

Remembering and knowing: Electrophysiological distinctions at encoding but not retrieval

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ABSTRACT

Contemporary memory theories often distinguish between contextual recollection and acontextual familiarity as two fundamentally different types of recognition memory. It is currently unclear whether recollection and familiarity are supported by two correspondingly distinct retrieval mechanisms, or whether the same type of retrieval processing supports both phenomena. Electrophysiological findings in humans have widely been cited as support for the former, two-process position, in that late-onset parietal “LPC” potentials have been linked to recollection and earlier frontal “FN400” potentials to familiarity. However, recognition memory is generally studied using conceptually rich stimuli such as words, which leaves open an alternative interpretation that one or both of these electrophysiological signals reflect conceptual processing distinct from recollection and familiarity per se. We tested this hypothesis using conceptually impoverished kaleidoscope images, such that opportunities for conceptual processing were minimized. Recollection-based and familiarity-based recognition in a remember/know paradigm were both indexed by LPC potentials. Old/new amplitude differences were greater for recollection compared to familiarity. Despite ample familiarity-based recognition, FN400 old/new effects were not observed, consistent with the contention that these potentials index conceptual processing rather than familiarity. These results cast doubt on interpretations of prior electrophysiological evidence obtained using conceptually rich stimuli as dissociating neural mechanisms of recollection and familiarity. We also found that neural events during encoding differentially predicted later recollection versus later familiarity. Collectively, these findings suggest that the engagement of distinct encoding processes can preferentially lead to recollection or to familiarity even if one type of retrieval process is responsible for both memory expressions.

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Introduction

The neurocognitive foundations of recollection and familiarity are currently under considerable debate. *Recollection* refers to a memory expression that is substantiated by the retrieval of specific contextual detail from a learning episode, whereas *familiarity* refers to an acontextual memory expression (Mandler, 1980; Yonelinas, 2002). For instance, encountering a familiar face can trigger retrieval of details such as the person's name or where, how, and when she was met (recollection). Conversely, the encounter can instead leave one puzzling over the identity of this seemingly familiar person (familiarity). In an experimental setting, recollection and familiarity are often operationalized as the recognition of repeated stimuli either with or without the simultaneous retrieval of contextual detail from the learning episode (Eichenbaum et al., 2007; Yonelinas, 2002). Dual-process models of recognition typically attribute the recollection/

familiarity distinction to qualitatively distinct retrieval mechanisms. An alternative possibility is that a single type of retrieval process supports recognition memory, yielding recollection when highly effective and familiarity when less effective, particularly with regard to retrieving contextual information.

Recordings of event-related potentials (ERPs) from the human brain have been widely portrayed as supporting dual-process models, because spatio-temporally distinct ERPs have purportedly been associated with recollection versus familiarity. ERP data have become increasingly central in this debate, because recent arguments have raised doubts about the meaning of apparent neural dissociations between recollection and familiarity obtained using other methods, including human neuropsychological assessment, non-invasive brain imaging, and animal models (e.g., Kirwan et al., 2008; Shrager et al., 2008; Squire et al., 2007; Wais, 2008; Wais et al., 2006; Wixted and Squire, 2004). Indeed, ERP evidence is increasingly being used to provide face validity on which to build more detailed elaborations of dual-process models of recognition (e.g., Eichenbaum et al., 2007). Assessing the validity of ERP dissociations between recollection and familiarity is thus essential for future progress in this area.

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The proposal that recollection is indexed by late-onset potentials typically showing a parietal-maximum distribution—“LPC” potentials—is not controversial (reviewed in Curran et al., 2006b; Friedman and Johnson, 2000; Mecklinger, 2000; Paller and Kutas, 1992; Paller et al., 2007; Rugg and Curran, 2007; Voss and Paller, 2008a). Views on ERP correlates of familiarity, however, are more contentious. Familiarity has most frequently been associated with earlier-onset potentials with a frontal distribution—“FN400” potentials or midfrontal old/new effects (reviewed in Curran et al., 2006b; Mecklinger, 2000; Rugg and Curran, 2007). It should be noted that FN400 and LPC potentials frequently co-occur during recognition testing, though this would not conflict with dual-process accounts, as most suggest that familiarity and recollection are not mutually exclusive. The majority of the evidence used in support of mapping the LPC/FN400 dissociation onto the recollection/familiarity dissociation consists of demonstrations that experimental manipulations that influence recollection but not familiarity also can influence LPC potentials but not FN400 potentials. For example, Curran (2000) tested recognition using some words that appeared with an inconsistent plurality from encoding to retrieval (either singular to plural or plural to singular), whereas plurality was consistent for other words. Plurality change reduced estimates of recollection and LPC potentials, relative to the consistent plurality condition, whereas plurality change did not influence estimates of familiarity and FN400 potentials. This and other evidence putatively linking FN400 potentials to familiarity merely shows that both are insensitive to the same experimental manipulations (Paller et al., 2007).

Furthermore, because recollection and familiarity are almost always studied using conceptually rich stimuli such as words and nameable pictures, it is possible that these ERPs reflect changes in

conceptual processing due to repetition instead of the hypothesized memory functions. Specifically, an alternative explanation for supposed ERP dissociations between recollection and familiarity is that familiarity has been conflated with conceptual implicit memory (Paller et al., 2007; Voss and Paller, 2008b). *Conceptual implicit memory* occurs when stimulus repetition enhances the neurocognitive processing of conceptual information independent of the awareness of this influence, as measured behaviorally in tests of conceptual priming (Gabrieli, 1998; Henson, 2003; Schacter and Buckner, 1998). Based on our review of the ERP literature (Paller et al., 2007), we argued that familiarity and conceptual implicit memory were likely to be operative concurrently in recognition tests with conceptually rich stimuli, and that various experimental factors would have influenced the two types of memory in a similar fashion. By this account, the extant evidence is insufficient for attributing FN400 potentials to familiarity versus conceptual implicit memory.

Results from a set of three recent studies are especially relevant in this regard. First, Yovel and Paller (2004) sought to examine ERP correlates of familiarity using facial stimuli. Faces of unknown people convey far less conceptual information than do verbal stimuli, such that influences from conceptual implicit memory were arguably less than in many other studies of recognition memory. In a learning phase, faces were randomly paired with spoken occupations. ERPs were examined during successful face recognition as a function of whether the occupation or any other details from learning were simultaneously retrieved (recollection) versus when no details were retrieved (familiarity). For both outcomes, recognition was associated with LPC potentials but not FN400 potentials, suggesting that FN400 potentials might be more strongly aligned with conceptual memory processing than with familiarity.

