (RT) was faster than 650 ms or slower than 10 s for RKN judgments during the test phase, or faster than 450 ms during the corresponding trial of the study phase.

ERPs for each electrode site and event (onset of test word) were created by averaging all artifact-free epochs according to the recognition memory judgment. Correctly endorsed studied items were segregated into three bins: R responses accompanied by correct source judgments (R+), R responses accompanied by incorrect or Don't Know source responses (R−), and trials attracting a K (familiar only) response. Correctly rejected new items (CR) were also included; due to low trial numbers, ERPs for item misses and false alarms (R or K responses to new items) were not included in any analyses.

2.7. Statistical analyses

The overall design included one between-participants factor (age group) and one within-participants factor (memory judgment). As stated above, we collapsed across the encoding duration factor because there were no differences in memory performance between the short and long durations.

Statistical analyses were conducted using *R* software version 3.3.2 (R Core Team, 2017). ANOVA models were computed using the functions from the *afex* package version 0.16–1 (Singmann et al., 2016). Degrees of freedom for repeated-measures factors were corrected for non-sphericity using the Greenhouse-Geisser procedure in all reported ANOVAs (Greenhouse and Geisser, 1959). Effect size measures for ANOVA results are reported as partial η^2 (Cohen, 1988). The threshold for statistical significance was $p < .05$.

2.7.1. Behavioral analysis

Behavioral analyses were conducted to confirm the pattern of results reported by Koen et al. (2018), since the sample of participants yielding usable data for the retrieval phase of the experiment did not completely overlap with the sample of participants analyzed for the encoding phase. Dependent variables of interest from the behavioral data included three estimates of memory performance. These included estimates of recollection and familiarity derived from the RKN procedure and a measure of source memory accuracy derived from the judgments that followed R responses. Estimates of recollection and familiarity were calculated (regardless of source accuracy) using the independent Remember/Know estimation procedure (Yonelinas and Jacoby, 1995). Recollection was computed using the following formula:

$$Recollection = R_{old} - R_{new}$$

R_{old} and R_{new} represent the proportion of R responses to old and new items, respectively. Familiarity estimates were derived from the following set of formulas:

$$F_{old} = \frac{K_{old}}{1 - R_{old}}$$

$$F_{new} = \frac{K_{new}}{1 - R_{new}}$$

$$Familiarity = F_{old} - F_{new}$$

In the above formulae, K_{old} and K_{new} represent the proportion of K responses to old and new items, respectively.

Source memory was computed using a single-high threshold model (Snodgrass and Corwin, 1988; for prior examples of its use, see Gottlieb et al., 2010; Mattson et al., 2014) modified to account for the rate of guessing. This measure, pSR, was computed using the following formula:

$$pSR = \frac{p(Hit) - .5^*[1 - p(DK)]}{1 - .5^*[1 - p(DK)]}$$

$p(Hit)$ and $p(DK)$ refer to the proportion of R responses accompanied by a correct source judgment or a Don't Know source judgment, respectively.

Trials with RTs >10 s were excluded from all behavioral and ERP analyses. For each participant, median RTs for trials from the four bins of interest in the ERP analysis were calculated.

2.7.2. ERP analyses

Analysis of the ERP data was conducted on epochs time-locked to the onset of the test word spanning two time windows. The windows were selected to correspond to recollection-related ERP effects typically reported in the literature (see section 1): 500–800 ms (left parietal effect), 800–2000 ms (late negative and right frontal effects; see below). ERP amplitude was computed within each time window as the mean voltage (μV) relative to the mean voltage in the 500 ms pre-stimulus baseline period.

For each time window, we focused analyses on *a priori* electrode clusters chosen based on the latency and topography of retrieval (recollection) effects previously reported in the episodic memory literature, namely, the 'left parietal' effect associated with recollection and the 'right frontal' and two 'late negative' effects associated with post-retrieval processes in young and older adults, respectively (for reviews see Friedman, 2013; Mecklinger et al., 2016). Virtual electrodes (i.e., mean ERP amplitude across all electrodes included in each cluster) were subjected to 4 (memory judgment: R+, R−, K, CR) x 2 (age group: young, older) ANOVAs, with post-hoc comparisons as warranted by the outcomes. For the 500–800 ms time window, a left parietal cluster (comprising TP7, CP5, CP3, P7, P5, and P3 electrodes) was used to investigate whether the left parietal recollection effects were present in one or both age groups. During the late time window (800–2000 ms), analyses focused on i) a mid-central cluster (comprising C1, Cz, C2, CP1, CPz, and CP2 electrodes) to quantify the late negative slow wave identified in prior reports in older adults, ii) a mid-posterior cluster (comprising P1, Pz, P2, PO3, POz, and PO4 electrodes) to examine the LPN previously identified in young adults, and iii) a right frontal cluster (comprising AF4, AF8, F4, F6, and F8 electrodes), where a right frontal effect, held to be a correlate of 'post-retrieval monitoring' (Mark and Rugg, 1998; Rugg et al., 2002) is typically evident.

ANOVA effects involving the factor of memory judgment were followed up with subsidiary ANOVAs and pairwise comparisons to determine which response categories were associated with significantly different ERP amplitudes. Post hoc t-tests were computed with a pooled error term using the lsmeans function in R (calculated within the ANOVA model motivating the comparisons). The Holm-Bonferroni method (Holm, 1979) was used to correct for multiple comparisons based on the six possible post hoc tests between pairs of memory judgments in each instance (R+ vs. R−, R+ vs. K, R+ vs. CR, R− vs. K, R− vs. CR, and K vs. CR). Both corrected and uncorrected p-values are reported for these contrasts.

3. Results

3.1. Neuropsychological test scores

Results of the neuropsychological tests are presented in Table 1 (these data were also reported in Koen et al., 2018 for a largely overlapping sample of participants; see section 2). Relative to young adults, older adults demonstrated equivalent levels of performance on tests of vocabulary, fluency and digit-span, along with decreased performance on measures of memory, reasoning, and processing speed. This pattern is typical of prior reports involving samples of well-educated, healthy young and older adults (e.g., de Chastelaine et al., 2016; Mattson et al., 2014; Wang et al., 2012).

