

Separating Event-related Potential Effects for Conceptual Fluency and Episodic Familiarity

Regine Bader and Axel Mecklinger

Abstract

■ ERP old/new effects have been associated with different sub-processes of episodic recognition memory. The notion that recollection is reflected in the left parietal old/new effect seems to be uncontested. However, an association between episodic familiarity and the mid-frontal old/new effect is not uncontroversial. It has been argued that the mid-frontal old/new effect is functionally equivalent to the N400 and hence merely reflects differences in conceptual fluency between old and new items. Therefore, it is related to episodic familiarity only in situations in which conceptual fluency covaries with familiarity. Alternatively, the old/new effect in this time window reflects an interaction of episodic familiarity and conceptual processing with each making a unique functional contribution. To test this latter account, we manipulated conceptual fluency and episodic familiarity orthogonally in an in-

cidental recognition test: Visually presented old and new words were preceded by either conceptually related or unrelated auditory prime words. If the mid-frontal old/new effect is functionally distinguishable from conceptual priming effects, an ERP contrast reflecting pure priming (correct rejections in the related vs. unrelated condition) and a contrast reflecting priming plus familiarity (hits in the related vs. correct rejections in the unrelated condition) should differ in scalp distribution. As predicted, the pure priming contrast had a right-parietal distribution, as typically observed for the N400 effect, whereas the priming plus familiarity contrast was significantly more frontally accentuated. These findings implicate that old/new effects in this time window are driven by unique functional contributions of episodic familiarity and conceptual processing. ■

INTRODUCTION

Recollection of a prior episode comprises remembering contextual details, whereas familiarity indexes oldness of a stimulus by a mere context-free feeling of knowing. According to dual-process models of recognition memory, these two phenomenological descriptions of retrieval experiences are reflections of different neurocognitive processes (for a review, see Yonelinas, 2002). This notion has been widely supported using different neuroscientific methodologies (e.g., Montaldi & Mayes, 2010; Aggleton & Brown, 2006; Diana, Reder, Arndt, & Park, 2006) but also contested (e.g., Squire, Wixted, & Clark, 2007).

Comparing ERPs to correctly classified old and correctly classified new items in an episodic recognition memory task, one can reliably observe that old items elicit more positive-going waveforms than new items. These so-called ERP old/new effects have been subdivided according to time course and scalp distribution as well as their associated functional significance. Two of these effects have been associated with familiarity and recollection across a variety of experimental manipulations, which is why they have been in the focus of recognition memory research during the last decades (see Rugg & Curran, 2007, for a review). It is claimed that the left parietal old/new effect,

which can be observed between 500 and 700 msec after stimulus onset, is an index of recollection whereas an earlier occurring (300–500 msec) mid-frontal old/new effect has been linked to familiarity. The validity of these differential associations is of theoretical importance as they are taken as support for dual-process models. Moreover, the high temporal resolution of ERPs provides the unique possibility to track online the involvement of familiarity and recollection under different experimental conditions without imposing additional response requirements on participants.

Although the association of the left parietal old/new effect with recollection seems to be uncontroversial, the link between the mid-frontal effect and familiarity has recently been intensively debated. In support of the view that the mid-frontal old/new effect is a neural correlate of familiarity, experimental manipulations were found to influence the mid-frontal old/new effect in a way that would be theoretically expected from a neural correlate of a fast-acting strength-based memory process. For instance, the effect is sensitive to the gist rather than contextual details of a study episode (Curran, 2000), covaries with subjective expressions of familiarity strength (Yu & Rugg, 2010; Woodruff, Hayama, & Rugg, 2006), and it is not impeded by a response deadline (Mecklinger, Brunnemann, & Kipp, 2010). The main contraposition to this view is the notion that the mid-frontal old/new effect reflects differences in conceptual fluency for old and

new items that are inherent in most recognition memory tasks and are not necessarily bound to episodic familiarity. According to this position, the mid-frontal old/new effect can be associated with familiarity only under limited conditions, that is, when conceptual fluency covaries with familiarity (Paller, Lucas, & Voss, 2012). In line with this view, the mid-frontal old/new effect is not observed when the to-be-remembered stimuli are conceptually meaningless as is the case for kaleidoscope images (Voss & Paller, 2009). For pre-experimentally unfamiliar stimuli such as line drawings of non-objects or rare words with unknown meanings, a mid-frontal old/new effect can only be observed when these stimuli are subjectively perceived as meaningful by the participants (Voss, Lucas, & Paller, 2010; Voss, Schendan, & Paller, 2010; but see Speer & Curran, 2007). In one study, Voss and Federmeier (2010) claimed that the mid-frontal old/new effect is functionally equivalent to the N400, an electrophysiological measure of the ease of semantic processing (Kutas & Federmeier, 2011). N400 effects crystallize in less negative-going waveforms for items that are conceptually more fluent due to expectancy or semantic priming. Indeed, with a peak latency of about 400 msec, the N400 has a similar time course as the mid-frontal old/new effect. The topographical distribution of the N400 effect, however, has a parietal and not a frontal focus. Voss and Federmeier (2010) employed a continuous recognition memory paradigm, in which words were either preceded by semantically related or unrelated words. As a topographic comparison of the semantic priming contrast and the old/new contrast did not reveal a significant difference, the authors concluded that the N400 effect and the mid-frontal old/new effect are functionally indistinguishable. However, recognition memory and priming were highly confounded in this study as hits in the unrelated condition, which were used for the recognition contrast, were primed with a related prime during their first presentation. Thus, hits did not only have a study history but also a priming history, which eliminated the mid-frontal old/new effect (Stróžak, Abedzadeh, & Curran, 2016, Experiment 2). Moreover, as another limitation of the aforementioned study, the requirement to first rate the pleasantness of the word and then make an old/new decision might have obscured recognition-related ERPs. In an effort to overcome these limitations, Bridger, Bader, Kriukova, Unger, and Mecklinger (2012) integrated the priming manipulation into the study phase of a standard study-test recognition memory paradigm and assessed recognition memory without additional tasks during the test phase. This allowed a more valid comparison of these two effects on the same set of stimuli by clearly separating the involved cognitive processes. Intriguingly, topographic comparisons between ERP semantic priming (N400) and the mid-frontal old/new effect revealed significant differences implying a functional dissociation between these two effects (see Stróžak et al., 2016, Experiment 2, for a recent replication).

Nevertheless, the findings that only meaningful stimuli can elicit a mid-frontal old/new effect are reconcilable with a familiarity account of this effect (Bridger et al., 2012) as some studies show that familiarity and conceptual processing have overlapping neural generators (Dew & Cabeza, 2013; Meyer, Mecklinger, & Friederici, 2010; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010; Henson, Cansino, Herron, Robb, & Rugg, 2003); and it is well conceivable that meaningfulness is a prerequisite for familiarity to occur. Moreover, some models of recognition memory explicitly assume that conceptual fluency can be attributed to familiarity in situations in which fluency varies within a test situation or is discrepant to the expected fluency for a given item (Bruett & Leynes, 2015; Whittlesea & Williams, 2001; Jacoby, Kelley, & Dywan, 1989). Thus, to reconcile the ERP findings described above, we consider it most likely that the mid-frontal old/new effect reflects episodic familiarity but that its magnitude can be modulated by the degree of conceptual processing. One way to reveal such a modulation would be to manipulate old/new status and conceptual fluency of an item orthogonally in a recognition test by preceding old and new items with semantically related and unrelated primes. On a behavioral level, this leads to an increase in “old” responses for studied and unstudied primed items because their conceptual fluency is enhanced (e.g., Dew & Cabeza, 2013; Wolk et al., 2004; Whittlesea & Williams, 2001; Rajaram & Geraci, 2000). Wolk and colleagues contrasted old/new status and conceptual fluency also on the electrophysiological level and found a mixed pattern of results. They tested participants on incidentally studied single words (e.g., “boat”), that were either preceded by predictive sentence stems (“The stormy seas tossed the...”) or nonpredictive sentence stems (“She saved up her money and bought a...”). The behavioral finding of an increase in “old” responses after predictive sentence stems was mirrored by the ERP results: In the time window between 300 and 550 msec, predictive stems led to more positive amplitudes than nonpredictive stems for both old and new words. As the effect was smaller for old compared with new words, the authors reasoned that, as old words were conceptually more fluent due to prior study, the priming manipulation may have been less effective for these words. Surprisingly, however, the comparison of “old” and “new” responses did not yield any differences in this time window. Only in later time windows (800–1200 msec, 1200–1600 msec), “new” responses elicited more positive going waveforms than “old” responses. As this late positivity was also negatively correlated with a behavioral measure of fluency, the authors take this late effect to reflect the successful inhibition of an erroneous fluency attribution for primed new words. Such an interpretation implies that in the early time window only conceptual processing takes place and familiarity comes into play only in a late time interval in the form of a (mis) attribution of fluency to a prior experience. This view

is questionable as familiarity would be expected to be present well before responses are made as it led to an increase in “old” responses. More likely, processing old and new words within a sentence might have prioritized conceptual processing over recognition memory processing, causing the lack of reliable old/new effects in time windows before 800 msec. This, of course, complicates analyzing the interplay of fluency on the one hand and familiarity and recollection on the other hand. Moreover, the results by Wolk et al. are difficult to interpret as the authors analyzed “old” and “new” responses irrespective of accuracy, which precludes comparison with standard old/new effects.