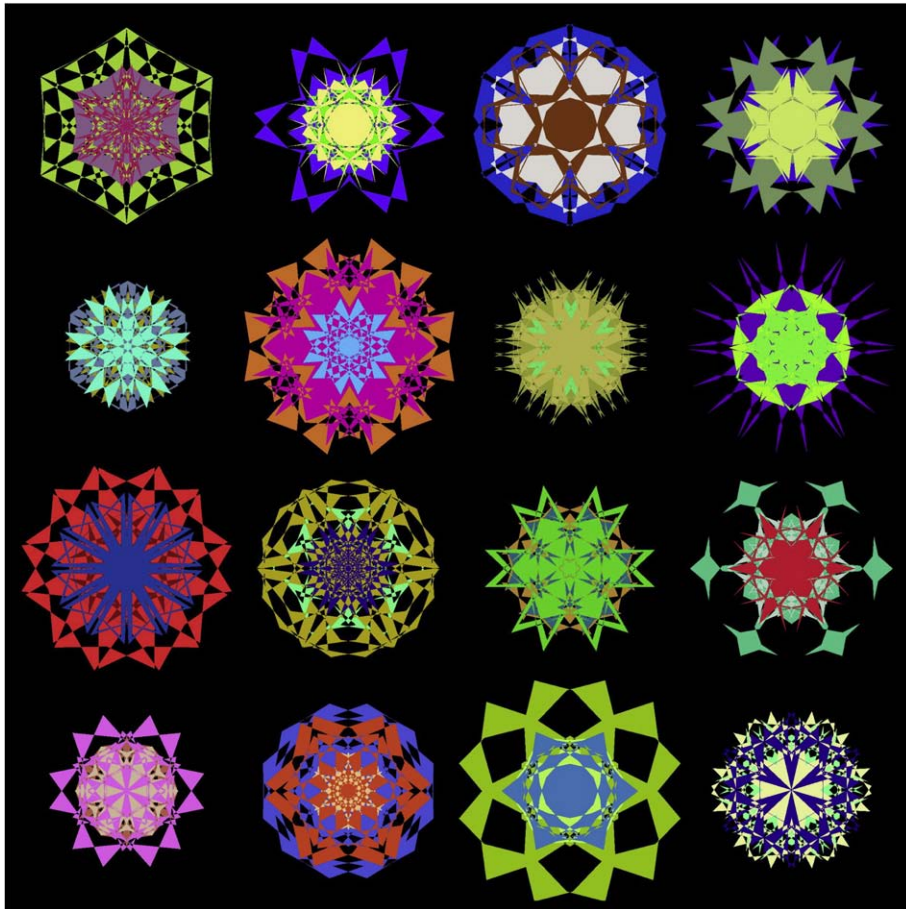


Fig. 1. Example kaleidoscope images.

Two subsequent studies that sought to replicate these findings produced conflicting results. MacKenzie and Donaldson (2007) found that familiarity and recollection for novel faces were indexed by LPC potentials. Additionally, the scalp topography of these potentials was more anterior for recollection than for familiarity (confirming a trend also observed by Yovel and Paller, 2004). In contrast, Curran and Hancock (2007) found that familiarity for novel faces was associated with FN400 potentials. In a companion commentary (Donaldson and Curran, 2007), authors of the two conflicting papers highlighted potential differences between studies that could have accounted for the different results. One intriguing possibility concerns the nature of the faces used. Yovel and Paller (2004) and MacKenzie and Donaldson (2007) both used sets of face stimuli that were relatively homogeneous in terms of race, hairstyles, and other characteristics, whereas Curran and Hancock (2007) used a set of face stimuli with marked variation in distinguishing features. We would postulate that the meaningfulness and variety of facial features could function to make conceptual memory processing more robust in a recognition paradigm (Paller et al., 2007). Collectively, these three studies are thus consistent with the notion that FN400 correlates of familiarity are more likely to be identified when processing of repeated items would support conceptual implicit memory.

One way to evaluate this interpretation and thereby achieve a better understanding of relationships between familiarity and recollection is to examine neural correlates of familiarity for stimuli with varying levels of conceptual features. Indeed, we recently found that FN400 correlates of familiarity for minimalist “squiggle” images varied as a function of whether the stimulus supported conceptual implicit memory (Voss and Paller, 2007). Squiggles were segregated into high- and low-meaningfulness categories via subjective ratings, and only those in the high-meaningfulness category were able to support conceptual implicit memory as measured behaviorally in a priming test. Critically, FN400 correlates of familiarity during a recognition test were present for the high-meaningfulness category but not for the low-meaningfulness category, despite approximately matched familiarity-based recognition (Voss and Paller, 2007; Voss et al., submitted for publication). Furthermore, FN400 amplitudes for high-meaningfulness squiggles varied systematically across subjects in proportion to each subject’s reaction-time measure of conceptual priming for the same squiggles (Voss et al., submitted for publication). These results demonstrate that putative FN400 correlates of familiarity depend on whether stimuli can also trigger conceptual implicit memory.

In the current study, we sought to determine whether ERP signals of recollection-based recognition would differ from those of familiarity-based recognition when confounding influences of conceptual processing were eliminated. We therefore used conceptually impoverished kaleidoscope images (Fig. 1) to elicit ERP correlates of memory in a recognition test. Although conceptual implicit memory was not directly assessed, we reasoned that it would be negligible, given that any conceptual processing induced by these stimuli would be extremely minimal.¹ Recollection and familiarity were operationalized via “remember” and “know” responses (Gardiner and Java, 1991; Tulving, 1985), which respectively indicated recognition with concomitant retrieval of detail from the encoding episode versus

recognition based solely on an unsubstantiated, acontextual feeling of familiarity. Know responses were subdivided into four confidence levels in order to characterize neural measures that track familiarity strength for comparison to recollection (cf. Woodruff et al., 2006; Yonelinas et al., 2005). Another key characteristic of the current study was that the large stimulus count (400 old and 400 new images) permitted analyses of ERP correlates of familiarity confidence for repeat items and, separately, for false alarms to new items. Such analyses are important, given that retrieval has been examined by identifying neural processing that leads an individual to erroneously claim that a novel item had been seen previously (e.g., Curran, 2000; Woodruff et al., 2006; but see footnote 4). The large stimulus set thus provided sufficient power for ERP analyses focused on false alarms to new items. The current design was thus suitable for thoroughly characterizing neural correlates of familiarity without contamination from concomitant conceptual processing.

Prior evidence has also indicated that neural events during the initial encoding of stimuli can differ according to whether subsequent recognition is accompanied by recollection or familiarity (Duarte et al., 2004; Paller and Wagner, 2002; Yovel and Paller, 2004). We therefore sought to determine if comparable dissociations between recollection and familiarity would be obtained using conceptually impoverished materials.

Materials and methods

Visual stimuli included 800 kaleidoscope images (Fig. 1). Images were created by overlaying three opaque hexagons, each of a randomly selected color, and performing three rounds of distortion for each hexagon. Distortion was accomplished via bisection of each side and deflection of each half at a randomly selected angle from the line tangential to the center of the bisected side. Images were presented at the center of a computer monitor within a square subtending approximately 5° of visual angle.

Recognition memory was assessed in 18 right-handed subjects (ages 19–32 years, 11 female) using 20 study-test blocks. In each study session, 20 novel kaleidoscope images were presented at visual fixation for 1500 ms each with a randomized 1500–2500 ms interstimulus interval. Subjects were instructed to memorize each image. Each study session was separated from its corresponding recognition test by a 1-min break, during which subjects performed mental arithmetic and were reminded of test instructions.