Table 1
Neuropsychological test scores for young (left) and older adults (right); mean scores given (SD). CVLT: California Verbal Learning Test, WTAR: Wechsler Test of Adult Reading, WMS: Wechsler Memory Scale (WMS-IV). Differences between age groups were determined using Welch's t-tests; significant differences are marked with an asterisk.

	Younger Adults	Older Adults	Age Group Differences (p-values)
N	20	20	
Sex (M/F)	9/11	12/8	
Age	23.75 (3.58)	69.25 (3.75)	
Years of education	16.10 (2.29)	17.00 (2.75)	0.268
MMSE	29.50 (0.92)	29.30 (0.69)	0.443
CVLT SD - Free	13.35 (1.69)	10.20 (3.62)	0.002*
CVLT SD - Cued	13.85 (1.63)	11.45 (3.02)	0.004*
CVLT LD - Free	14.05 (1.57)	10.65 (3.69)	0.001*
CVLT LD - Cued	14.20 (1.47)	11.55 (3.25)	0.003*
CVLT Recognition - Hits	15.55 (0.83)	14.70 (1.53)	0.036*
CVLT Recognition - FAs	0.50 (0.61)	2.50 (2.65)	0.003*
SDMT	59.70 (10.10)	49.65 (8.11)	0.001*
Digit Span (Total)	21.05 (3.83)	19.50 (3.14)	0.170
Trails A	21.83 (8.41)	28.94 (9.33)	0.016*
Trails B	51.38 (17.27)	65.88 (23.14)	0.031*
FAS (Total)	47.55 (10.13)	47.45 (9.77)	0.975
Category Fluency (Animals)	23.65 (5.10)	20.85 (6.07)	0.123
WTAR (Raw)	40.50 (3.38)	44.00 (4.70)	0.011*
Logical Memory I	31.25 (3.80)	27.45 (6.31)	0.028*
Logical Memory II	28.50 (4.95)	23.45 (6.58)	0.010*
Raven's (List 1)	10.85 (1.09)	9.30 (2.03)	0.005*
Visual Acuity (logMAR)	−0.10 (0.11)	0.08 (0.13)	<0.001*

3.2. Behavioral performance

3.2.1. Memory test

To verify that performance did not differ by encoding condition, we first computed paired t-tests between short and long encoding durations for each memory estimate in each age group. No significant differences were found between encoding conditions for young [Recollection: t(19) = 0.80, p = .432; Familiarity: t(19) = 0.20, p = .845; Source accuracy: t(19) = 1.15, p = .264] or older adults [Recollection: t(19) = 0.74, p = .467; Familiarity: t(19) = 1.53, p = .144; Source accuracy: t(19) = 0.82, p = .423]. We thus collapsed test performance across the short and long encoding conditions. Table 2 lists the proportions of R (with and without correct source judgment), K, and N responses by item type (Studied or New), and Fig. 2 displays estimates of recollection (young adults: mean = 0.56, SD = 0.14, older adults: mean = 0.39, SD = 0.14), familiarity (young adults: mean = 0.33, SD = 0.13, older adults: mean = 0.24, SD = 0.14), and source accuracy (young adults: mean = 0.46, SD = 0.14, older adults: mean = 0.40, SD = 0.21). These estimates were contrasted using independent-samples t-tests (equal variance not assumed). As expected based on the previous analysis reported by Koen et al. (2018) on a largely overlapping sample, sizeable age-related differences in recollection estimates [t(37.91) = 3.69, $p < .001$, Cohen's d = 1.17], alongside a more modest age-related reduction in estimates of familiarity [t(37.85) = 2.10, p = .043, Cohen's d = 0.66], were evident. Source accuracy (pSR) did not significantly differ between age groups [t(33.99) = 1.14, p = .262]. See Supplemental Materials for an analysis comparing the proportion of Don't Know responses for young and older adults.

3.2.2. Test RTs

Table 3 lists the group averages of median RTs for the RKN and subsequent source judgments (referenced to the onset of the test item and the subsequent response cue, respectively). Note that the RTs for the source judgment are only available for trials attracting an R response. A 2 (age group) x 4 (memory judgment: R+, R−, K, CR) ANOVA of the RTs for the initial RKN judgment revealed main effects of age group [F(1,38) = 8.25, MSE = 1365692, partial $\eta^2 = 0.18$, p = .007] and memory judgment [F(2.11, 80.05) = 23.15, MSE = 256162, partial $\eta^2 = 0.38$, $p < .001$], but no age group x memory judgment interaction [F(2.11,80.05) = 2.36, MSE = 256162, partial $\eta^2 = 0.06$, p = .100]. Older

Table 2
Test response proportions (SD) by item type (Studied, New) and RKN memory judgment (with source accuracy for R judgments) for young and older adults. R + SC: Remember with correct source, R + SI: Remember with incorrect source, R + DK: Remember with Don't Know response, K: Know, N: New.