Recently, Stróžak et al. (2016) reported a study (Experiment 1) in which they manipulated conceptual fluency and episodic familiarity orthogonally in a recognition test using a semantic priming manipulation. Although effects of priming and old/new status were present, they only found a quantitative interaction of both factors, but not a topographical dissociation between these effects. They concluded that conceptual fluency and familiarity cannot be dissociated when both factors are manipulated within the same test phase of a recognition test. However, several factors might have contributed to this null effect. First, as in the Voss and Federmeier (2010) study, participants had to make a valence judgment before making a recognition judgment, which likely diminished the influence of recognition processes on the ERPs during word presentation. Second, the delayed recognition response, an intentional encoding task, and relatively short study–test cycles might have increased participants’ reliance on recollection (see, e.g., Cary & Reder, 2003, for list length effects). Third and most importantly, to dissociate conceptual fluency and familiarity, Stróžak et al. compared the old/new effect for semantically primed words to the priming effect for hits. However, as acknowledged by the authors, the latter contrast is confounded by priming as it is possible that there are interactive effects of familiarity and conceptual fluency when both are manipulated within the same test phase.

Thus, to be able to investigate the relationship between the mid-frontal old/new effect and the N400 under ideal conditions, it is necessary to employ a design optimized for the occurrence of the mid-frontal old/new effect and choose a more suitable comparison. In the current study, we employed an incidental test to prevent participants from applying encoding strategies that might boost recollection and reduce the contribution of familiarity. After the study phase, in which participants made pleasantness judgments to single words, we visually presented a randomized list of old (studied) and new (unstudied) words that were preceded by either semantically related or unrelated auditory prime words. Responses were only required for old and new words but not for primes. In contrast to the previous studies that emphasized conceptual processing (processing within a sentence frame in Wolk et al., 2004, and pleasantness judgments in Stróžak et al., 2016), this trial structure

was intended to emphasize recognition memory processes for the target. We opted for auditory primes to minimize the risk that participants do not attend to the primes.

Given overlapping neural generators and the behavioral findings that fluency can be attributed to familiarity in situations in which fluency varies across trials (Bruett & Leynes, 2015), we expected an interaction between conceptual processing and familiarity. On the behavioral level, we hypothesized priming to generally increase “old” judgments irrespective of old/new status. In contrast, priming effects on RTs were primarily expected to speed up correct “old” responses (hits) whereas this prediction was not made for correct “new” responses (correct rejections [CRs]) as fluency and novelty should provide conflicting signals in this case (see Woollams, Taylor, Karayanidis, & Henson, 2008, for the same argument). On the electrophysiological level, given that the mid-frontal old/new effect is the ERP correlate of familiarity, we expected that the mid-frontal old/new effect should be greater in the related than the unrelated condition as attribution of fluency to familiarity should boost familiarity in the related condition. However, importantly, on the basis of the Bridger et al. (2012) data, we expected to observe also unique contributions of conceptual processing and familiarity in the early time interval in which the N400 and the mid-frontal old/new effect tend to occur. We operationalized pure conceptual priming on the electrophysiological level as the ERP contrast between CRs in the related and CRs in the unrelated condition because familiarity should be absent for unstudied words. In line with the typical topography of N400 effects, we expected a posterior maximum for this contrast. A priming plus familiarity contrast was computed by subtracting CRs in the unrelated condition from hits in the related condition as the latter should be associated with both, enhanced familiarity and enhanced conceptual fluency, compared with the former. Thus, if episodic familiarity can be dissociated from conceptual fluency when both processes are simultaneously available in a recognition test, the comparison between the priming plus familiarity contrast and the pure priming contrast should reveal the qualitatively unique features of a familiarity-related old/new effect. Therefore, the topography of the priming plus familiarity contrast was expected to exhibit a significantly more frontal distribution.

These two contrasts were supplemented by the priming contrast for hits and the old/new contrast in the related condition. These two effects were central to the conceptual fluency versus familiarity comparison made by Stróžak et al. (2016). Although we would agree that these contrasts differ in the degree to which they reflect conceptual fluency and familiarity, we assume that hits in the related condition reflect an interaction of priming and familiarity, and thus, this comparison is not suitable to dissociate the two processes. To demonstrate this, we compared the priming effect for hits to the (pure)

priming effect for CRs as we expected that the contribution of familiarity to this contrast shifts the topographic distribution more frontally.

In addition to the early time window, we also investigated the interaction of conceptual fluency and recognition memory in later time intervals. In the 500–800 msec time window, we either expected no effect of priming on the left parietal old/new effect or a greater old/new effect in the related condition as results of previous behavioral studies are mixed (Taylor & Henson, 2012; Rajaram & Geraci, 2000). On the basis of the late positivity for “new” responses in the Wolk et al. study, we also analyzed the time window between 1200 and 1600 msec. However, we had no clear predictions as we expected familiarity attribution to modulate respective ERP components in an earlier time window in our experiment.

METHODS

Participants

Twenty-four students from Saarland University took part in the experiment. Two participants were excluded from the analysis because of recognition performance close to chance (χ^2 tests for independence of Item Status and Response, $ps > .6$). The mean age of the remaining 22 participants (12 women) was 22.05 years (range = 18–28). All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and were native German speakers. All participants had normal or corrected-to-normal vision and no known neurological problems. Participants received course credit or participated voluntarily. All of them provided informed consent before the start of and were debriefed after the experiment. The study was in line with the Declaration of Helsinki and approved by the local ethics committee.

Stimuli and Design

Stimuli comprised 240 semantically related German prime–target pairs. Primes and targets were predominantly concrete nouns with a moderate mean lexical frequency (dlexDB occurrences per million: primes: 47, targets: 58; Heister et al., 2011). Word lengths ranged from 3 to 13 for primes and from 3 to 11 for targets. Association norms from the Edinburgh Associative Thesaurus (Kiss, Armstrong, Milroy, & Piper, 1973) for English translations were available for 220 of the pairs. The mean forward association strength was 0.13. Relatedness in German was approved by two independent German speakers. Word pairs were divided into four lists of 60 pairs each. Within these lists, primes were reallocated to targets creating unrelated prime–target pairs. For each participant, the targets of two lists were presented randomly intermixed as study items. At test, targets were preceded by auditorily presented prime words. Targets of one list were preceded by related primes and targets

of the other lists were preceded by unrelated primes. New items were taken from the remaining two lists. Again, new items from one list were preceded by a related prime, whereas new items from the other list were preceded by an unrelated prime. Old and new items were presented intermixed in pseudorandom order: Not more than five old or new items nor more than five related or unrelated prime–target pairs appeared in a row.