In each test session, the 20 kaleidoscope images from the previous study session (old images) were randomly intermixed with 20 entirely novel images (new images). Stimuli were presented individually at visual fixation for 1500 ms with a randomized 1500–2500 ms interstimulus interval. Subjects were instructed to discriminate old from new kaleidoscope images and simultaneously report the subjective quality of the recognition experience using a 5-choice button-press response. The choices were based on a modified “remember/know” paradigm intended to assess recollection and four levels of familiarity confidence (Woodruff et al., 2006; Yonelinas et al., 2005). Choices for old items included “remember” for recognition plus simultaneous retrieval of contextual detail from the study session, and four levels of “know” confidence (high, medium, low, and none). The last response, no-confidence know, was tantamount to a “new” response such that the subject could indicate viewing a new image. The kaleidoscope images assigned to the old and new conditions (400 for each condition) were counterbalanced across subjects.

Continuous EEG recordings were made during the study and test sessions from 59 scalp locations using tin electrodes embedded in an elastic cap. Impedance was less than 5 k Ω . Recordings were digitally sampled at 1000 Hz with a bandpass of 0.05 to 200 Hz. Recordings were collected with a right mastoid reference, and were rereferenced offline to averaged mastoids. Stimulus-locked ERPs were calculated for each condition of interest in 1100-ms epochs beginning 100 ms

¹ This reasoning was further supported by meaningfulness ratings collected from a separate group of 10 individuals (two male, ages 23–26). Subjects viewed 100 randomly selected kaleidoscope images (see Materials and methods) and 100 randomly selected squiggle images (Voss and Paller, 2007) in randomized order for two seconds each, and made ratings using a five-point scale with 1 indicating “no meaning whatsoever” and 5 indicating “high in meaning for an abstract image.” The average ratings for squiggles and kaleidoscopes were 3.5 and 1.8, respectively [$t(9) = 7.1, p < 0.001$]. The mean rating for squiggles was higher than that for kaleidoscope images in every subject. Our previous findings demonstrated that conceptual priming was found only in the subset of squiggles rated relatively higher in meaningfulness (Voss and Paller, 2007; Voss et al., submitted for publication). By extension, the mean meaningfulness rating of 1.8 for kaleidoscopes makes it unlikely that these stimuli would consistently elicit conceptual priming.

Table 1

Summary of recognition performance, showing mean percentage of old and new items endorsed in each of the five response categories, with response times and corresponding number of trials for each ERP

Endorsement: Word type:	Remember		High-confidence know		Medium-confidence know		Low-confidence know		New (no-confidence know)	
	Old	New	Old	New	Old	New	Old	New	Old	New
% Endorsed	22.7 (3.3)	2.8 (0.8)	18.4 (1.4)	9.3 (1.2)	20.8 (1.7)	20.3 (2.3)	26.1 (1.7)	36.5 (1.9)	11.9 (1.8)	31.1 (4.1)
Hits–false alarms	19.9		9.1		0.5		–10.4		–19.2 ^a	
Response times in ms	1298 (61)	1464 (104)	1448 (112)	1472 (125)	1424 (117)	1463 (131)	1420 (129)	1431 (130)	1415 (103)	1359 (102)
ERP trials	80 (14)	8 ^b (4)	70 (6)	30 (5)	69 (7)	65 (9)	91 (7)	120 (9)	15 ^c (8)	111 (17)

Standard error of the mean is provided in parentheses.

^a Computed as misses to old items minus correct rejections to new items.

^b The trial count was too low to constitute an ERP average.

^c The trial count was too low (<20 in five subjects), and so this ERP condition was excluded.

prior to stimulus onset. Baseline correction was performed by subtracting the average prestimulus amplitude from each poststimulus sample. An additional four channels were used for monitoring horizontal and vertical eye movements. Trials contaminated by electro-ocular or other artifact were excluded from analysis. ERP waveforms were smoothed with a 40-Hz zero-phase-shift Butterworth filter for presentation purposes only.

Statistical analyses of ERP waveforms focused on amplitude values averaged over latency intervals and electrode clusters. Latency intervals (300–500, 500–700, and 700–900 ms) were selected based on inspection of the waveforms and on a priori hypotheses regarding FN400 and LPC potentials, as were electrode clusters. Differences between conditions were assessed using repeated-measures analysis of variance (RM-ANOVA) with Geisser–Greenhouse correction when necessary.

Results

Recognition performance is summarized in Table 1. Accuracy was high for two response categories, in that far more old than new items were endorsed with remember and high-confidence know responses. Conversely, more new than old items were endorsed with low- and no-confidence know responses. The impression that recognition accuracy varied systematically across response type was confirmed by RM-ANOVA with factors response type (remember, high-confidence know, medium-confidence know, low-confidence know, and no-confidence know) and repetition (old and new), yielding a significant interaction [$F(2,8,46.9) = 43.1, p < 0.001$]. Furthermore, the number of hits was reliably greater than the number of false alarms only for remember and high-confidence know responses [$t(17) = 7.1, p < 0.001$ and $t(17) = 4.9, p < 0.001$, respectively], approximately the same number of hits and false alarms were produced for medium-confidence know responses, false alarms significantly outnumbered hits for low-confidence know responses [$t(17) = 6.6, p < 0.001$], and correct rejections significantly outnumbered misses for the new (no-confidence know) response category [$t(17) = 7.5, p < 0.001$].

Accurate recognition can also be indicated by greater than zero values for the percentage of hits minus the percentage of false alarms, which were calculated separately for each response option. Greater than zero values were evident only for remember and high-confidence know responses (Table 1). Whereas recognition was poor for responses made with lower confidence, both the remember and the high-confidence know response categories were associated with high accuracy and, as presented below, with robust ERP effects. Furthermore, a receiver operating characteristic (ROC) curve formed by treating the five response options as a confidence scale indicated that old/new discrimination was successful overall (Supplemental Fig. 1).

Recognition ERPs for old items

The primary ERP comparisons focused on correctly recognized old items (remember and know responses) contrasted with correctly

rejected new items. Very few trials were available for old items that were incorrectly endorsed as new (i.e., misses, <20 trials in five subjects), and this ERP condition was thus excluded. As shown in Fig. 2A, ERPs for old items in the remember and high-confidence know conditions were more positive than ERPs for correct rejections. ERPs for the medium- and low-confidence know conditions (two conditions not associated with accurate recognition, Table 1) were virtually identical to ERPs for correct rejections for all latencies and recording sites.

The old/new ERP differences for the high-confidence know and remember conditions both displayed a positive centro-parietal zenith from approximately 500–900 ms. There was markedly greater positivity for remember compared to know ERPs. Topographic maps for these two old/new ERP differences for latency intervals from 300 to 500, 500 to 700, and 700 to 900 ms are shown in Fig. 2A. The distributions appear qualitatively similar for the two contrasts, and, as discussed further below, both appear to lack an FN400 effect at 300–500 ms.