	Memory judgment				
Item type	R + SC	R + SI	R + DK	K	N
	Young adults				
Studied	0.42 (0.14)	0.05 (0.04)	0.17 (0.09)	0.20 (0.09)	0.15 (0.07)
New	~	0.04 (0.04)	0.05 (0.06)	0.22 (0.14)	0.69 (0.18)
	Older adults				
Studied	0.32 (0.12)	0.10 (0.05)	0.06 (0.06)	0.25 (0.10)	0.26 (0.09)
New	~	0.08 (0.07)	0.02 (0.04)	0.22 (0.13)	0.69 (0.19)

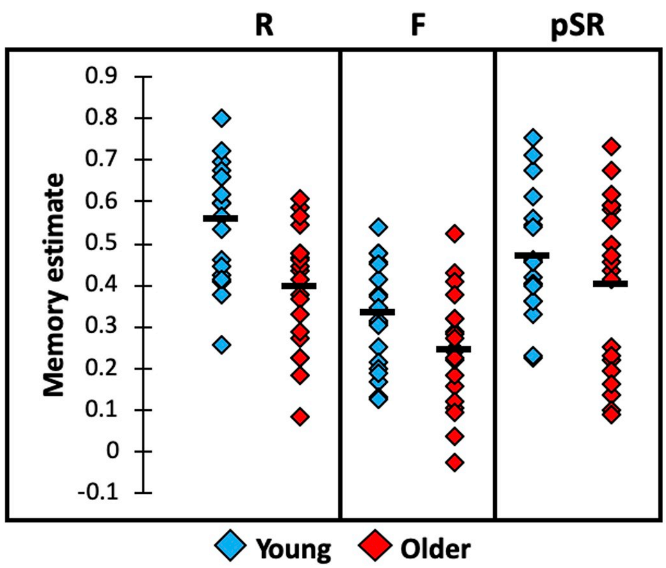

Fig. 2. Memory estimates for young and older adults; horizontal bars indicate group means of memory estimates. R: Recollection, F: Familiarity, pSR: Source accuracy. See Methods for details on how memory estimates were calculated.

Table 3
Average median RT in ms (SD) by age group for the initial RKN judgment (top) and the source judgment following R judgments (bottom).

	Young	Older
RKN judgment		
R+	1507 (494)	2127 (597)
R−	1687 (505)	2407 (822)
K	2225 (573)	2765 (961)
CR	1683 (653)	1925 (776)
Source judgment		
R+	693 (408)	828 (524)
R−	922 (491)	1030 (538)

adults were, in general, slower to respond than young adults. In addition, post-hoc comparisons of median RTs for each memory judgment (collapsed across age group) revealed that K trials gave rise to slower responses than all other categories (K vs. CR: $t(114) = 7.28$, $p < .001$, corrected $p < .001$; K vs. R−: $t(114) = 4.72$, $p < .001$, corrected $p < .001$; K vs. R+: $t(114) = 7.15$, $p < .001$, corrected $p < .001$), R− trials were associated with slower responses than R+ and CR trials [R− vs. R+: $t(114) = 2.43$, $p = .017$, corrected $p = .036$; R− vs. CR: $t(114) = 2.56$, $p = .012$, corrected $p = .036$], and R+ and CR trials did not significantly differ [R+ vs. CR: $t(114) = 0.13$, $p = .896$, corrected $p = .896$].

A 2 (age group) x 2 (source accuracy: R+, R−) ANOVA of RTs for the source judgments that followed R responses revealed a main effect of source accuracy [$F(1,38) = 5.44$, MSE = 53899, partial $\eta^2 = 0.13$, $p = .025$], but no effect of age group [$F(1,38) = 2.16$, MSE = 431448, partial $\eta^2 = 0.06$, $p = .150$] or age group x source accuracy interaction [$F(1,38) = 0.07$, MSE = 53899, partial $\eta^2 = 0.00$, $p = .791$]. Both young and older adults' RTs associated with inaccurate or Don't Know source judgments were slower than the RTs associated with accurate source judgments.

3.3. ERP results

To provide an overview of ERP effects in the two age groups, ERP waveforms for the four response categories of interest (R+, R−, K, CR) are illustrated for the four *a priori* electrode clusters in Figs. 3 and 4. Mean trial numbers (and ranges) for each response category of interest included in ERP analyses are given in Table 4. It is clear from examining the figures that the patterns of activity observed in young and older adults differ markedly in some of the time windows. Before describing the results of the statistical analyses for each time window in detail, a brief qualitative description of the ERP effects follows.

In young adults, the ERP effects appear to be broadly consistent with numerous prior reports. There is a positive-going effect over the left parietal scalp between around 500–1000 ms that is seemingly graded according to the specificity of information recollected. Additionally, there is a prominent, later-onsetting, right frontal effect that is present for all studied items relative to correct rejections. This effect overlaps temporally with a posterior-maximum negative-going effect for R+ items relative to all other response categories. In addition, there appears to be a negative deflection in the ERPs for K trials relative to other trial types in the right frontal cluster (Fig. 3D) during the early time window (500–800 ms). At the request of a reviewer, we conducted an exploratory analysis to examine the reliability of this effect which is reported and discussed in the Supplementary Materials.

In striking contrast to the ERPs in the young adults, older adults' waveforms are dominated by a marked negative-going effect for R+ and R− items relative to K items and correct rejections. The effect emerges around 800 ms post-stimulus and is evident over much of the scalp, albeit with a central-posterior maximum. The effect reverses over the right frontal scalp, giving rise to a right-frontal effect similar to that demonstrated by the young participants.

3.3.1. 500–800 ms latency region

3.3.1.1. Left parietal electrode cluster. ANOVA of the mean amplitude of the left parietal electrode cluster (Figs. 3A and 4A) revealed a main effect of memory judgment [$F(2.62,99.40) = 13.26$, MSE = 0.91, partial $\eta^2 = 0.26$, $p < .001$] and an age group x memory judgment interaction [$F(2.62,99.40) = 9.06$, MSE = 0.91, partial $\eta^2 = 0.19$, $p < .001$]. Separate group-wise ANOVAs revealed no significant memory judgment effect for the older adults [$F(2.61,49.59) = 2.09$, MSE = 0.63, partial $\eta^2 = 0.10$, $p = .121$] but a significant effect for the young group [$F(2.60,49.45) = 15.98$, MSE = 1.20, partial $\eta^2 = 0.46$, $p < .001$]. Pairwise post-hoc contrasts revealed that the amplitude for R+ trials exceeded that for all other response categories [R+ vs. R−: $t(57) = 2.79$, $p = .007$, corrected $p = .014$; R+ vs. K: $t(57) = 5.93$, $p < .001$, corrected $p < .001$; R+ vs. CR: $t(57) = 5.82$, $p < .001$, corrected $p < .001$], and the amplitude for R− trials exceeded that for K and CR trials [R− vs. K: $t(57) = 3.14$, $p = .003$, corrected $p = .011$; R− vs. CR: $t(57) = 3.03$, $p = .004$, corrected $p = .011$]. K and CR trials did not significantly differ [K vs. CR: $t(57) = 0.11$, $p = .914$, corrected $p = .914$].