Procedure

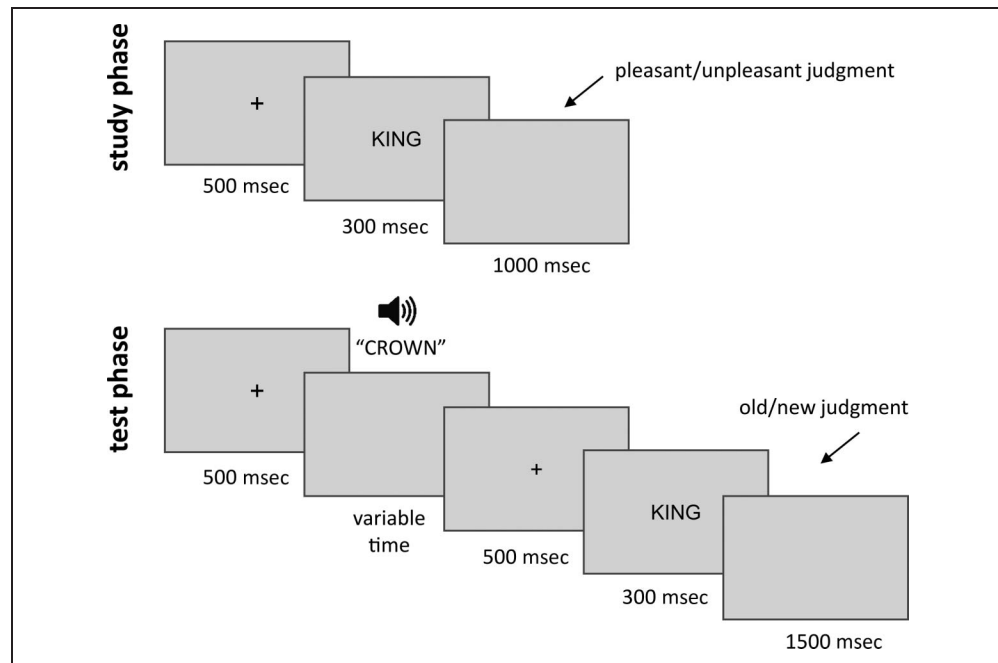
Overall, the experimental session consisted of one study and one test phase interrupted by an approximately 30-min retention interval, which was filled with an unrelated auditory oddball task. Until they were instructed for the test phase, participants were not aware of the final memory test. They were told that the experiment was about the electrophysiological signature of valence judgments. EEG caps were fitted before the start of the study phase. The experiment was presented using E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA) on a 19-in. monitor. Participants were seated approximately 75 cm in front of the screen and were tested one at a time in an electrically shielded and sound attenuated chamber. Trial procedures are depicted in Figure 1. All targets were presented in 28 pt. Arial font in black on gray background. The vertical visual angle was approximately 1.2°, and the horizontal visual angles ranged from approximately 1.5° to 6.1°.

In the study phase, each trial began with a 500-msec fixation cross in the center of the screen. Afterward, the study item was presented for 300 msec followed by a 1000-msec fixed response interval consisting of a blank screen. In each trial, the participants’ task was to rate the pleasantness of the word’s meaning by pressing either “c” or “m” on a standard keyboard. At the beginning of the study phase, participants performed a short practice phase (four trials). Midway through the study phase, participants had the chance to take a self-paced break.

Test phase trials began with a 500-msec fixation cross, which was followed by a blank screen and the auditory presentation of the prime. Directly after the end of prime presentation, a fixation cross was presented for 500 msec. The target word was presented visually for 300 msec. At the end of the trial, participants had another 1500 msec to indicate whether they thought the visually presented word was “old” or “new” by pressing the keys “c” or “m.” For the auditorily presented primes, participants were told to listen carefully. Before the test phase began, participants practiced the task with the four study practice items and four new items. After every 60 trials, they had the opportunity to take a self-paced break.

Assignment of stimulus lists to conditions and assignments of keys to “pleasant” and “unpleasant” judgments as well as “old” and “new” judgments was fully counter-balanced across participants.

Figure 1. Schematic illustration of the trial procedures in the study phase (top) and the test phase (bottom). Example stimuli are English translations of the original German words.



Electrophysiological Recording Parameters and Analysis

EEG was continuously recorded from 59 scalp sites (Fp1, Fpz, Fp2, AF3, AF4, F1, Fz, F2, F7, F5, F3, FT7, FC5, FC3, T7, C5, FC1, FCz, FC2, C3, C1, Cz, C2, C4, F4, F6, F8, FC4, FC6, FT8, C6, T8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, TP7, CP5, CP3, P7, P5, P3, CP1, CPz, CP2, P1, Pz, P2, CP4, CP6, TP8, P4, P6, P8, A2) according to the extended 10–20 system (Jasper, 1958) using BrainVision Recorder 1.0 (Brain Products, München, Germany). Electrode AFz served as ground electrode, and the EEG was amplified referenced to the left mastoid electrode. Data were acquired with a sampling rate of 500 Hz and online filtered with a band-pass of 0.016 to 100 Hz. Impedances were kept below 5 k Ω . EOG activity was recorded with four additional electrodes placed on the outer canthi and above and below the right eye.

Offline, the EEG was filtered using a 0.05–30 Hz Butterworth filter (slope: 12 dB/oct). For EOG and cardiac artifact correction, independent component analysis was employed using the classic biased restricted infomax algorithm implemented in BrainVision Analyzer 2.0 (Brain Products). After re-referencing the EEG to the average of both mastoids, all further processing was conducted using EEProbe (ANT Software). Epochs from –200 to 1600 msec around target onset were constructed, baseline-corrected to the 200 msec before stimulus onset, and visually checked for remaining artifacts. The mean proportion of artifact-free trials was as follows (range; number of rejected trials): 40.5 (27–54; 5.8) for hits in the related condition, 40.6 (35–52; 4.4) for CRs in the related condition, 39.8 (21–54; 4.7) for hits in the unrelated condition, and 42.5 (27–55; 4.6) for CRs in the unrelated condition.

Inferential statistics were performed on mean amplitudes in the following time windows: 300–500 msec, 500–800 msec, and 1200–1600 msec. Repeated-measures ANOVAs included factors of Response Type (hits, CRs) and Priming (related, unrelated) as well as the location factors Anterior–Posterior (AntPost: F = frontal, FC = frontocentral, C = central, CP = centroparietal, P = parietal) and Sagittal Plane (SP: 3 = left midlateral, 1 = left superior, z = midline, 2 = right superior, 4 = right midlateral) to capture all relevant regions for the effects of interest. Follow-up tests were also conducted using ANOVAs. Significance level was set to $\alpha = .05$. When interactions with topographical factors were followed up on all five levels, p values are compared with a Bonferroni-corrected $\alpha = .01$. Whenever the assumption of sphericity was violated as determined by Mauchly's Test, we report uncorrected degrees of freedom, but used p values according to the Greenhouse–Geisser correction. We report all main effects for the factors Response Type and Priming. Interactions involving these factors are reported only when they are significant. η_p^2 is provided as a measure of effect size.

Behavioral Data Analysis

For the analysis of the behavioral data, we excluded those trials where no response was given and trials with outlying RTs (i.e., RTs 1.5 interquartile ranges above the third or below the first quartile for each participant/priming condition/item status/response combination; Tukey, 1977). Mean number of excluded trials ranged from 1.09 to 3.23 per priming condition/item status/response combination. For inferential statistics, hit and false alarm

(FA) rates were subjected to a 2 (Priming: related vs. unrelated) \times 2 (Response Type: hits vs. FAs) repeated-measures ANOVA. RT data were analyzed for hits and CRs by means of a 2 (Priming: related vs. unrelated) \times 2 (Response Type: hits vs. CRs) ANOVA. We report η_p^2 and Cohen's d as indicators of effect sizes for ANOVAs and t tests, respectively. Discrimination ($Pr = p(\text{hit}) - p(\text{FA})$) and bias ($Br = p(\text{FA}) / (1 - (p(\text{hit}) - p(\text{FA})))$) indices were calculated for each Priming condition separately (Snodgrass & Corwin, 1988).

RESULTS

Behavioral Data

Mean response rates for "old" responses (i.e., hits and FAs) and RTs for correct responses are displayed in Table 1. A Priming (related, unrelated) \times Response Type (hits, FAs) repeated-measures ANOVA on hits and FAs revealed significant main effects of Priming ($F(1, 21) = 17.18, p < .001, \eta_p^2 = 0.450$) and Response Type ($F(1, 21) = 282.25, p < .001, \eta_p^2 = 0.93$). The interaction was not significant ($F(1, 21) = 0.70, p = .414, \eta_p^2 = 0.032$), which is in line with comparable Pr scores across Priming conditions (related: 0.50, $SE: 0.028$; unrelated: 0.52, $SE: 0.037$). Whereas the Response Type effect assures overall above chance performance, the Priming effect was due to generally more "old" responses in the related condition than the unrelated condition, for both old and new items, confirming a generally more liberal bias after related primes ($Br = 0.45, SE: 0.037$) than after unrelated primes ($Br = 0.39, SE: 0.032; t(21) = 3.39, p = .003, d = 0.722$). It should, however, be noted that the difference between the related and the unrelated condition was only significant for FAs ($t(21) = 2.70, p = .013, d = 0.576$), but not for hits ($t(21) = 0.95, p = .355, d = 0.202$) when analyzed separately.