Statistical assessment of ERP waveforms for the remember, high-confidence know, and correct rejection conditions were made using RM-ANOVA with factors: condition, latency interval (300–500, 500–700, and 700–900 ms), and electrode cluster (anterior, middle, and posterior).² The anterior electrode cluster was centered on the Fz electrode and encompassed electrodes at which FN400 effects are commonly measured. The middle and posterior clusters encompassed electrodes for which LPC potentials are commonly measured.

A significant two-way interaction indicated that the condition effects differed across latency intervals [$F(2,2,37.0) = 9.4, p < 0.001$]. Additional RM-ANOVAs for each latency interval, with condition and cluster as factors, showed significant main effects of condition for each latency interval [respectively, $F(1.5,26) = 5.9, p = 0.01$; $F(1.5,26.3) = 23, p < 0.001$; and $F(1.6,27.9) = 17.5, p < 0.001$], but no significant interaction effects. These results indicate that old/new ERP differences did not vary significantly as a function of electrode cluster (but see below for direct tests for topographic differences).

For each latency interval, pairwise comparisons for (1) remember minus correct rejection, and for (2) high-confidence know minus correct rejection, were thus made using amplitude values averaged over all three clusters. All significant differences in these comparisons took the form of greater positive ERPs for old than for new stimuli. For the 300–500 ms interval, remember old/new differences were significant [$t(17) = 2.9, p = 0.01$], whereas high-confidence know old/new differences were not [$t(17) = 1.6, p = 0.1$]. For the 500–700 ms interval, both old/new differences were significant [$t(17) = 5.3, p < 0.001$ and $t(17) = 2.3, p = 0.03$, respectively]. Likewise, both

² The anterior cluster comprised electrodes: Fza, F3s, F4s, Fzp, FC1, FC2, and Cz. The middle cluster comprised electrodes: Cz, C1a, C2a, C1p, C2p, and Pzs. The posterior cluster comprised electrodes: Pzi, PO1, PO2, Ozs, O1i, O2i, and Ozi. The lowercase letters indicate that the given electrode was slightly anterior, posterior, inferior, or superior to the corresponding electrode from the International 10–20 system.

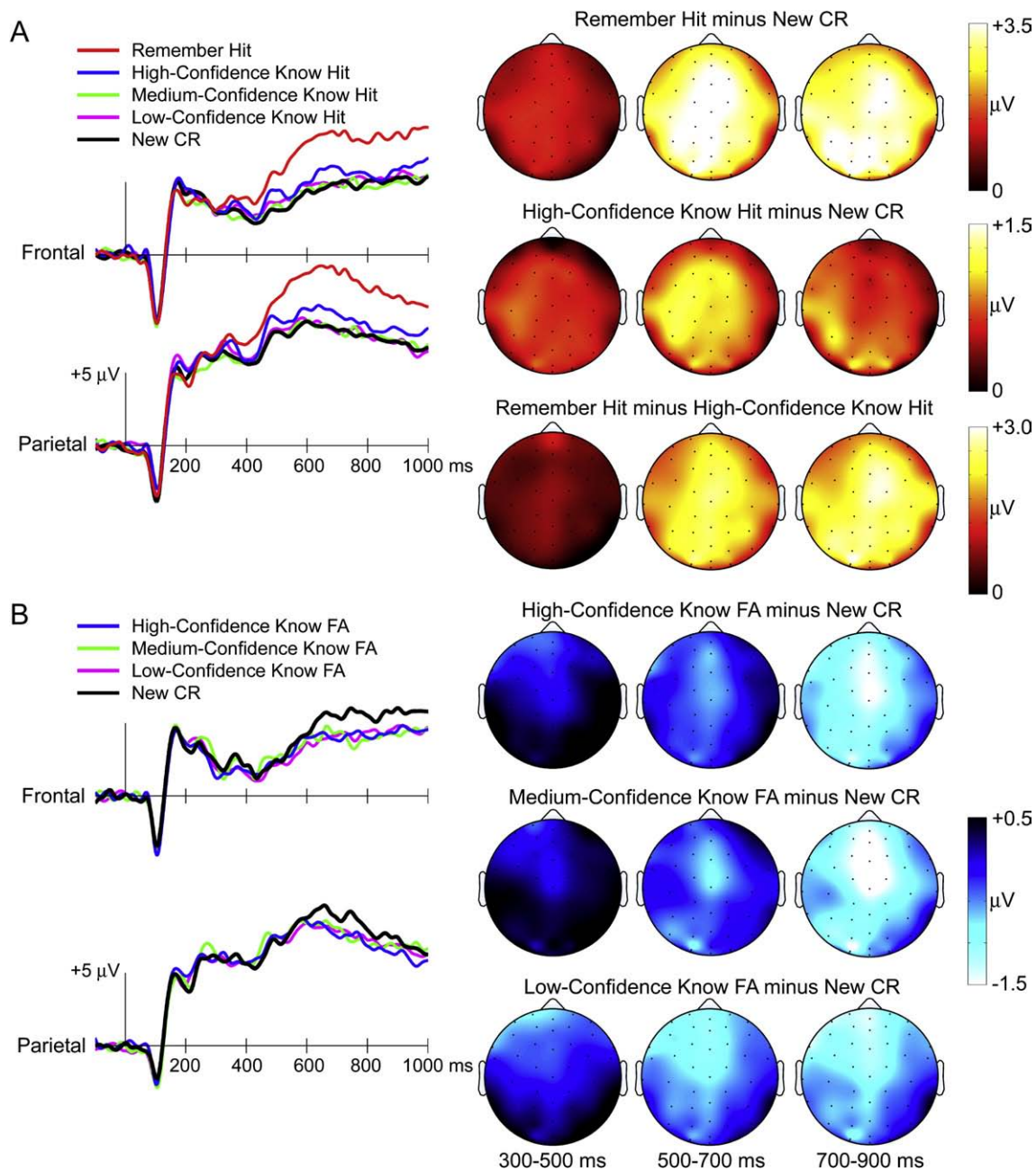


Fig. 2. Recognition test ERPs. (A) ERP waveforms for new correct rejections (CR) and old hits averaged as a function of recognition response type appear on the left for midline frontal and parietal recording sites. The frontal site was slightly anterior to Fz, and the parietal site was slightly inferior to Pz. Topographic plots of the old versus new ERP differences appear on the right for the remember and high-confidence know conditions, averaged over 300–500 ms, 500–700 ms, and 700–900 ms latency intervals. Topographic plots for remember minus high-confidence know are also provided for the same latency intervals (used in the targeted analysis of recollection, see Results). Each schematic head is shown as viewed from above, with the nose at the top, and difference amplitudes are indicated by the calibration bar, scaled differently for different contrasts. (B) The same type of ERP information is provided for the new CR condition and new false alarms (FA) averaged as a function of recognition response type. These data were computed for a subset of subjects (14 out of 18) for whom a sufficient number of trials were available, such that new CR waveforms differ slightly between panels A and B.

old/new differences were significant for the 700–900 ms interval [$t(17) = 4.7, p < 0.001$ and $t(17) = 2.2, p = 0.04$, respectively]. In addition, remember ERPs were significantly more positive than high-confidence know ERPs for all three latency intervals [$t(17) = 2.5, p = 0.02$; $t(17) = 5.4, p < 0.001$, and $t(17) = 5.5, p < 0.001$, respectively].

