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RESEARCH ARTICLE

Is what goes in what comes out? Encoding and retrieval event-related potentials together determine memory outcome

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Abstract Understanding memory function amounts to identifying how events (cognitive and neural) at study eventually influence events at test. Many of the proposed cognitive correlates of memory-related event-related potentials (ERPs) at study resemble proposed cognitive correlates of other memory-related ERPs, recorded at test. We wondered whether a given known ERP feature at study might in fact reflect an effective-encoding process that is, in turn, tapped by another specific ERP feature, recorded at test. To this end, we asked which pairs of known memory-related ERP features explain common variance across a large sample of participants, while they perform a word-recognition task. Two early ERP features, the Late Positive Component (study) and the FN400 (test), covaried significantly. These features also correlated with memory success (d′ and response time). Two later ERP features, the Slow Wave (study) and the Late Parietal Positivity (test), also covaried when lures were incorporated into the analysis. Interestingly, these later features were uncorrelated with memory outcome. This novel approach, exploiting naturally occurring subject variability (in strategy and ERP amplitudes), informs our understanding of the memory functions of ERP features in several ways. Specifically, they strengthen the argument that the earlier ERP features may drive old/new recognition (but perhaps not the later features). Our findings suggest the Late Positive Component at study, in some degree, may cause the FN400 to increase at test, together producing effective recognition memory. The Slow Wave at study appears to relate the Left Parietal Positivity at test, but these may play roles in more complex memory judgments and may be less critical for simple old/new recognition.

Keywords Subsequent memory effect · Old/new effect · Recognition memory · Event-related potentials

Introduction

Memory experiments include two distinct phases: a study phase, during which materials are learned, and a later test phase, during which the participant is tested on their memory for the target materials. A major goal of memory research is therefore to understand how encoding processes affect processes at a later retrieval phase, in turn, to produce effective memory. In electroencephalographic (EEG) studies, encoding and retrieval phases have been studied separately, and researchers have identified event-related potentials (ERPs) associated with memory outcome during both phases. Subsequent memory effects (Brewer et al. 1998; Paller and Wagner 2002; Wagner et al. 1998) or differences due to memory (Paller et al. 1987) identify brain activity during study that differentiates later-successful (remembered) versus later-unsuccessful (forgotten) items. Similarly, old/new effects identify brain activity during the memory test that differentiates correctly responded target items (hits) from correctly responded lure items (correct rejections; Rugg 1995). Two well-studied encoding ERP features, the Late Positive Component and the Slow

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Wave, both show subsequent memory effects. Similarly, two well-studied retrieval ERP features, the FN400 and the Late Parietal Positivity, both show old/new effects (Warren 1980). A natural question is: Is there a functional relationship between those features? For example, does the Late Positive Component reflect some effective study process that results in better memory retrieval, which, in turn, is indexed by the FN400? Many studies have found that a single experimental manipulation, such as levels of processing (Fabiani et al. 1990) or recollection versus familiarity (Guo et al. 2004), can affect both an encoding and a retrieval ERP feature. However, a single variable might affect the two brain-activity measures in unrelated ways. For example, the Late Positive Component and the FN400 both show greater coupling to memory outcome when participants apply rote memorization strategies than elaborative/intentional strategies (Karis et al. 1984; Rugg and Curran 2007). This could be because both deflections reflect conceptual priming (Kutas and Federmeier 2011), or because one reflects conceptual priming effects (Voss and Federmeier 2011), whereas the other reflects familiarity. Indeed, these are both currently defensible interpretations of these two ERP peaks. One approach would be to continue to try to fractionate memory processes via experimental manipulations until the two peaks are dissociated. This approach has been, and should continue to be, extensively pursued. We suggest enriching this body of knowledge with a complementary approach: asking which pairs of memory-related ERP features might be related, in the sense that they explain some common variance across participants. Prior researchers have proposed similar cognitive functions of subsequent memory effect and old/new effect ERP features, but for every example of a parallel between a proposed function of a study- and test-ERP feature, it is straightforward to find evidence suggesting they differ. One outcome of our approach is that we may find out which memory-relevant ERP features might be promising to study together, which can in turn inform current ERP research fractionating memory function. Next, we briefly review prior evidence suggesting which study- and test-related ERP features might be functionally related.