An ANOVA with the factors Priming (related, unrelated) and Response Type (hits, CRs) on RTs for correct responses yielded no significant main effect of Priming ($F(1, 21) = 0.28, p = .603, \eta_p^2 = 0.013$), but a significant main effect of Response Type ($F(1, 12) = 11.93, p = .002, \eta_p^2 = 0.362$) and a significant interaction ($F(1, 21) = 15.69, p = .001, \eta_p^2 = 0.428$). The interaction was due to a significant priming effect (faster RTs in the related than unrelated condition) for old items ($t(21) = 2.91, p = .008, d = 0.619$) and a reversed priming effect for

new items, which was non-significant with a Bonferroni-corrected α level of .025 ($t(21) = 2.03, p = .055, d = 0.433$).

ERP Data

ERP waveforms are depicted in Figure 2. To get an overall picture whether recognition memory processes and priming interact in the time windows of interest, we performed Response Type (hits, CRs) \times Priming (related, unrelated) \times AntPost (F = frontal, FC = frontocentral, C = central, CP = centroparietal, P = parietal) \times SP (3 = left mid-lateral, 1 = left superior, z = midline, 2 = right superior, 4 = right mid-lateral) repeated-measures ANOVAs.

300–500 msec Time Window

In the early time window, the overall ANOVA yielded significant main effects of Response Type ($F(1, 21) = 8.92, p = .007, \eta_p^2 = 0.298$) and Priming ($F(1, 21) = 11.99, p = .002, \eta_p^2 = 0.363$) as well as a significant two-way interaction of Response Type \times Priming ($F(1, 21) = 7.68, p = .011, \eta_p^2 = 0.268$). In addition, the Priming effect was qualified by a significant Priming \times SP ($F(4, 84) = 11.18, p < .001, \eta_p^2 = 0.347$) interaction.

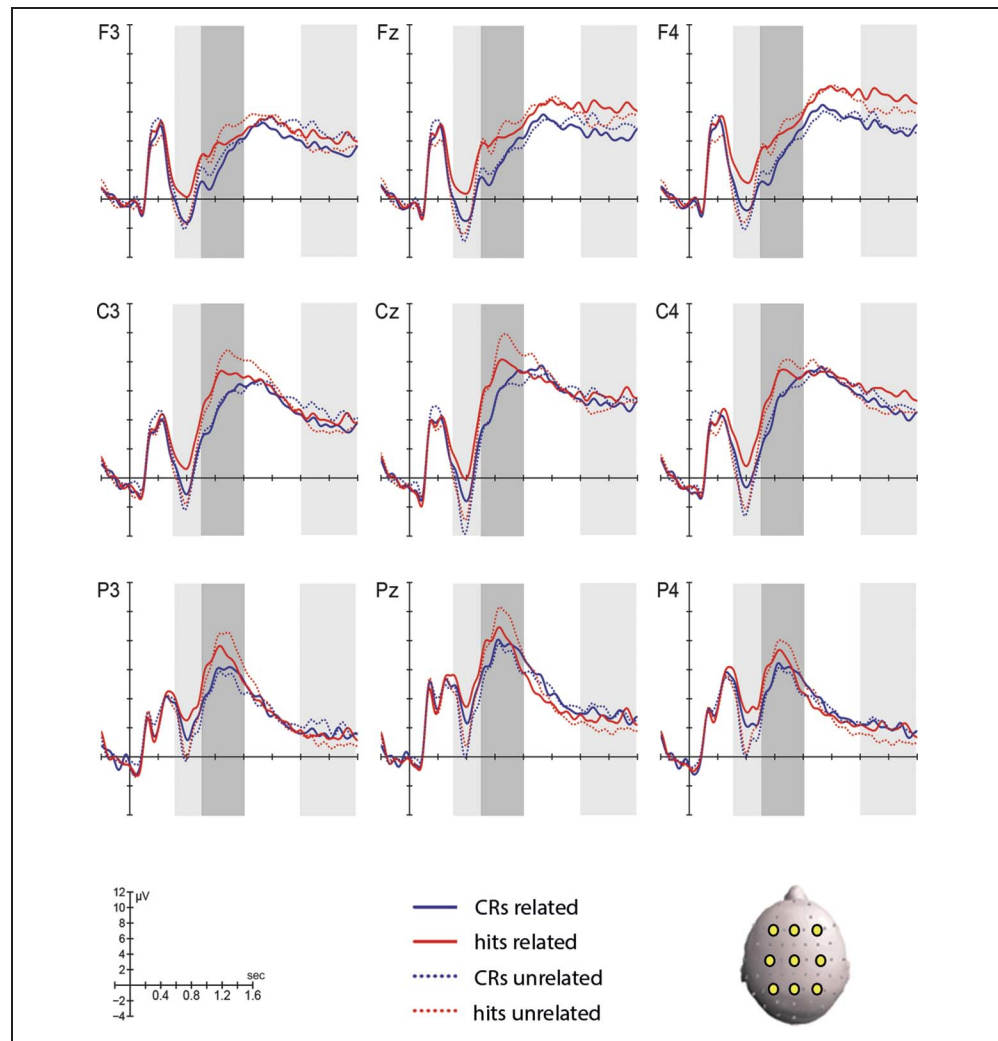
To follow-up on the significant two-way interaction, we performed separate ANOVAs for hits and CRs to analyze the Priming effect as well as separate ANOVAs in the related and unrelated condition to test old/new effects. For hits, a Priming \times AntPost \times SP ANOVA revealed a significant Priming effect ($F(1, 21) = 20.17, p < .001, \eta_p^2 = 0.490$) and a significant Priming \times SP interaction ($F(4, 84) = 5.05, p = .012, \eta_p^2 = 0.194$). Follow-up ANOVAs revealed significant Priming effects at all levels of SP ($ps \leq .002$) with effects being greatest over the right hemisphere (3: $\eta_p^2 = 0.365, 1: \eta_p^2 = 0.436, z: \eta_p^2 = 0.472, 2: \eta_p^2 = 0.544, 4: \eta_p^2 = 0.564$). For CRs, the main effect of Priming was only marginally significant ($F(1, 21) = 3.64, p = .070, \eta_p^2 = 0.148$), but the interactions of Priming \times AntPost ($F(4, 84) = 7.41, p = .005, \eta_p^2 = 0.261$) and Priming \times SP ($F(4, 84) = 9.05, p < .001, \eta_p^2 = 0.301$) were both significant. Follow-up ANOVAs on each level of AntPost as well as on each level of SP revealed a parietal focus of the priming effect (P: $p = .010, \eta_p^2 = 0.279$, all other $ps > .022$). Analyzing old/new effects, there was a significant main effect of Response Type ($F(1, 21) = 15.12, p = .001, \eta_p^2 = 0.419$) in the related condition, but no significant effects were found in the unrelated condition (main effect of Response Type: $F(1, 21) = 1.30, p = .268, \eta_p^2 = 0.058$).

To sum up, the preceding set of analyses support the idea that priming and study history interact with each other: Although priming effects (i.e., more positive going waveforms for words in the related than the unrelated condition) were observable for hits and CRs, effect sizes were larger for hits than for CRs. Moreover, the old/new

Table 1. Mean Rates of "Old" Responses and Mean RTs for Correct Answers (*SEM*)

	Old Responses		RTs (msec)	
	Hits	FAs	Hits	CRs
Related	0.72 (0.025)	0.22 (0.020)	771 (23)	832 (27)
Unrelated	0.71 (0.029)	0.18 (0.019)	793 (21)	816 (25)

Figure 2. ERP waveforms for nine sample electrodes on frontal, central, and parietal locations (see scalp bottom right) in the four experimental conditions. Shaded parts indicate the three main analysis windows. Waveforms were filtered with a 12-Hz low-pass filter for illustrative purposes.



effect was significant only in the related but not in the unrelated condition.