Topographic comparisons were also made for the same two old/new ERP contrasts, utilizing the vector normalization method, in which ERP amplitudes are normalized across conditions to permit comparisons of ERP distributions (McCarthy and Wood, 1985). Significant condition-by-electrode interactions for normalized values from all 59 electrodes indicate different scalp topographies for the

tested conditions, but not necessarily different neural generators (Urbach and Kutas, 2002). The first analysis sought to assess the consistency of the effects for each condition over time. Thus, the normalized difference topography for remember minus correct rejection was compared for the 300–500, 500–700, and 700–900 ms latency intervals, and the same was done for the high-confidence know minus correct rejection normalized difference topography. For the remember old/new difference, a nonsignificant electrode-by-interval interaction [$F(4.5, 76.3) = 1.5, p = 0.2$] indicated that the topographic distribution was consistent over time (the same outcome was obtained using comparisons between each pair of latency

intervals, $ps > 0.17$). A nonsignificant interaction was also identified for the know old/new difference [$F(4.9, 83.8) = 1.3$, $p = 0.3$; with $ps > 0.24$ for all pairwise comparisons of latency intervals]. These comparisons indicated that LPC correlates of recognition with remember and high-confidence know responses did not vary spatially across the three latency intervals.

Another topographic analysis sought to directly compare remember and know topographies. For each latency interval, the remember old/new difference topography was compared to the high-confidence know old/new difference topography. Electrode-by-condition interactions were nonsignificant for each interval [respectively, $F(58, 986) = 0.7$, $p = 0.9$; $F(5.4, 91.5) = 1.7$, $p = 0.1$; $F(58, 986) = 0.8$, $p = 0.8$], indicating similar old/new difference topographies for remember and high-confidence know recognition.

Based on these ERP findings, it is tempting to conclude that the same retrieval processing led to both remember and high-confidence know responses. Indeed, ERP old/new effects for each response type included LPC potentials that were qualitatively similar. However, remember responses probably signify recollection along with familiarity (Yonelinas, 2002). To the extent that this was the case, our ERP analyses could have been biased against finding differences between remember and high-confidence know conditions.

To provide a more sensitive test for such differences, we calculated the ERP difference between remember and high-confidence know responses. Whereas the remember-minus-new contrast could reflect both recollection and familiarity, the remember-minus-know contrast would hypothetically isolate ERP correlates of recollection by subtracting out ERP correlates of familiarity. These ERP differences appear as topographic maps in Fig. 2A. To determine if ERPs isolated by this contrast differed from ERP correlates of familiarity, we compared ERP topographies for remember minus high-confidence know versus high-confidence know minus correct rejection using the vector normalization approach. For the 300–500, 500–700, and 700–900 ms latency intervals, nonsignificant condition-by-electrode interactions indicated that difference topographies were indistinguishable [$F(58, 986) = 0.79$, 0.34, and 0.86, respectively]. This sensitive test for ERP differences between remember and high-confidence know responses thus corroborates the results from the

initial analysis in providing no evidence for a recollection/familiarity dissociation. Moreover, these results provided no evidence to link familiarity with FN400 potentials.

Recognition ERPs for new items

We also analyzed ERPs to new items as a function of the type of recognition response made (i.e., false alarms). The number of remember false alarms was too small to permit ERP analysis of this condition (Table 1). For the remaining analyses, four subjects were excluded because there were less than 15 trials for ERP calculation in one or more of the other conditions. Counterbalancing of stimuli to the old and new conditions was complete for this subset of 14 included subjects.

ERP waveforms for high-, medium-, and low-confidence know false alarms and new correct rejections are shown in Fig. 2B. Waveforms for the three false alarm conditions were strikingly similar throughout the recording epoch and for all recording sites. ERPs for all false alarm conditions were more negative than ERPs for correct rejections starting at approximately 600 ms. Topographic plots of the false-alarm versus correct-rejection ERP differences for each response type (Fig. 2B, right) indicated that the relative negativity over the interval from 700 to 900 ms was maximal at midline frontal and central locations, and appeared similar for the three contrasts.

Statistical assessments for these ERPs were made for the three electrode clusters described above and for the 500–700 and 700–900 ms latency intervals (the 300–500 ms interval was excluded because inspection indicated that conditions were virtually identical). A marginal three-way interaction [$F(2.9, 37.3) = 2.5$, $p = 0.08$] indicated that differences between the four conditions tended to vary by cluster and interval. Follow-up RM-ANOVAs for the 500–700 ms interval did not yield a significant main effect of condition [$F(3, 39) = 1.0$, $p = 0.4$] or condition-by-cluster interaction [$F(6, 78) = 0.9$, $p = 0.5$]. For the 700–900 ms interval, there was a significant main effect of condition [$F(2.6, 33.9) = 3.1$, $p = 0.04$] and a nonsignificant condition-by-cluster interaction [$F(6, 78) = 1.5$, $p = 0.2$], indicating that the greater negativity for false-alarm conditions did not vary by cluster. Pairwise comparisons on amplitude values at 700–900 ms

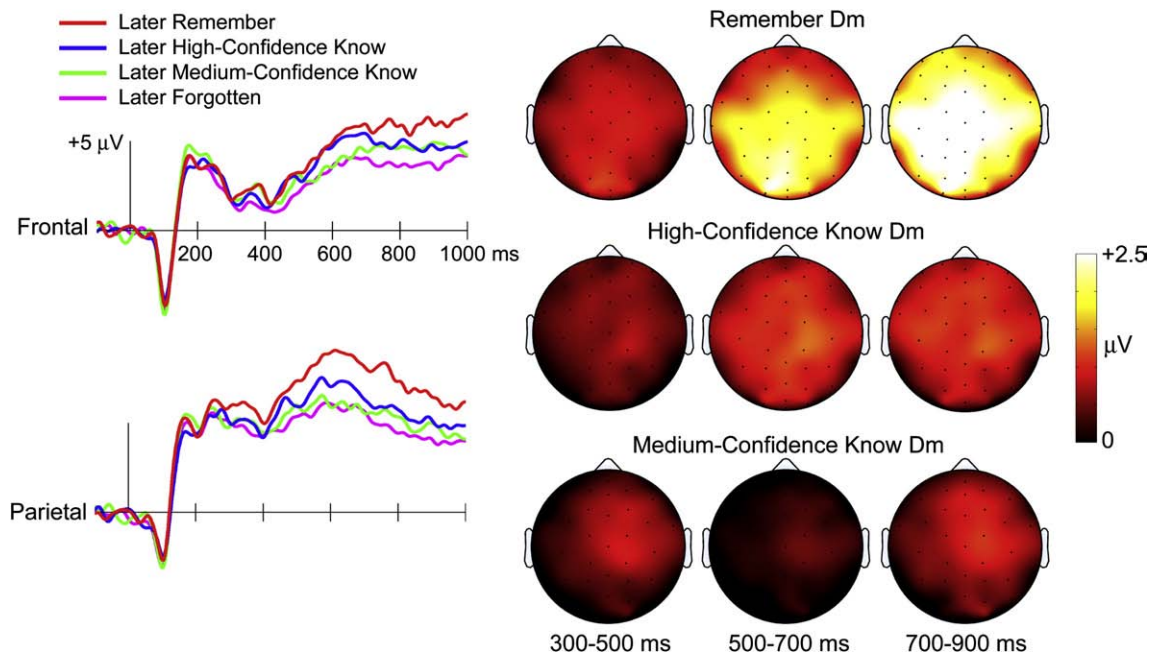


Fig. 3. Encoding ERPs showing Dm effects. For items in the study phase, ERP results are displayed paralleling those in Fig. 2. ERPs were averaged as a function of the responses given to the same items during the subsequent recognition test. ERP difference topographies for the three higher confidence conditions (Dm for remember, Dm for high-confidence know, and Dm for medium-confidence know) were computed relative to the baseline, later-forgotten, condition (low-confidence know and miss).