3.3.2. 800–2000 ms latency region

3.3.2.1. Mid-central electrode cluster. ANOVA of the mean amplitude of the mid-central electrode cluster (Figs. 3B and 4B) revealed main effects of memory judgment [$F(2.31,87.60) = 11.16$, MSE = 3.45, partial $\eta^2 = 0.23$, $p < .001$] and age group [$F(1,38) = 7.12$, MSE = 34.57, partial $\eta^2 = 0.16$, $p = .011$], and a memory judgment x age group interaction [$F(2.31,87.60) = 6.60$, MSE = 3.45, partial $\eta^2 = 0.15$, $p = .001$]. Separate ANOVAs for each age group revealed no significant effect of memory judgment in young adults [$F(2.39,45.40) = 0.52$, MSE = 3.18, partial $\eta^2 = 0.03$, $p = .629$], along with a significant effect for older adults [$F(1.96,37.22) = 16.50$, MSE = 4.26, partial $\eta^2 = 0.47$, $p < .001$]. Pairwise post-hoc contrasts indicated that ERPs elicited by items accorded R judgments (regardless of source accuracy) were significantly more negative relative to items judged K and correct rejections [R+ vs. CR: $t(57) = 5.33$, $p < .001$, corrected $p < .001$; R− vs. CR: $t(57) = 4.63$, $p < .001$, corrected $p < .001$; R+ vs. K: $t(57) = 5.27$, $p < .001$, corrected $p < .001$; R− vs. K: $t(57) = 4.57$, $p < .001$, corrected $p < .001$]. R judgments did not significantly differ [R+ vs. R−: $t(57) = 0.70$, $p = .489$, corrected $p = .978$], and nor did K and CR trials [K vs. CR: $t(57) = 0.06$, $p = .952$, corrected $p = .978$].

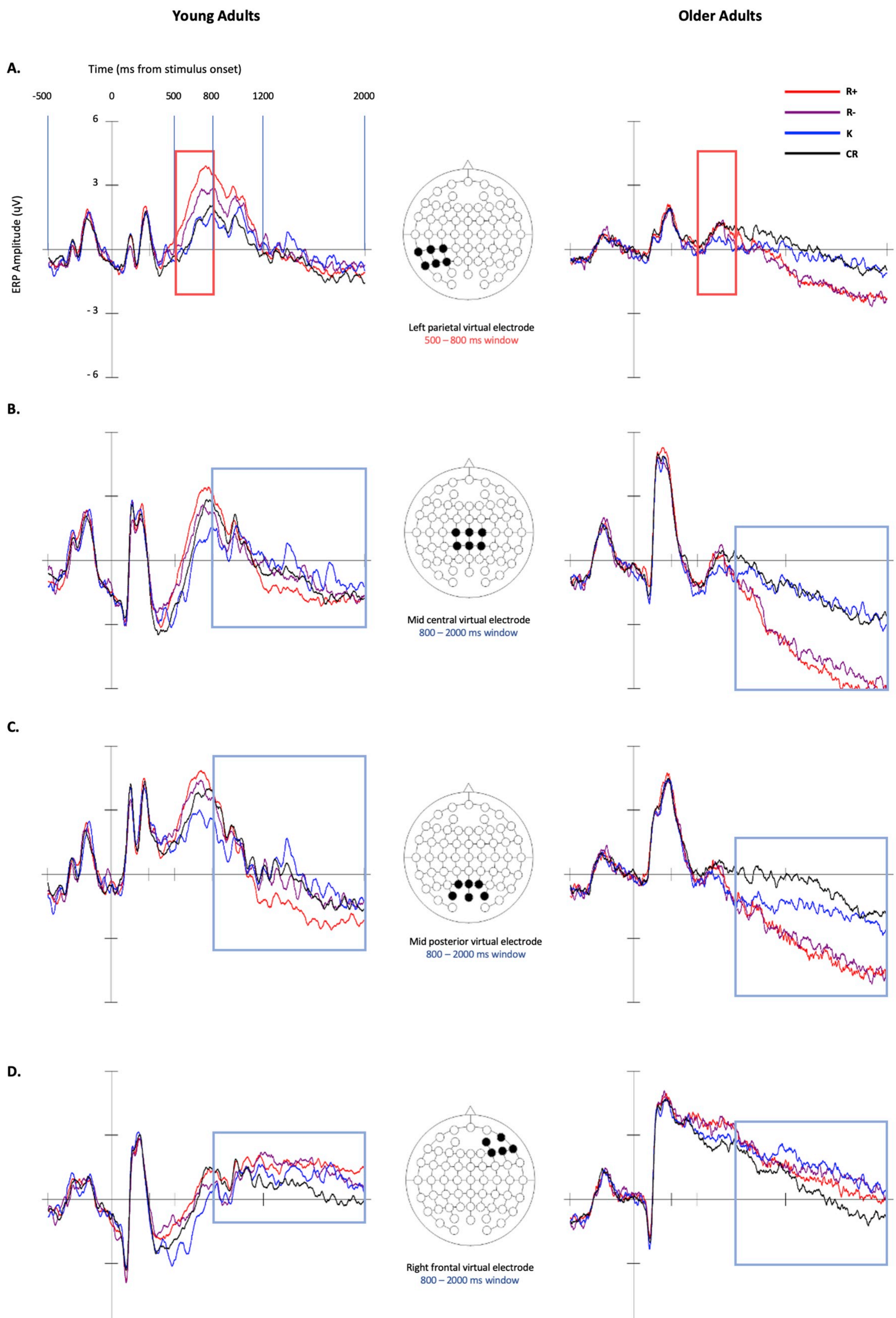

Fig. 3. ERP waveforms of the virtual electrode (averaged across all electrodes in the cluster) for each *a priori* cluster of interest in young (left) and older adults (right). Scalp schematics depict each electrode cluster, and rectangular frames depict the time window of interest for each cluster. See top left plot for amplitude scale. Response categories depicted: R+ (Remember with source correct), R− (Remember with source incorrect or Don't Know), K (Know response), CR (New response to new item).