500–800 msec Time Window

In the 500–800 msec time window, the overall ANOVA revealed a significant main effect of Response Type ($F(1, 21) = 10.30, p = .004, \eta_p^2 = 0.329$) and a significant interaction of Priming \times AntPost \times SP ($F(16, 336) = 2.43, p = .037, \eta_p^2 = 0.104$). The main effect of Priming was not significant ($F(1, 21) = 0.45, p = .508, \eta_p^2 = 0.021$). To break down the interaction, we performed separate ANOVAs with the factors Response Type, Priming, and AntPost on each level of SP and with the factors Response Type, Priming, and SP on each level of AntPost. We did not find any significant effects of Priming or two-way interactions with Priming that survived correction for multiple comparisons ($ps > .108$).

In summary, the foregoing analyses showed that old/new effects were present for words in the related and the unrelated condition and that priming effects were not reliable in this time interval.

1200–1600 msec Time Window

To compare the current results to those reported by Wolk et al. (2004), we compared waveforms in the time window from 1200 to 1600 msec. The overall ANOVA yielded neither a significant main effect of Response Type ($F(1, 21) = 0.02, p = .900, \eta_p^2 = 0.001$) nor a significant main effect of Priming ($F(1, 21) = 0.43, p = .518, \eta_p^2 = 0.020$); however, there was a significant interaction between Response Type and Priming ($F(1, 21) = 6.30, p = .020, \eta_p^2 = 0.231$). Moreover, the interactions of Response Type \times AntPost ($F(4, 84) = 10.19, p = .002, \eta_p^2 = 0.327$), Priming \times SP ($F(4, 84) = 3.84, p = .035, \eta_p^2 = 0.155$), and the three-way interaction of Response Type \times AntPost \times SP ($F(16, 336) = 2.84, p = .043, \eta_p^2 = 0.119$) reached significance. Because of the significant Response Type \times Priming interaction, we looked at Priming effects for hits and CRs separately, as well as old/new effects for words in the related and unrelated condition separately. For hits, there was a significant main effect of Priming, which took the form of more positive going waveforms for hits in the related than in the unrelated condition ($F(1, 21) = 5.28, p = .032, \eta_p^2 = 0.201$). In

contrast, for CRs, the main effect of Priming failed to reach significance ($F(1, 21) = 2.79, p = .110, \eta_p^2 = 0.117$), but there was a significant interaction of Priming \times SP ($F(4, 84) = 3.54, p = .043, \eta_p^2 = 0.144$). None of the follow-up comparisons on each level of SP survived correction for multiple comparisons (p values $> .024$). Further analyzing old/new effects, there was no main effect of Response Type ($F(1, 21) = 2.51, p = .128, \eta_p^2 = 0.107$) in the related condition, but a significant interaction of Response Type \times AntPost ($F(4, 84) = 10.28, p = .002, \eta_p^2 = 0.329$). To follow-up on the interaction with AntPost, we ran separate analyses for all levels of AntPost, which revealed that the main effect of Response Type was only significant at frontal and frontocentral electrodes (F: $p = .005, \eta_p^2 = 0.313$; FC: $p = .013$, all other p s $> .14$). In the unrelated condition, there was no main effect of Response Type ($F(1, 21) = 1.26, p = .274, \eta_p^2 = 0.057$).

In summary, the preceding set of analyses shows that priming effects in the very late time interval were only reliable for hits. Moreover, only words in the related condition showed an old/new effect with a right frontal distribution in this late time window.

Topographic Comparisons

To further elucidate topographical differences between effects, we performed a set of ANOVAs on rescaled difference scores for effects of interest using the vector-scaling method (McCarthy & Wood, 1985).

300–500 msec Time Window

To test our prediction regarding the differences in the ERP correlates of episodic familiarity and conceptual fluency, we first compared whether the contrast reflecting priming plus familiarity, that is, hits in the related condition to CRs in the unrelated condition (Figure 3A), exhibited a different topographical distribution than the pure priming effect (new items in the related vs. new items in the unrelated condition, Figure 3B). As predicted, the ANOVA revealed that the Priming plus Familiarity contrast has a significantly more frontal and less right maxi-

imum than the pure Priming contrast (Contrast \times AntPost ($F(4, 84) = 6.86, p = .010, \eta_p^2 = 0.246$); Contrast \times SP ($F(4, 84) = 4.34, p = .027, \eta_p^2 = 0.171$)). For comparison with the findings by Strózak et al. (2016), we compared the topographic distributions of the priming effect for hits (Figure 3C) and the mid-frontal old/new effect in the related condition (Figure 3D). There was only a trend for an interaction of Contrast by AntPost ($F(4, 84) = 3.13, p = .082, \eta_p^2 = 0.130$). An additional analysis by which we examined the influence of old/new status on priming effects showed that hits exhibit a more frontal priming effect than CRs (Figure 3C vs. B), which was evident in a significant Contrast (priming hits, priming CRs) \times AntPost interaction ($F(4, 84) = 4.71, p = .033, \eta_p^2 = 0.183$). Summing up, when differences in familiarity strength between hits and CRs contribute to the scalp distribution, it is tentatively more anteriorly distributed whereas differences in conceptual fluency between related and unrelated words shift the topographic distribution to more posterior and right hemisphere recording sites.

Post hoc Analyses

150–230 msec Time Window

Visual examination of the ERP waveforms suggests that there were unexpected differences between conditions in an early time window preceding the effects of interest in the 300–500 msec interval. We assumed that the unexpected early positivity for CRs compared with hits in the unrelated condition is at least partially the reason why we did not find a significant old/new effect in the 300–500 msec time window in this condition. Therefore, we performed post hoc analyses in this time window at electrode Fz to further explore these effects. An ANOVA with factors Response Type and Priming revealed a trend for a main effect of Response Type ($F(1, 21) = 3.27, p = .085, \eta_p^2 = 0.135$), no main effect of Priming ($F(1, 21) = 0.06, p = .810, \eta_p^2 = 0.003$), and a significant interaction of Response Type \times Priming ($F(1, 21) = 8.188, p = .009, \eta_p^2 = 0.281$). Follow-up t tests revealed that there was no significant difference between hits and CRs in the related condition ($t(21) = .26, p = .796, d = 0.056$),

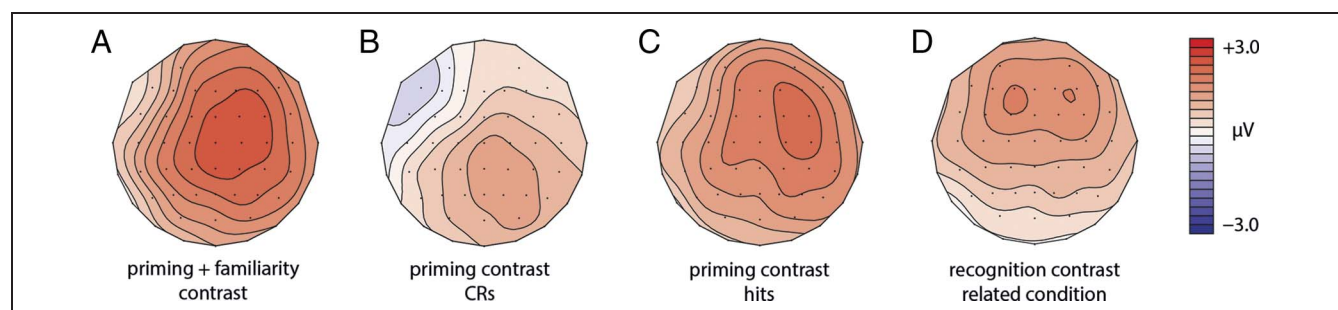


Figure 3. Topographic distributions in the 300–500 msec time window for (A) the priming + familiarity contrast (hits related–CRs unrelated), (B) the priming contrast for correct rejections (CRs related–CRs unrelated), (C) the priming contrast for hits (hits related–hits unrelated), and (D) the recognition contrast in the related condition (hits related–CRs related).

but that CRs were significantly more positive than hits in the unrelated condition ($t(21) = 3.09, p = .006, d = 0.658$). Furthermore, if the early positivity in the 150–230 msec time window for CRs compared with hits in the unrelated condition can indeed account for the absence of the mid-frontal old/new effect in this condition, there should be a negative correlation between the negative polarity old–new difference score in this early time window and the old–new difference score in the 300–500 msec time window in the unrelated condition at electrode Fz. An across-subject Pearson’s correlation of $r(20) = -.674$ ($p = .001$) confirmed this assumption. This relationship was specific to the unrelated condition as the respective correlation in the related condition was not significant ($r(20) = -.207, p = .356$) and significantly smaller than the correlation in the unrelated condition (Fisher’s $Z = 1.874, p = .03$). That is, the larger the negative polarity old–new difference in the 150–230 msec time window, the smaller the mid-frontal old/new effect in the unrelated condition.