averaged over the three clusters indicated that ERPs were significantly more negative for the high-, medium-, and low-confidence know false alarms relative to correct rejections ($t(13) = 2.2, p = 0.04$; $t(13) = 2.8, p = 0.02$; and $t(13) = 2.2, p = 0.04$, respectively). From 700 to 900 ms, the average difference amplitude for all three false-alarm conditions relative to the correct rejection condition was $-1.2 \mu\text{V}$ at the vertex electrode (Cz).

Topographic comparisons made using the vector normalization method (as above) were used to determine if the distribution of the ERP difference between false alarms and correct rejections from 700–900 ms varied as a function of false alarm response type (high, medium, and low confidence know). A nonsignificant condition-by-electrode interaction [$F(116,1508) = 1.0, p = 0.6$] indicated that the distributions did not vary significantly.

Encoding ERPs

To investigate whether recollection and familiarity could be dissociated during encoding, the Dm method (analyzing neurophysiological Differences based on subsequent memory performance) was used to assess encoding events that predicted performance during the recognition tests (Paller and Wagner, 2002). ERPs were computed for encoding trials segregated according to the corresponding response to that item during recognition testing. Because low-confidence know and no-confidence know (new) responses were both made with significantly higher frequency for new items than for old items, study items subsequently endorsed in either of these two conditions were considered “later forgotten,” the baseline for Dm analyses. ERPs for three later recognition hit conditions—recollection, high-confidence know, and medium-confidence know—were thus compared to ERPs for later forgotten items. These ERPs are shown in Fig. 3, along with topographic plots for remember Dm, high-confidence know Dm, and medium-confidence know Dm. All three Dm effects displayed a centro-parietal scalp distribution, with largest amplitudes for recollection Dm, intermediate amplitudes for high-confidence know Dm, and smallest amplitudes for medium-confidence know Dm.³

Statistical assessments were conducted using average amplitude values for each of the four conditions shown in Fig. 3 for the three electrode clusters and for the 500–700 ms and 700–900 ms latency intervals. A significant main effect of condition [$F(1.9,31.6) = 5.4, p = 0.01$] and condition-by-interval interaction [$F(1.9,31.6) = 6.9, p < 0.001$] indicated that differences between conditions varied by latency interval, but not by cluster. Dm amplitudes were thus averaged over the three clusters and assessed via pairwise comparisons for the three effective encoding conditions, each versus the baseline condition. The remember Dm and high-confidence know Dm were significantly positive at 500–700 ms [$t(17) = 3.5, p = 0.003$ and $t(17) = 2.9, p = 0.01$, respectively] and at 700–900 ms [$t(17) = 4.2, p < 0.001$ and $t(17) = 2.6, p = 0.02$, respectively]. The medium-confidence know Dm was not reliable for either interval [$t(17) = 0.9, p = 0.38$ and $t(17) = 1.6, p = 0.13$, respectively].

Topographic comparisons for the 500–700 and 700–900 ms intervals were used to determine if the distribution of the significant ERP differences between later remember and baseline conditions differed from that between the later high-confidence know and baseline conditions. The condition-by-electrode interaction was significant only for the 700–900 ms interval [$F(3.0,51.4) = 3.2, p = 0.03$; for the 500–700 ms interval, $F(58,986) = 1.1, p = 0.29$], validating the impression that the remember Dm was more posterior than the high-confidence know Dm. To more closely scrutinize the

difference between remember Dm and high-confidence know Dm, the ERP difference between these two conditions was computed (Supplemental Fig. 2). The topography of this difference was left-posterior and maximal during the 700–900 ms latency interval, confirming the results from the aforementioned statistical tests.

Discussion

We characterized ERP correlates of individually assessed recollection and familiarity experiences for kaleidoscope images. Memory performance was highly accurate, even though the memorial information was conceptually impoverished. Successful recognition was associated with LPC effects for recollection and for high-confidence familiarity. LPC amplitude differences were much greater for recollection compared to high-confidence familiarity, but there were no topographic differences between these two conditions. These results are consistent with the hypothesis that recollection and familiarity were both supported, at least in part, by the neural processing that produced LPC potentials.

FN400 effects were not identified in association with either recollection or familiarity. Because opportunities for conceptual processing were negligible, as were FN400 effects, these results are consistent with our previous proposal that FN400 potentials reflect conceptual implicit memory processing rather than familiarity-based recognition (Paller et al., 2007; Voss and Paller, 2006, 2007, 2008b; Voss et al., submitted for publication; Yovel and Paller, 2004). It is important to note, however, that implicit memory processing was not assessed in this experiment. The current findings are therefore also consistent with the notion that FN400 potentials reflect explicit conceptual processing. On the other hand, our previous studies have shown that FN400 potentials directly track conceptual implicit memory processing for faces (Voss and Paller, 2006) and squiggles (Voss et al., submitted for publication). Meaningfulness ratings made to kaleidoscope images were extremely low, even relative to ratings made to squiggle images (footnote 1). We previously found that only the most meaningful squiggle images were capable of supporting conceptual implicit memory (Voss and Paller, 2007; Voss et al., submitted for publication). These results collectively suggest that any conceptual processing, explicit and implicit, was negligible for kaleidoscopes. On the other hand, familiarity memory was likely operative for kaleidoscopes recognized either with high-confidence know responses or with remember responses; in violation of the hypothesis that FN400 effects signal familiarity, neither of these two conditions yielded FN400 old/new effects.

The current results differ from the results reported in some previous examinations of ERP correlates of familiarity for stimuli ostensibly devoid of meaning. Groh-Bordin et al. (2007, 2006) identified FN400 potentials as putative correlates of familiarity for minimalist squiggle images. However, many of these images were not devoid of meaning; participants in memory experiments often believe that many of these images look like abstract representations of common, nameable objects. Group-normalized ratings of squiggle meaningfulness were used by Groh-Bordin et al. (2006) in an attempt to rule-out potential influences from conceptual implicit memory by showing FN400 effects independent from variations in meaningfulness. However, the extent to which most of these same abstract images evoked meaning-based associations varied markedly across viewers (Voss and Paller 2007), such that normalized ratings were inadequate for assessing the relevance of squiggle meaningfulness. Indeed, when we characterized squiggle meaningfulness on a subject-by-subject basis, conceptual priming was reliably exhibited for the most meaningful items, and our ERP results showed that FN400 potentials tracked conceptual implicit memory processing rather than familiarity (Voss and Paller 2007, Voss et al., submitted for publication).