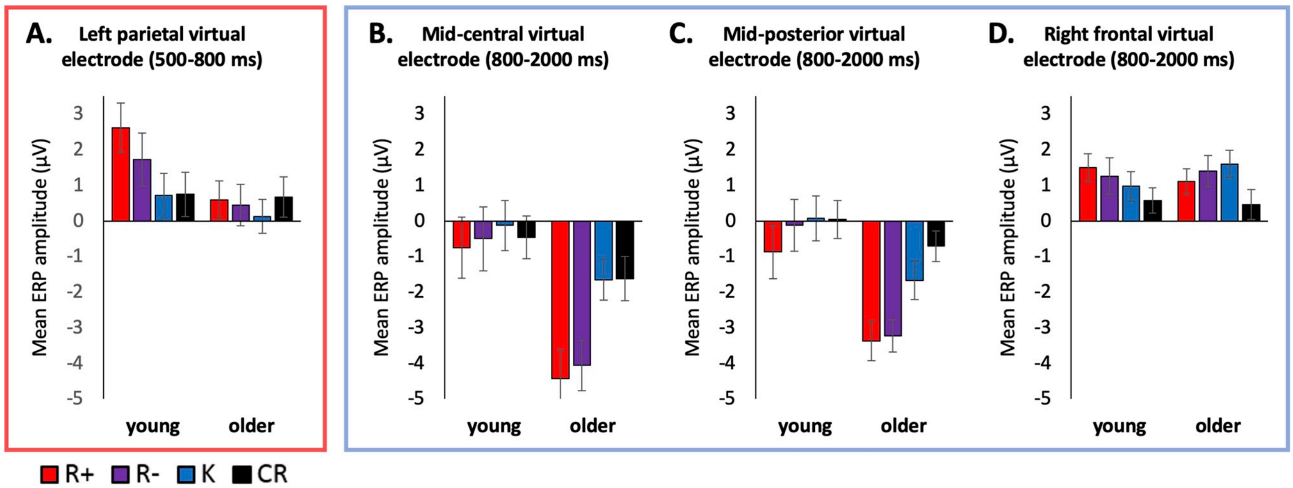

Fig. 4. Mean amplitudes of ERPs for each virtual electrode (averaged across all electrodes in the cluster) for each *a priori* cluster of interest. See Fig. 3 for scalp schematics of electrode clusters. A) Left parietal virtual electrode, 500–800 ms. B) Mid-central virtual electrode, 800–2000 ms. C) Mid-posterior virtual electrode, 800–2000 ms. D) Right frontal virtual electrode, 800–2000 ms.

Table 4
Mean trial numbers (range) for the response categories of interest included in ERP analyses. Mean trial numbers are rounded down to the nearest whole number.

Age Group	Response Type			
	R+	R−	K	CR
young	95 (45–157)	47 (16–83)	45 (16–83)	82 (44–122)
older	75 (17–116)	38 (16–68)	59 (21–115)	85 (33–118)

3.3.2.2. Mid-posterior electrode cluster. ANOVA of the mean amplitude of the mid-posterior electrode cluster (Figs. 3C and 4C) also revealed main effects of memory judgment [F(2.36,89.63) = 12.62, MSE = 2.66, partial η^2 = 0.25, p < .001] and age group [F(1,38) = 7.59, MSE = 21.65, partial η^2 = 0.17, p = .009], and a memory judgment x age group interaction [F(2.36,89.63) = 4.98, MSE = 2.66, partial η^2 = 0.12, p = .006]. Separate ANOVAs for each age group revealed no significant effect of memory judgment for young adults [F(2.48,47.05) = 1.79, MSE = 2.62, partial η^2 = 0.09, p = .170], and a significant effect for older adults [F(2.17,41.23) = 16.36, MSE = 2.78, partial η^2 = 0.46, p < .001]. Pairwise post-hoc contrasts indicated that, similarly to the results from the mid-central cluster, ERPs associated with R judgments were significantly more negative than ERPs associated with K judgments and correct rejections [R+ vs. CR: t(57) = 5.93, p < .001, corrected p < .001; R− vs. CR: t(57) = 5.63, p < .001, corrected p < .001; R+ vs. K: t(57) = 3.79, p < .001, corrected p = .001; R− vs. K: t(57) = 3.49, p < .001, corrected p = .003]. R judgments did not significantly differ [R+ vs. R−: t(57) = 0.30, p = .765, corrected p = .765], and nor did ERPs associated with K and CR trials [K vs. CR: t(57) = 2.14, p = .037, corrected p = .074], although this contrast approached significance.

3.3.2.3. Right frontal electrode cluster. ANOVA of the mean amplitude of the right frontal cluster revealed a main effect of memory judgment [F (2.50,94.86) = 3.86, MSE = 1.92, partial η^2 = 0.09, p = .017], but no main effect of age group [F(1,38) = 0.02, MSE = 8.61, partial η^2 = 0.00, p = .883] or age group x memory judgment interaction [F(2.50,94.86) = 1.16, MSE = 1.92, partial η^2 = 0.03, p = .325]. Post-hoc contrasts revealed that ERPs associated with correctly endorsed old items (regardless of RK distinction or source accuracy) were significantly more positive-going than correct rejections [R+ vs. CR: t(114) = 2.75, p = .007, corrected p = .034; R− vs. CR: t(114) = 2.86, p = .005, corrected p = .030; K vs. CR: t(114) = 2.71, p = .008, corrected p = .034]. ERPs elicited by correctly endorsed items did not significantly differ from one another [R+ vs. R−: t(114) = 0.11, p = .916, corrected p = 1.00; R+ vs. K: t(114) = 0.05, p = .964, corrected p = 1.00; R− vs. K: t(114) = 0.15, p = .880, corrected p = 1.00].