DISCUSSION

In line with our predictions, both the behavioral as well as the electrophysiological measures of our study show an interaction of conceptual fluency and familiarity during recognition memory judgments. Consistent with models of recognition memory that assume that conceptual fluency under some circumstances is (mis-)attributed to oldness (Whittlesea & Williams, 2001; Jacoby et al., 1989), related primes led to more “old” responses, irrespective of response type, although when analyzed separately, the difference was only significant for FAs. Whereas the pattern is very consistent for FAs (Stróžak et al., 2016; Wolk et al., 2004; Whittlesea & Williams, 2001; Rajaram & Geraci, 2000), not all studies find that conceptual fluency increases hit rates (Stróžak et al., 2016; Voss & Federmeier, 2010). This is usually accounted for by the notion that, although FAs are primarily driven by familiarity, hits can also be based on recollection, which is less likely influenced by conceptual priming (but see Taylor, Buratto, & Henson, 2013; Taylor & Henson, 2012). According to this view, whether or not one finds an influence of conceptual priming on the number of hits depends on the degree to which participants rely on familiarity to give correct “old” responses. However, even when the analysis is constrained to “know” responses in the aforementioned studies by Stróžak et al. and Voss and Federmeier, there was no influence of priming on “old” responses. Interestingly, Whittlesea and Williams postulate in their discrepancy attribution hypothesis that a person must have had an implicit and uncertain expectation concerning the outcome of an event to attribute perceived fluency for this event to familiarity. In the studies by Stróžak et al. and Voss and Federmeier, a clear prime–target relationship was presumably not experienced by the participants as responses

were required for targets and primes. As a consequence, no expectancies were built up, and fluency was not attributed to familiarity. In the current design, prime–target relationships within a trial were highly salient as primes were presented auditorily whereas targets were presented visually and responses had to be made for targets only. Moreover, half of the trials were related. In line with the importance of expectancies, a fluency-driven increase in “old” responses (for both hits and FAs) was only observed in the second half of the experiment.¹ Moreover, the use of a relatively long study list together with an incidental encoding task very likely increased the contribution of familiarity (see Introduction). RTs for hits provide further behavioral evidence for the influence of conceptual fluency on recognition decisions as related primes speeded up responses in contrast to unrelated primes. No such effect was found for CRs probably because CRs in the related condition are slowed down as fluency and novelty provide contradictory signals (Woollams et al., 2008).

The main goal of the current experiment was to shed light on the interaction of the putative electrophysiological markers of episodic familiarity and conceptual fluency, the mid-frontal old/new effect and the N400, respectively. First of all, in contrast to the study by Wolk et al. (2004), we found significant ERP priming and old/new effects enabling us to investigate the relationship between the processes associated with these effects. As expected, the N400 effect varied with response type, and the priming manipulation also modulated the mid-frontal old/new effect. As can be seen in Figure 2, the priming effect in the 300–500 msec interval was greater for hits than for CRs, which is consistent with the notion that priming and repetition facilitate conceptual processing in an additive manner. Moreover, a mid-frontal old/new effect was revealed in the related condition whereas it was virtually absent in the unrelated condition. This finding supports the view that, when multiple sources of fluency such as repetition and conceptual fluency are available when recognition judgments are made, these memory signals seem to intermix and contribute to feelings of familiarity (Bruett & Leynes, 2015).

Most importantly, as can be seen in the topographical distributions depicted in Figure 3, familiarity and conceptual processing seem to interact in a qualitative manner. Consistent with the assumption that the difference between CRs in the related and unrelated conditions reflects a pure priming contrast (as episodic familiarity should be absent for CRs), it has a typical right parietal maximum (Figure 3B) that resembles the topography of the N400 effect (Kutas & Federmeier, 2011). On the contrary, a contrast that we claim captures both priming and familiarity, namely hits in the related condition minus CRs in the unrelated condition, exhibits a significantly more frontal distribution in this time interval (Figure 3A). The latter distribution resembles those found in many ERP recognition memory studies, in which

familiarity and conceptual fluency presumably act concertedly. Given that differences in the neural representation of the stimuli between conditions can be excluded (Rugg & Coles, 1995), it is most likely that different topographical distributions imply different cognitive functions. Thus, the current study adds to the increasing evidence that the N400 and the mid-frontal old/new effect are functionally distinct (Bridger et al., 2012; Experiment 2 in Stróžak et al., 2016). A further clue for a functional dissociation between both effects is provided by the topographical difference between the priming contrasts for hits and CRs. Although the priming contrast for hits also exhibits a typical right-shifted topographical distribution as the one for CRs, it was more frontally distributed than the latter one (Figure 3C vs. B). Inspection of the waveforms in Figure 2 gives the impression that the topographical difference arises from related hits being more positive than related CRs at frontal sites. As the dissociation above, this is consistent with the notion that differences due to episodic familiarity are mostly visible at anterior recording sites. Moreover, this illustrates that contrasting hits in the related and unrelated condition, as done in the Stróžak et al. study, does not isolate the effect of priming as hits in the related condition presumably reflect an interaction of conceptual fluency and familiarity.

The current findings are in opposition to the findings of Experiment 1 in the study by Stróžak et al. (2016). Employing a very similar paradigm to the current one, they did not find a topographical dissociation between priming and familiarity. We think that in addition to the procedure (valence judgment before recognition judgment, see Introduction), the critical comparison Stróžak et al. made is problematic. They compared the old/new effect for semantically primed words to the priming effect for hits. Using hits for the priming contrast confounds recognition and priming. In contrast, in the comparison we chose, in particular by exploring the priming effect for CRs only, the differences between the two effects can be isolated. Note, however, that when we made the same comparison as in the Stróžak et al. study, the mid-frontal old/new effect in the related condition also tended to be more frontally accentuated than the N400 effect for hits (Figure 3D and C). Thus, prioritizing recognition memory processes over conceptual processing as in the current study might provide better conditions to isolate ERP effects related to familiarity and conceptual fluency.

One unexpected finding was the virtually absent mid-frontal old/new effect in the unrelated condition. A similar finding was obtained by Stróžak et al. (2016), who reasoned that the mid-frontal old/new effect might only be observed when familiarity is enhanced due to conceptual priming—as in the related condition. However, we think that this account is rather unlikely as mid-frontal old/new effects have been found in numerous recognition memory studies where conceptual fluency was not specifically enhanced. It seems more reasonable to assume that the presence of the related primes and a possible built-up of