In another study, Curran et al. (2002) identified FN400 correlates of recognition for visual “blob” stimuli. However, these investigators

³ In a separate analysis, Dm effects were computed using the later low-confidence know response as the baseline (excluding items later endorsed as new). Given that the number of old items later endorsed as new was relatively small (Table 1), the pattern of Dm findings in this separate analysis was indistinguishable from that reported in the main analysis.

noted that many subjects reported that the blobs looked like nameable shapes (e.g., “Texas”), so blobs in this experiment might very well have prompted conceptual processing suitable for supporting conceptual implicit memory. We thus presume that, on average, kaleidoscope stimuli are less likely to evoke conceptual processing than either squiggle stimuli (Groh-Bordin et al., 2006, 2007; Voss and Paller, 2007; Voss et al., submitted for publication) or blob stimuli (Curran et al., 2002). Moreover, our subsidiary analysis of meaningfulness ratings (footnote 1) showed that, on average, subjects found kaleidoscope images much less meaningful than squiggles.

Subjects in the current ERP study were asked, during debriefing, if any kaleidoscope stimuli were meaningful in any way. All but one subject reported that nameable objects were perceived in some stimuli—subjects are astonishingly capable of creating meaning in such situations. Example reports included crab claws, buildings, insects, and faces. These subjects furthermore reported that “remember” responses were preferentially made to these items during the recognition test. Thus, if conceptual processing contributed to any ERP measures here, it would have been for a few trials in the recollection condition. There was a nonsignificant trend for more positive potentials at midfrontal electrodes in the 300–500 ms latency interval for this condition compared to correct rejections (1.0 μV on average, $\text{SE}=0.9$, Fig. 2A). Perhaps FN400 effects were present in the recollection condition on some trials, but such effects may have been too infrequent, weak, poorly time-locked to stimulus onset, and/or obscured by LPC potentials to be detected reliably. Curran et al. (2002) in their study of blobs did not segregate recollection from familiarity, such that FN400 effects in their experiment may have related to conceptual implicit memory processing for striking visual features that also led to recollection, instead of to familiarity.

One of the major results from the present study is that familiarity was associated with LPC potentials rather than FN400 potentials, and it is thus important to note that in one sense this represents a null finding with respect to the association between familiarity and FN400 potentials. Additional consideration is warranted, in light of the possibility that various extraneous factors could have resulted in no association between familiarity and FN400 potentials. First, high-confidence familiarity decisions were not exceedingly rare or based on weak memory experiences; this response choice elicited approximately twice as many hits as false alarms, on par with other recent studies that have identified FN400 correlates of recognition (Curran, 2004; Curran and Hancock, 2007; Woodruff et al., 2006). Recognition accuracy (and presumably, familiarity) was also very high for recollection responses, and FN400 potentials were not identified during this condition either. It is therefore unlikely that the failure to identify FN400 potentials resulted from weak memory. Another important point is that the ERP trial count for the high-confidence familiarity condition (70 on average) was very high compared to that in previous studies, indicating that the failure to identify FN400 potentials was not a trivial outcome of excessive EEG noise or poor signal-to-noise ratio. One final consideration is related to the nature of the ERP method—it can be difficult to dissociate two ERP effects that overlap in time and space. In the current experiment, it is conceivable that LPC effects, if produced during the 300–500 ms latency, could have obscured genuine FN400 effects. LPC effects superimposed on FN400 effects could conceivably shift the topography at 300–500 ms from a frontal maximum to a parietal maximum. However, waveform examination at 300–500 ms (Fig. 2A) weighs against this possibility, because difference amplitudes were unreliable at frontal locations (approximately 0.5 μV for old high-confidence know versus new correct-rejection; $t(17)=0.9$, $p=0.4$). Indeed, this is the latency interval and scalp location typically used for measuring FN400 (300–500 ms and electrodes near the Fz electrode). There is thus no reason to conclude that FN400 effects were present but obscured by LPC effects. Furthermore, in other studies we used the identical ERP recording and analysis techniques to separate FN400 potentials from

partially-overlapping LPC potentials, and the outcome was that FN400 potentials were linked to conceptual implicit memory (Voss et al., in revision; Voss and Paller, 2006, 2007; Voss et al., submitted for publication). Accordingly, a reasonable conclusion is that if FN400 indexed familiarity in a general sense, as has been widely claimed, then FN400 effects would have been observed in the present experiment.

In the published literature on ERPs and recognition memory, one fact that has not received sufficient emphasis is that FN400 potentials are very similar to N400 potentials, which have been extensively characterized as neural correlates of semantic/conceptual priming and linguistic processing (Kutas and Federmeier, 2000; Kutas and Hillyard, 1980; Kutas et al., 2006). Like FN400 potentials, these N400 potentials entail a negative deflection in the ERP waveform with a peak amplitude at approximately 400 ms after stimulus onset. The scalp distribution of N400 potentials has classically been characterized as parietal, which is why FN400 potentials, which are maximal at mid-frontal recording sites, were denoted as Frontal N400s. However, the anterior-posterior loci of N400 effects aren't invariably parietal, but rather vary greatly as a function of many factors, including the nature of the stimuli (Kutas et al., 2006). The extent to which FN400 potentials can be associated or dissociated from N400 potentials is largely unexplored and deserves further investigation.

As summarized above, LPC potentials were associated with familiarity for repeated kaleidoscope images. In addition, ERP correlates of new items mistakenly endorsed as old (false alarms) provide additional information relevant to determining the functional significance of LPC potentials. False alarms primarily comprised “know” responses, indicating false recognition based on a feeling of familiarity. False alarms at low, medium, and high confidence levels were associated with very similar late-onset (approximately 600 ms), centrally distributed negative ERPs relative to the correct-rejection baseline (Fig. 2B). Given that these ERPs were similar to LPC potentials identified in the old/new ERP contrast in latency and spatial distribution, one possibility is that they reflect a common memory process in the following sense. Amplitudes were greatest for recollection, less for high-confidence familiarity, less yet for correct rejections of new items (which can entail accurate retrieval of old items in order to correctly reject the new item), and least for false alarms (Fig. 4). Prior studies have revealed similar correlations