4. Discussion

We investigated the relationship between ERP correlates of recollection in young and older adults and the specificity of the retrieved information. Here, we operationalized recollection specificity by contrasting studied items attracting a 'Remember' response according to the accuracy of a subsequent source memory judgment for a specific detail of the study episode (i.e., the encoding task). Consistent with prior findings (Vilberg et al., 2006; Vilberg and Rugg, 2009a; Wilding, 2000), ERP correlates of recollection over the left parietal scalp in young adults were modulated by source accuracy. In older adults, however, we were unable to identify any evidence that their ERPs were modulated by this variable; rather, older adults' recollection-related ERPs were dominated by a centrally maximal late negative deflection that did not vary in its magnitude with the specificity of the retrieved information. In both age groups, a late-onsetting, temporally sustained right frontal effect was elicited by all test items attracting correct 'old' judgments. Below, we discuss these findings and their implications.

4.1. Behavioral findings

Consistent both with the findings we reported for a largely overlapping sample of participants (Koen et al., 2018), and with the conclusions of recent reviews (Koen and Yonelinas, 2014; Schoemaker et al., 2014), we identified a substantial age-related reduction in recollection, as operationalized by proportion of R judgments, alongside a smaller but reliable reduction in familiarity-based recognition memory. Contrary to numerous prior reports (e.g., Boywitt et al., 2012; Duarte et al., 2008; Kuhlmann and Boywitt, 2016; Mark and Rugg, 1998; Spencer and Raz, 1995), we did not find an effect of age on source memory performance. This null finding might be attributable to the fact that successful memory judgments could be supported by retrieval of multiple, redundant features of the study episode. Each study task (Manmade or Shoebox judgment) was consistently associated both with a specific task cue (X or O) and a different hand of response. Therefore, a correct source judgment could have been supported by the retrieval of task (Manmade vs. Shoebox), perceptual (X vs. O) or effector (left vs. right hand) information. We conjecture that this redundancy in source-specifying information attenuated potential age differences in source memory performance. This hypothesis, however, requires further study and empirical evaluation.

4.2. ERP modulations specific to young adults

Recollection-related ERP effects over the left parietal scalp in young adults were sensitive to the specificity of recollected information, as reported previously (Murray et al., 2015; Vilberg et al., 2006; Vilberg and Rugg, 2009a; Wilding, 2000). Importantly, the present experimental procedure allowed us to contrast ERPs associated with differing levels of retrieval specificity using a combination of subjective (RK) and objective (source accuracy) measures of recollection, extending prior findings in which specificity of information recollected was indexed solely by a subjective judgment (Vilberg et al., 2006; Vilberg and Rugg, 2007; but see Murray et al., 2015) or was inferred from a study manipulation (Estrada-Manilla and Cansino, 2012; Vilberg and Rugg, 2009a; Wilding, 2000).

The present findings bear comparison with those from an fMRI study in which a similar experimental procedure was employed. Yu et al. (2012a) reported greater BOLD activity in the left angular gyrus for items accorded an R judgment that went on to attract a correct, high-confidence source judgment relative to items endorsed R that attracted a low-confidence or an incorrect judgment. In addition, left angular gyrus BOLD activity elicited by these latter items tended to exceed the activity elicited by items afforded K judgments (whether the contrast achieved the nominal significance level depended on the composition of the trial types comprising the K judgments). These findings parallel those reported here for the left parietal ERP 'recollection effect' and, together, they add to the evidence that the ERP effect is the electrophysiological correlate of the recollection-related fMRI BOLD effects consistently observed in left angular gyrus (for reviews see Rugg and King, 2018; Vilberg and Rugg, 2008).

The left parietal effect is widely regarded as a specific neural correlate of recollection (e.g., Curran, 2000; Rugg et al., 1998a; Wang et al., 2012; Wilding and Rugg, 1996; Woodruff et al., 2006; Yu and Rugg, 2010; for reviews see Friedman, 2013; Rugg and Curran, 2007). However, debate remains over the nature of the memory signal(s) underlying recognition memory. Some researchers (e.g., Donaldson, 1996; Dunn, 2004) propose that recognition memory is supported by a single, continuously varying, 'strength-like' memory signal, rather than by two qualitatively distinct signals. This single-process perspective motivated a recent ERP study by Brezis et al. (2017). In this study, ERPs were obtained during a memory test in which participants first assigned a confidence rating to an old/new judgment, and subsequently made an R/K/guess judgment for items judged as old. The rationale for this design (see also Wixted and Mickes, 2010) is that confidence ratings can be employed as a proxy measure of memory strength. Largely on the basis of the finding that no ERP differences could be detected between test items attracting a combination of a low confidence rating and an R judgment and items attracting a high confidence rating and a K judgment, the authors concluded that the consistently reported finding of an enhanced left parietal effect for R relative to K judgments reflects differences in average memory strength between the two classes of judgment, rather than a neural correlate of recollection. Applying the same logic to the present data, it would be argued that the findings illustrated in Figs. 3 and 4 for our younger participants' left parietal ERPs (along with analogous prior findings: e.g., Vilberg et al., 2006; Vilberg and Rugg, 2009a) merely reflect a graded difference in memory strength (K $<$ R$-$ $<$ R$+$). There are however reasons to question this interpretation. Notably, due to limited trial numbers, ERPs elicited by correct rejections were not available as a 'baseline' condition in the study of Brezis et al. (2017). Thus it is unclear whether either critical class of test items – i.e., items that were 'weakly' remembered or 'strongly' familiar – actually elicited a reliable left parietal effect. This leaves open the possibility that the findings indicate that unconfident R responses do not elicit the effect, rather than that confident K responses elicit it. In support of this possibility, other studies employing a combination of the RKN procedure and confidence ratings have failed to find evidence that left parietal ERPs are modulated by memory strength, as this is operationalized by response confidence. For example, in the studies of Woodruff et al. (2006) and Wang et al. (2012; see also Yu and Rugg, 2010), ERPs elicited by items that were judged old with high confidence but not endorsed as R failed to elicit a reliable left parietal effect relative to items attracting confident new judgments, in marked contrast to items endorsed as Remembered.