expectancies also changed processing of the words in the unrelated condition. In the post hoc analyses of the 150–230 msec (P200) time window, we found that new words were significantly more positive than old words in the unrelated condition. Moreover, our correlation analysis revealed that the larger the negative polarity (CRs > hits) old/new effect in the P200 time window, the smaller the succeeding mid-frontal old/new effect. This suggests that differential processing of old and new items in the unrelated condition at a very early stage may have influenced later recognition processes. But what does this early differential processing reflect? Previous ERP studies reporting less positive ERPs for primed compared with unprimed items with long-lag repetition priming (Voss & Paller, 2010), immediate masked repetition priming (Li, Gao, Wang, & Guo, 2015), or when stimuli were presented in a clear versus blurry version across trials (Leynes & Zish, 2012) take this effect to index perceptual fluency. In the current study, hits and CRs should indeed differ in the degree of perceptual fluency. It is, however, unclear why perceptual fluency should only play a role in the unrelated condition. In contrast, studies that observed an enhanced P200 for predicted versus unpredicted words in sentence contexts (Federmeier, Mai, & Kutas, 2005) and one-word contexts (Lau, Holcomb, & Kuperberg, 2013) rather suggest that the P200 in word processing is enhanced when processing is facilitated. This fits well with the current pattern of results as CRs in the unrelated condition, which elicit the largest P200, are the only category that is not associated with any kind of fluency signal (neither from priming nor from oldness) and can therefore be processed in a conflict-free, that is, facilitated, manner. For all other conditions, participants either experience a fluency signal due to priming, to oldness, or both. In these cases, participants have to determine the origin of the fluency signal before they are able to respond correctly. Interestingly, for one-word contexts, the P200 effect in the Lau et al. study was only found in a condition where related targets were highly expected suggesting that the P200 effect is driven by top-down processes (Lau et al., 2013). In earlier studies, in which the P200 effect was not found (Stróžak et al., 2016; Voss & Federmeier, 2010), the prime–target relationship was presumably not as obvious to the participants and no expectancies were built up (see Discussion above). In contrast, in the current study, participants probably experienced the existence of possibly conflicting fluency signals (from oldness and priming) during the course of the test phase. Hence, CRs preceded by unrelated primes might have become a unique trial sequence, in that they signal conflict-free processing (no fluency neither from oldness nor from priming). As a consequence of the early P200 effect in the unrelated CRs, the subsequent mid-frontal old/new effect was attenuated. It is not clear from the data at hand, however, whether this was just a superposition of the two opposing effects or whether familiarity was indeed diminished

in this condition. Future studies have to more systematically investigate the influence of response strategies on memory-based decision-making and its ERP correlates when multiple fluency signals covary as in the current paradigm.

In the 500–800 msec time window, we found no significant differences between old/new effects in the related and the unrelated condition. This adds to the growing evidence that recollection is mostly unaffected by priming manipulations (Stróžak et al., 2016; Voss & Paller, 2010; Rajaram & Geraci, 2000) although an increase in recollection for primed words seems to be possible under some circumstances (Taylor et al., 2013; Taylor & Henson, 2012).

Whereas in the study by Wolk et al. (2004), a positivity for “new” responses for primed words over right frontal electrodes from 1200 to 1600 msec was considered to be crucially involved in inhibiting a fluency-driven “old” judgment for new items, the pattern we observed in this late time window does not support this interpretation. In the current experiment, there was no difference for CRs between the two relatedness conditions at right frontal sites. However, hits in the related condition elicited more positive ERPs than hits in the unrelated condition. Visual inspection of the waveforms at posterior sites suggests that hits in the unrelated condition elicited a greater late posterior negativity (LPN) than the other conditions. Because of its rather broad topographic distribution, this late negativity may have also contributed to the difference between hits in the related and unrelated condition at frontal sites (see Nessler & Mecklinger, 2003, for similar considerations). The LPN has been associated with reconstructive and evaluative processing of retrieval outcomes at a late retrieval stage whenever monitoring demands are high, for example, due to high response conflict (Mecklinger, Rosburg, & Johansson, 2016). In the current experiment, response conflict was high for old words in the unrelated condition as conceptual fluency and familiarity provide contradictory signals, and this may have boosted the processes reflected in the LPN at this late processing stage.

The main finding of this study is that the N400 effect and the mid-frontal old/new effect make independent contributions to condition differences found in the 300–500 msec time window. This poses the question: What exactly constitutes the difference between the N400 and the early mid-frontal old/new effect? As already mentioned in the Introduction and discussed elsewhere (Bridger et al., 2012), previous research suggests that the N400 and the early mid-frontal old/new effect share common neural generators. On the one hand, the perirhinal cortex (PRC) is assumed to hold a key position in familiarity-based recognition memory (e.g., Yonelinas, Aly, Wang, & Koen, 2010; Bowles et al., 2007; Henson et al., 2003). On the other hand, several studies showed that the PRC is important for conceptual processing (Dew & Cabeza, 2013; Meyer et al., 2010; Wang et al., 2010; Taylor, Moss, Stamatakis, & Tyler, 2006). Moreover, a selective

PRC lesion was recently shown to affect both episodic familiarity and semantic knowledge representation (Bowles, Duke, Rosenbaum, McRae, & Köhler, 2016). Besides the common generators, the different distribution of the mid-frontal old/new effect strongly suggests that it is generated by a brain network that includes areas that serve a function specific to explicit recognition. One likely candidate is the lateral PFC, especially the inferior frontal gyrus. Activity in the inferior frontal gyrus was associated with behavioral estimates of familiarity (Angel et al., 2013; Yonelinas, Otten, Shaw, & Rugg, 2005) and was predicted by the mid-frontal old/new effect in an EEG-informed fMRI analysis (Hoppstädter, Baeuchl, Diener, Flor, & Meyer, 2015). Finally, patients with lateral PFC damage showed a selective increase in familiarity-based FAs (Aly, Yonelinas, Kishiyama, & Knight, 2011), suggesting that the lateral PFC might be involved in evaluating weaker familiarity signals or in setting decision criteria. Thus, although the PRC presumably generates a familiarity signal in these patients, they cannot base their episodic recognition judgments on it. This fits well with the notion that the dorsolateral PFC is generally associated with resolution of response competition (Badre & Wagner, 2007; see Angel et al., 2013, for a similar discussion). Thus, conceptual fluency and familiarity signals might be both generated in the PRC. However, to make a familiarity signal diagnostic in an episodic task, it has to be further processed by PFC.

In conclusion, the findings of the current study underline that episodic familiarity is associated with the mid-frontal old/new effect, which has a significantly more anterior topographical distribution than the N400 effect associated with conceptual fluency. This implies that episodic familiarity and conceptual processing have at least partly non-overlapping neural generators. Future research will have to clarify which brain regions and processing steps are shared and not shared by the two processes.

Acknowledgments

We thank Annika Raabe, Lisa Riedel, and Kristin Pfaff for assistance with data collection and analysis.

Reprint requests should be sent to Regine Bader, Experimental Neuropsychology Unit, Department of Psychology, Saarland University, Campus A2.4, 66123 Saarbrücken, Germany, or via e-mail: regine.bader@mx.uni-saarland.de.

Note

1. A three-way ANOVA on hits and FAs with the factors Response Type (hits, FAs), Priming (related, unrelated), and Experimental Halves (first, second) revealed a significant Priming \times Experimental Half interaction ($F(1, 21) = 6.31, p = .020, \eta_p^2 = 0.231$). Follow-up ANOVAs yielded a significant main effect of Priming in the second half ($F(1, 21) = 16.92, p < .001, \eta_p^2 = 0.446$), but not in the first half ($F(1, 21) = 0.376, p = .546, \eta_p^2 = 0.018$). Pairwise t tests revealed that related primes increased hits ($M_{\text{related}} = 0.74; M_{\text{unrelated}} = 0.67; t(21) = 2.40, p = .026, d = 0.511$) and FAs ($M_{\text{related}} = 0.21; M_{\text{unrelated}} = 0.17; t(21) = 2.54, p = .019, d = 0.541$).