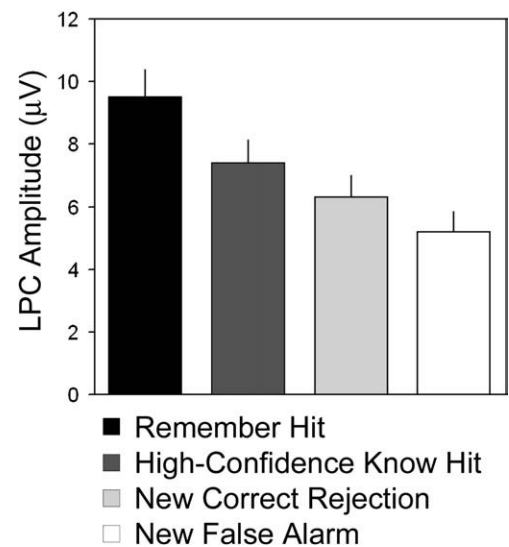


Fig. 4. LPC potentials tracked retrieval accuracy. ERP amplitudes were averaged from 500 to 900 ms for the middle and posterior electrode clusters used to assess LPC potentials. Four test-phase conditions were included: old remember, old high-confidence know, new correct rejection, and new false alarm. The false alarm condition comprised new items erroneously endorsed with high-, medium-, and low-confidence know responses. All pairwise differences were statistically significant ($N=18$, $p<0.05$).

between LPC potentials and recognition accuracy (Curran et al., 2006a; Voss and Paller, 2007; Wilding, 2000).⁴ We thus tentatively propose that a subset of the neural processes responsible for LPC potentials included the retrieval process that produced accurate recollection and familiarity. Previous evidence (e.g., Wilding, 2000) suggests that LPC potentials would have been yet greater in magnitude if recollection had been more robust. Because LPC potentials varied only in amplitude with whether the subjective content of the recognition experiences was one of recollection with detail versus familiarity with no detail, it is likely that these potentials reflect the operation of the retrieval processing that reactivates stored memory traces, rather than the reactivated content of those traces (as studied in Polyn et al., 2005).

Neural correlates of familiarity have been highly relevant to the evaluation of dual-process models of recognition in the literature. Distinctions between FN400 correlates of familiarity and LPC correlates of recollection have been taken as strong evidence in favor of these models (Curran et al., 2006b; Eichenbaum et al., 2007; Rugg and Curran, 2007; Yonelinas, 2002). The hypothetical distinction between recollection and familiarity has also been supported by a other types of evidence, including human behavior, single-unit recordings, and surgical ablation studies in nonhuman animals (Aggleton and Brown, 2006; Eichenbaum et al., 2007; Yonelinas, 2002). However, it has been cogently argued that the brunt of this evidence is consistent with the notion that a single type of retrieval process supports both recollection and familiarity (Squire et al., 2007; Wixted, 2007). Recollection and familiarity may indeed correspond to distinct memory experiences, but they may result from retrieval processes that are either highly effective in the case of recollection, or relatively less effective with minimal contextual information from the learning episode in the case of familiarity. The present results indicate that familiarity and FN400 potentials are not inexorably linked. Taken with other evidence from our laboratory that FN400 correlates of familiarity are only identified when conceptual implicit memory is also possible (Voss and Paller, 2007), and that FN400 magnitude is positively correlated with the magnitude of conceptual priming (Voss and Paller, 2006; Voss et al., submitted for publication), we suggest that recollection and familiarity are both indexed by LPC potentials. Thus, the extant ERP evidence should not be taken as supporting dissociations between retrieval processing relevant for recollection and familiarity.

ERPs recorded during memory encoding in the present study (Fig. 3) are relevant for exploring other dimensions of the qualitative differences between the memory expressions of recollection and familiarity. Successful memory formation was associated with widespread positive ERPs that onset approximately 500 ms after stimulus onset. These potentials differentiated subsequent recollection from subsequent high-confidence familiarity; Dm for recollection had a more posterior distribution compared to Dm for high-confidence familiarity. Other studies have also identified neural dissociations between later recollection and later familiarity during encoding

(Davachi, 2006; Diana et al., 2007; Paller and Wagner, 2002; Yovel and Paller, 2004). However, most studies have used conceptually rich stimuli, and ERP studies using abstract stimuli have either failed to identify Dm effects (e.g., Van Petten and Senkfor, 1996), or identified unusual Dm effects (e.g., Otten et al., 2007). The present findings demonstrate that conceptual content is not a prerequisite for Dm effects. The greater parieto-occipital distribution for subsequent recollection versus subsequent familiarity in the present study could reflect a multitude of neurocognitive processes that are potentially correlated with successful encoding. One possibility is that these effects partially reflected conceptual processing for the subset of somewhat meaningful items that were later endorsed with remember responses. Indeed, we have previously found that parieto-occipital potentials at encoding vary with meaningfulness for abstract shapes (Voss et al., submitted for publication). Future studies will be necessary to determine what operations are indexed by encoding processing that differentiates later recollection from later familiarity, and how these processes differ when conceptual content is present versus absent. Moreover, it is yet to be determined if neural measures that predict recollection versus familiarity reflect differential long-term memory processing *per se* (a position argued by Davachi, 2006), rather than the recruitment of additional resources that merely correlate with long-term memory processing, such as selective or sustained attention (e.g., Kirwan et al., 2008; Staresina and Davachi, 2008). Based on the current results, a reasonable hypothesis is that the strength of memory traces can vary depending on the resources recruited during encoding, and that a retrieval process indexed by LPC potentials acts to reactivate these memory traces, producing recollection for relatively strong traces and familiarity for relatively weak traces.

In conclusion, we examined familiarity-based recognition for conceptually impoverished images, and the electrophysiological correlates of recognition did not include FN400 potentials; our key finding was that recollection and familiarity were both associated with LPC potentials. These results are consistent with the interpretation that FN400 potentials reflect conceptual implicit memory processing (Paller et al., 2007; Voss and Paller, 2008b), which was negligible for kaleidoscope images recognized with familiarity. Thus, we suggest that ERP evidence at-large is consistent with the hypothesis that distinct encoding processes lead to recollection and familiarity, but that both nonetheless rely on a common type of retrieval process, the effectiveness of which is indexed by LPC potentials. The position that supposed neural distinctions between recollection and familiarity can be boiled down to variations on a continuum from strong to weak memories (Shrager et al., 2008; Squire et al., 2004, 2007; Wais, 2008; Wais et al., 2006; Wixted, 2007; Wixted and Squire, 2004) thus appears to accurately describe electrophysiological correlates of recognition.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.01.048.

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⁴ In contrast, Woodruff et al. (2006) reported that FN400 amplitudes for words tracked familiarity confidence, with greatest amplitudes for high-confidence know responses. However, as we have previously argued (Paller et al., 2007), this finding is suspect due to the conflation of familiarity strength and old/new status. Old and new items were collapsed together to form the ERP for each confidence level. Therefore, the ratio of old items to new items was high for the highest confidence level and low for the lowest confidence level. If FN400 potentials merely differed overall between old and new items, FN400 old/new effects would be titrated across confidence levels, producing the illusion that FN400 potentials tracked familiarity strength. A subsidiary analysis of old-new differences equated for familiarity using matched numbers of old and new trials in each confidence condition was insufficient for ruling-out this possibility, because the result was a null FN400 finding and the subsidiary analysis was very heavily weighted with low-confidence trials, which might reflect poor encoding and could thus be expected to show minimal FN400 differences by either account. Therefore, FN400 results from Woodruff et al. (2006) could be attributed to either conceptual priming or familiarity, as no convincing relationship between FN400 amplitude and familiarity confidence was demonstrated.

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