Together, these considerations persuade us that the present findings do indeed reflect the modulation of neural activity associated specifically with recollection, rather than a more generic memory signal that does not honor the distinction between familiarity and recollection (for similar conclusions derived from behavioral findings, see Koen and Yonelinas, 2010; Koen et al., 2013; Yonelinas, 2001). However, we note that ERPs for R$-$ trials include a mix of incorrect and 'Don't Know' source responses. Contrasting the ERPs elicited by these two classes of trials might provide more insight into adjudicating between the above mentioned competing dual process and memory strength accounts. If ERPs for incorrect source responses were to resemble the ERPs associated with correct source judgments and to differ from those for Don't Know trials, this would arguably offer support for the memory strength interpretation, on the grounds that the putative ERP 'recollection' effects were driven by confident source judgments rather than veridical recollection. While insufficient trial numbers precluded this analysis in the present study, it would be a promising avenue for future research.

4.3. ERP modulations in older adults

We found no evidence in our older participants of the left parietal recollection effect that was so prominent in the young age group. Rather, in the later of the two analysis windows (extending from 800 to 2000 ms post-stimulus onset), a sustained, centrally maximal negative-going deflection was elicited by items attracting R judgments relative to correct rejections.

It is not possible to determine whether a left parietal recollection effect would have been evident in our older participants' ERPs had the aforementioned negative deflection, the onset of which likely overlapped the parietal effect, been absent. Similar age-specific late negativities have been reported in several prior studies (Dulas and Duarte, 2013; James et al., 2016; Kamp and Zimmer, 2015; Li et al., 2004; Scheuplein et al., 2014; Trott et al., 1997, 1999; Wegesin et al., 2002). In some of these studies, as in the present case, the negative effect was not accompanied by a detectable parietal effect (Kamp and Zimmer, 2015; Scheuplein et al., 2014; see also Duarte et al., 2006; Swick et al., 2006 for reports of a similar but seemingly more frontally distributed retrieval-related negativity). In other studies, however, the negative effect co-existed with a robust left parietal effect (Dulas and Duarte, 2013; James et al., 2016; Trott et al., 1997, 1999; Wegesin et al., 2002) and, in one case, the negativity co-occurred with a parietal effect that was evident only over the right hemisphere (Li et al., 2004). Clearly, the left parietal effect and the sustained retrieval-related negativities frequently identified in older participants are not mutually exclusive. However, the relationship between the effects is unclear, as are the circumstances that dictate whether they will co-occur or whether the parietal effect will be obscured by the evolving negativity. In the present case, these issues preclude a determination of whether, as in young individuals, the left parietal ERP effect in older adults was modulated by the specificity of the recollected information.

The present finding that the retrieval-related late negative effect evident in older adults was insensitive to source accuracy significantly extends previous results. With only one exception (see below), prior reports describing analogous age-dependent effects did not contrast the effects according to either subjective (RK) or objective (source accuracy) operationalizations of recollection. Rather, the contrasts identifying these effects employed ERPs elicited by correct rejections as a 'baseline'

(Dulas and Duarte, 2013; James et al., 2016; Kamp and Zimmer, 2015; Li et al., 2004; Scheuplein et al., 2014; Wegesin et al., 2002), potentially confounding the neural correlates of recollection and familiarity. To our knowledge, the present experiment is only the second study (after that of Trott et al., 1997, 1999) to examine whether this age-dependent late negativity is sensitive specifically to recollection, rather than reflecting a more generic retrieval process. The results stand in striking contrast to those reported by Trott and colleagues. As noted in section 1, these researchers examined ERPs in young and older adults in a procedure that allowed waveforms to be segregated according to source accuracy or, alternately, on the basis of an RK judgment. In agreement with the present data, Trott and colleagues reported that a prominent, age-dependent central-maximum late negativity (assessed relative to correct rejections) was insensitive to source accuracy. However, in contrast to the present results, the late negativity reported in the earlier study was also insensitive to the RK distinction: ERPs elicited by items accorded either judgment were equally negative-going relative to correct rejections. The reasons for these discordant findings are unclear. One potentially relevant factor, however, is that Trott and colleagues recorded ERPs during an initial old/new memory judgment, which was followed by 'off-line' source and RK judgments that were made some seconds later following re-presentation of the test item.

The findings of Li et al. (2004) demonstrate a somewhat similar pattern of ERP effects in older adults to that observed here. In that study, and unlike here, the sustained retrieval-related negativity was strongly left lateralized, although the contrast yielding the effects reported by Li and colleagues was between source-correct and correct rejection trials. Of importance, Li et al. (2004) employed a study manipulation (number of study exposures) that allowed ERPs to be contrasted across age groups while equating source accuracy, thus ruling out the possibility that the marked age differences in ERP retrieval effects that they observed resulted from a confound between age and memory performance (see Dulas and Duarte, 2013, for similar findings). Although Li et al. (2004) did not employ a contrast allowing recollection-specific effects to be identified, we take their findings as evidence that the present results are unlikely merely to be a reflection of age-related differences in memory performance (see Rugg, 2016, for discussion of this issue).