REFERENCES

- Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences*, *10*, 455–463.
- Aly, M., Yonelinas, A. P., Kishiyama, M. M., & Knight, R. T. (2011). Damage to the lateral prefrontal cortex impairs familiarity but not recollection. *Behavioural Brain Research*, *225*, 297–304.
- Angel, L., Bastin, C., Genon, S., Balteau, E., Phillips, C., Luxen, A., et al. (2013). Differential effects of aging on the neural correlates of recollection and familiarity. *Cortex*, *49*, 1585–1597.
- Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, *45*, 2883–2901.
- Bowles, B., Crupi, C., Mirsattari, S. M., Pigott, S. E., Parrent, A. G., Pruessner, J. C., et al. (2007). Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proceedings of the National Academy of Sciences, U.S.A.*, *104*, 16382–16387.
- Bowles, B., Duke, D., Rosenbaum, S. R., McRae, K., & Köhler, S. (2016). Impaired assessment of cumulative lifetime familiarity for object concepts after left anterior temporal-lobe resection that includes perirhinal cortex but spares the hippocampus. *Neuropsychologia*, *90*, 170–179.
- Bridger, E. K., Bader, R., Kriukova, O., Unger, K., & Mecklinger, A. (2012). The FN400 is functionally distinct from the N400. *Neuroimage*, *63*, 1334–1342.
- Bruett, H., & Leynes, P. A. (2015). Event-related potentials indicate that fluency can be interpreted as familiarity. *Neuropsychologia*, *78*, 41–50.
- Cary, M., & Reder, L. M. (2003). A dual-process account of the list-length and strength-based mirror effects in recognition. *Journal of Memory and Language*, *49*, 231–248.
- Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory & Cognition*, *28*, 923–938.
- Dew, I. T., & Cabeza, R. (2013). A broader view of perirhinal function: From recognition memory to fluency-based decisions. *Journal of Neuroscience*, *33*, 14466–14474.
- Diana, R. A., Reder, L. M., Arndt, J., & Park, H. (2006). Models of recognition: A review of arguments in favor of a dual-process account. *Psychonomic Bulletin & Review*, *13*, 1–21.
- Federmeier, K. D., Mai, H., & Kutas, M. (2005). Both sides get the point: Hemispheric sensitivities to sentential constraint. *Memory & Cognition*, *33*, 871–886.
- Heister, J., Würzner, K.-M., Bubbenzer, J., Pohl, E., Hanneforth, T., Geyken, A., et al. (2011). dlexDB—Eine lexikalische Datenbank für die psychologische und linguistische Forschung [dlexDB—A lexical database for psychological and linguistic research]. *Psychologische Rundschau*, *62*, 10–20.
- Henson, R. N., Cansino, S., Herron, J. E., Robb, W. G. K., & Rugg, M. D. (2003). A familiarity signal in human anterior medial temporal cortex? *Hippocampus*, *13*, 301–304.
- Hoppstädter, M., Baeuchl, C., Diener, C., Flor, H., & Meyer, P. (2015). Simultaneous EEG–fMRI reveals brain networks underlying recognition memory ERP old/new effects. *Neuroimage*, *116*, 112–122.
- Jacoby, L. L., Kelley, C. M., & Dywan, J. (1989). Memory attributions. In H. L. Roediger III & F. I. M. Craik (Eds.), *Varieties of memory and consciousness: Essays in honour of Endel Tulving* (pp. 391–422). Hillsdale, NJ: Erlbaum.
- Jasper, H. (1958). Report of the Committee on Methods of Clinical Examination in Electroencephalography. *Electroencephalography and Clinical Neurophysiology*, *10*, 370–375.
- Kiss, G. R., Armstrong, C., Milroy, R., & Piper, J. (1973). An associative thesaurus of English and its computer analysis. In A. J. Aitken, R. W. Bailey, & N. Hamilton-Smith (Eds.), *The computer and literary studies*. Edinburgh: University Press.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621–647.
- Lau, E. F., Holcomb, P. J., & Kuperberg, G. R. (2013). Dissociating N400 effects of prediction from association in single-word contexts. *Journal of Cognitive Neuroscience*, *25*, 484–502.
- Leynes, A. P., & Zish, K. (2012). Event-related potential (ERP) evidence for fluency-based recognition memory. *Neuropsychologia*, *50*, 3240–3249.
- Li, B., Gao, C., Wang, W., & Guo, C. (2015). Processing fluency hinders subsequent recollection: An electrophysiological study. *Frontiers in Psychology*, *6*, 863.
- McCarthy, G., & Wood, C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, *62*, 203–208.
- Mecklinger, A., Brunnemann, N., & Kipp, K. (2010). Two processes for recognition memory in children of early school age: An event-related potential study. *Journal of Cognitive Neuroscience*, *23*, 435–446.
- Mecklinger, A., Rosburg, T., & Johansson, M. (2016). Reconstructing the past: The late posterior negativity (LPN) in episodic memory studies. *Neuroscience & Biobehavioral Reviews*, *68*, 621–638.
- Meyer, P., Mecklinger, A., & Friederici, A. D. (2010). On the processing of semantic aspects of experience in the anterior medial temporal lobe: An event-related fMRI study. *Journal of Cognitive Neuroscience*, *22*, 590–601.
- Montaldi, D., & Mayes, A. R. (2010). The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. *Hippocampus*, *20*, 1291–1314.
- Nessler, D., & Mecklinger, A. (2003). ERP correlates of true and false recognition after different retention delays: Stimulus- and response-related processes. *Psychophysiology*, *40*, 146–159.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Paller, K. A., Lucas, H. D., & Voss, J. L. (2012). Assuming too much from “familiar” brain potentials. *Trends in Cognitive Sciences*, *16*, 313–315.
- Rajaram, S., & Geraci, L. (2000). Conceptual fluency selectively influences knowing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*, 1070–1074.
- Rugg, M. D., & Coles, M. G. H. (1995). The ERP and cognitive psychology: Conceptual issues. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event-related brain potentials and cognition* (pp. 27–39). Oxford: Oxford University Press.
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*, 251–257.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology: General*, *117*, 34–50.
- Speer, N. K., & Curran, T. (2007). ERP correlates of familiarity and recollection processes in visual associative recognition. *Brain Research*, *1174*, 97–109.
- Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews Neuroscience*, *8*, 872–883.
- Stróžak, P., Abedzadeh, D., & Curran, T. (2016). Separating the FN400 and N400 potentials across recognition memory experiments. *Brain Research*, *1635*, 41–60.

- Taylor, J. R., Buratto, L. G., & Henson, R. N. (2013). Behavioral and neural evidence for masked conceptual priming of recollection. *Cortex*, *49*, 1511–1525.
- Taylor, J. R., & Henson, R. N. (2012). Could masked conceptual primes increase recollection? The subtleties of measuring recollection and familiarity in recognition memory. *Neuropsychologia*, *50*, 3027–3040.
- Taylor, K. I., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2006). Binding crossmodal object features in perirhinal cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *103*, 8239–8244.
- Tukey, J. W. (1977). *Exploratory data analysis*. Reading, PA: Addison Wesley.
- Voss, J. L., & Federmeier, K. D. (2010). FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology*, *48*, 532–546.
- Voss, J. L., Lucas, H. D., & Paller, K. A. (2010). Conceptual priming and familiarity: Different expressions of memory during recognition testing with distinct neurophysiological correlates. *Journal of Cognitive Neuroscience*, *22*, 2638–2651.
- Voss, J. L., & Paller, K. A. (2009). Remembering and knowing: Electrophysiological distinctions at encoding but not retrieval. *Neuroimage*, *46*, 280–289.
- Voss, J. L., & Paller, K. A. (2010). Real-time neural signals of perceptual priming with unfamiliar geometric shapes. *Journal of Neuroscience*, *30*, 9181–9188.
- Voss, J. L., Schendan, H. E., & Paller, K. A. (2010). Finding meaning in novel geometric shapes influences electrophysiological correlates of repetition and dissociates perceptual and conceptual priming. *Neuroimage*, *49*, 2879–2889.
- Wang, W.-C., Lazzara, M. M., Ranganath, C., Knight, R. T., & Yonelinas, A. P. (2010). The medial temporal lobe supports conceptual implicit memory. *Neuron*, *68*, 835–842.
- Whittlesea, B. W., & Williams, L. D. (2001). The discrepancy-attribution hypothesis: II. Expectation, uncertainty, surprise, and feelings of familiarity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *27*, 14–33.
- Wolk, D. A., Schacter, D. L., Berman, A. R., Holcomb, P. J., Daffner, K. R., & Budson, A. E. (2004). An electrophysiological investigation of the relationship between conceptual fluency and familiarity. *Neuroscience Letters*, *369*, 150–155.
- Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research*, *1100*, 125–135.
- Woollams, A. M., Taylor, J. R., Karayanidis, F., & Henson, R. N. (2008). Event-related potentials associated with masked priming of test cues reveal multiple potential contributions to recognition memory. *Journal of Cognitive Neuroscience*, *20*, 1114–1129.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.
- Yonelinas, A. P., Aly, M., Wang, W.-C., & Koen, J. D. (2010). Recollection and familiarity: Examining controversial assumptions and new directions. *Hippocampus*, *20*, 1178–1194.
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, *25*, 3002–3008.
- Yu, S. S., & Rugg, M. D. (2010). Dissociation of the electrophysiological correlates of familiarity strength and item repetition. *Brain Research*, *1320*, 74–84.