As discussed above, recollection-related ERPs in older adults were dominated by a centrally maximal negativity. However, this is not to say that there was no evidence at all of a retrieval-related negativity in young adults. As can be observed in Fig. 3B and C, there appears to be a late-onsetting negative deflection for R+ judgments in young adults. To investigate this possibility, we performed a subsidiary analysis confined to a later, more restricted, time window (1200–2000 ms). The analysis identified a significant negative, mid-posterior ERP deflection that appeared to be specific to R+ judgments (see Supplemental Materials for a full account of these results). This negative-going effect appears to be an example of the canonical LPN (for reviews see section 1 and Mecklinger et al., 2016), which has been proposed as a neural correlate of the reconstruction of source information from retrieved contextual features (see also Rosburg et al., 2013). Although superficially similar, the above supplemental analysis suggests that the negative effects identified in the present samples of older and young adults might be functionally distinct: whereas the effect in the older sample does not differ between R+ and R− trials, the effect in the young participants is selective for R+ trials only (and hence is consistent with the above-mentioned 'source reconstruction' account of the LPN).

In light of this apparent dissociation, the question arises as to the functional significance of the retrieval-related negativity identified in older adults here and in prior studies. Prior proposals have converged on the general notion that the effect reflects a tendency in older adults to engage sustained, consciously mediated reconstructive processes in an effort to recover source-specifying information (e.g., Dulas and Duarte, 2013; Li et al., 2004; Scheuplein et al., 2014). The present findings are arguably consistent with these proposals, given that source judgments were required only for those items accorded an R response. At the same time, our findings (along with those of Trott et al., 1997, 1999) raise a difficulty for this account, in that the negativity appears to be insensitive to source accuracy. This finding is hard to reconcile with accounts of the negativity that tie it to a memory search process, since one would assume that the process would, on average, terminate sooner on trials associated with accurate judgments (consistent with the slower RTs for R− than R+ judgments – see Table 3 and associated analyses), leading to a larger or more prolonged negativity for trials associated with inaccurate judgments. Another possible explanation[1] for insensitivity of the retrieval-related negativity in the older adults' ERPs is that R− trials contain a significantly higher proportion of source misattribution errors than in the case of the young participants (e.g., Mitchell et al., 2003). By this argument, the negativity elicited on these trials in our older participants is a reflection of the high proportion of such trials on which source retrieval was 'successful', but non-veridical. Arguably, the behavioral data are consistent with this interpretation in that relative to young adults, older adults were more prone to make incorrect source judgments rather than use the Don't Know option (age x response type interaction $p < .001$; see Supplemental Materials for full analysis). As was noted previously, however, there are insufficient trial numbers to allow a direct contrast of ERPs elicited by items that went on to receive incorrect source vs. Don't Know judgments. Clearly, the precise functional significance of this age-specific ERP retrieval effect requires further research.

4.4. Age-invariant ERP modulations

Finally, we turn to the sustained positive-going effect evident over the right frontal scalp in both young and older adults during the 800–2000 ms time window. This finding is reminiscent of several prior reports of age-invariant right frontal ERP retrieval effects (e.g., Dulas and Duarte, 2013; Li et al., 2004; Mark and Rugg, 1998). Beginning with the earliest study in which this right frontal effect was reported (Wilding and Rugg, 1996), it has consistently been interpreted as a neural correlate of the engagement of post-retrieval monitoring operations – processes that act on the products of a retrieval attempt in service of behavioral goals (Cruse and Wilding, 2009; Hayama et al., 2008; Wilding and Rugg, 1996; Woodruff et al., 2006; for reviews see Rugg, 2004; Rugg et al., 2002). The effect we report here is however inconsistent with prior evidence that the right frontal effect is greater for items attracting correct source judgments relative to those accorded incorrect judgments (Wilding and Rugg, 1996). Nonetheless, along with evidence from prior aging studies (Dulas and Duarte, 2013; Li et al., 2004; Mark and Rugg, 1998), the present findings support the proposal that post-retrieval monitoring is relatively impervious to the effects of age. This proposal receives additional support from fMRI studies in which the neural correlates of post-retrieval monitoring were reported to be age-invariant (e.g., de Chastelaine et al., 2016; Duarte et al., 2010; Dulas and Duarte, 2014; Giovanello et al., 2010; Wang et al., 2015; but see also McDonough et al., 2013; Mitchell et al., 2013).

4.5. Limitations

One limitation of the present study stems from the test requirement to make source judgments only for items that attracted an R response. This leaves open the possibility that the late negativity observed in older adults reflects differential response demands, since only R, and not K or N, judgments required two responses. Although we cannot definitively reject this possibility, it seems highly unlikely in light of the large number of studies where highly similar age-related late negativities were reported with experimental procedures that equated the response demands for different trial types (Dulas and Duarte, 2013; James et al.,

[1] We thank an anonymous reviewer for bringing this possibility to our attention.

2016; Kamp and Zimmer, 2015; Li et al., 2004; Scheuplein et al., 2014; Trott et al., 1997, 1999; Wegesin et al., 2002). We note in addition that if the late negativity observed here was merely a reflection of the additional response demands associated with R judgments, a similar effect should have been present in the young adults' waveforms, which was clearly not the case (Fig. 3).

4.6. Conclusion

The present findings replicate and extend prior work by demonstrating that, in young adults, the electrophysiological correlates of recollection are sensitive to the specificity of recollected information (Murray et al., 2015; Vilberg et al., 2006; Vilberg and Rugg, 2009a; Wilding, 2000; Woroch and Gonsalves, 2010). Additionally, the findings indicate that a sustained, retrieval-related negative deflection reported previously in older adults (Dulas and Duarte, 2013; James et al., 2016; Kamp and Zimmer, 2015; Li et al., 2004; Scheuplein et al., 2014; Trott et al., 1997, 1999; Wegesin et al., 2002) is associated with recollection as estimated using the RKN procedure, but appears to be insensitive to the accuracy of a subsequent source memory judgment. The functional significance of this effect and its relationship with other retrieval-related ERP effects remain obscure, but our findings are consistent with prior evidence (for review, see Mecklinger et al., 2016) that this age-related negativity is functionally dissociable from the superficially similar LPN previously identified in studies of source memory in young adults.

Declaration of competing interest

None.

CRediT authorship contribution statement

Erin D. Horne: Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Joshua D. Koen:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing - review & editing. **Nedra Hauck:** Investigation, Project administration. **Michael D. Rugg:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2020.107394.

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