ERPs at encoding and retrieval

One common approach to identifying ERPs related to successful encoding has been termed the subsequent memory effect. In this approach, originally suggested by Sanquist et al. (1980) and first reported as statistically reliable by Karis et al. (1984), one isolates brain activity related to effective memory encoding by comparing ERPs during study between subsequently remembered items and subsequently forgotten items (see Friedman and Johnson 2000; Paller and Wagner 2002; Wagner et al. 1999, for reviews). The two most frequently reported subsequent memory effect deflections are distinguished mainly by their different latencies. The Late Positive Component, a positive-going peak, occurs around 400–700 ms after stimulus onset and is usually recorded at centro-parietal electrodes (i.e., electrode Pz, Fabiani et al. 1990; Friedman and Johnson 2000; Smith 1993). The Slow Wave is a relatively sustained voltage difference that usually starts around 800 ms after stimulus onset and is also typically recorded at both frontal and centro-parietal electrodes. The voltage difference between subsequently remembered items and subsequently forgotten items is thought to index cognitive processes that lead to successful memory encoding. The frontal Slow Wave is usually found in tasks that demand item–item associative encoding (Kim et al. 2009) or emotional processing (Diedrich et al. 1997; Simon-Thomas et al. 2005). The centro-parietal Slow Wave has also been suggested to relate to the use of more elaborative encoding strategies (Fabiani et al. 1986, 1990; Friedman and Trott 2000; Karis et al. 1984; Rushby et al. 2002; Weyerts et al. 1997). Because we tested memory for neutral items, not associations, nor emotional stimuli, we did not expect to find a frontal Slow Wave.

On the other hand, the most common means of investigating ERPs related to retrieval is by measuring the so-called old/new effect (Warren 1980). In this approach (see Rugg and Yonelinas 2003, for a review), ERPs are computed during the recognition-memory test, separately for target ("old") and lure ("new") items, usually confined to correct responses—hits and correct rejections, respectively—and the difference between these two ERPs is the old/new effect. Two chief features are consistently observed in old/new effects using verbal materials. First, the FN400 appears symmetrically at frontal electrodes (i.e., electrode Fz), as a negative-going potential peaking around 400 ms after probe onset. Second, the Left Parietal Positivity appears at left parietal electrodes (i.e., electrode P3), as a positive-going potential peaking around 500–800 ms after probe onset (Rugg and Curran 2007). For both the FN400 and the Left Parietal Positivity, old items elicit more positive waveforms than new items (hits > correct rejections). The usual inference is that this old/new difference reflects brain activity that contributes to successful memory retrieval.

One experimental manipulation that affects both subsequent memory effect and old/new effect ERPs is levels of processing. In the levels of processing framework, Craik and Lockhart (1972) proposed that target materials could be studied with at different levels of analysis, some of them considered "deeper" than others; the deeper-level strategies were proposed to result in better memory. Memory researchers have manipulated level of processing by instructing participants to study the material differently. With an incidental encoding procedure, Fabiani et al. (1990) found that participants who were instructed to use rote strategies (subvocal rehearsal) elicited a larger Late Positive Component for later-recalled than later-not-recalled items, whereas participants who employed elaborative strategies (combining multiple words into sentences or images) had no difference in the Late Positive Component between later-recalled and later-not-recalled items. On the other hand, the Slow Wave was more sensitive to elaborative strategies. In contrast, items studied with rote strategies produced no significant memory-related difference in the Slow Wave.

It is important to note that when one inspects subsequent memory effect ERPs, it is often not clear where the Late Positive Component ends and the Slow Wave begins (as exemplified in our ERP figures; see Fig. 2). One could thus argue that the subsequent memory effect begins at the onset of the Late Positive Component and the Slow Wave portion of the subsequent memory effect is simply a continuation of the deflection also known as the Late Positive Component, a single deflection, which would imply that the two ERP features could reflect the same cognitive process. We shall revisit this question in the data-analysis section, when we follow up our correlation analyses with partial correlation. Researchers taking this unitary-component perspective have reported that deep encoding strategies induced a larger subsequent memory effect than shallow strategies (Donaldson and Rugg 1998; Guo et al. 2004; Marzi and Viggiano 2010). Guo et al. (2004) had participants perform an incidental encoding task, judging either the meaning of an item (deep encoding) or its typeface (shallow encoding). The deeply encoded items elicited a larger subsequent memory effect than the shallowly encoded items, and this effect was sustained across their 200–800 ms time window. Thus, even if the Late Positive Component and the Slow Wave are distinct deflections, they may respond to some common cognitive processes.

The retrieval ERP waveforms also differ based on the level of processing at (prior) encoding. Participants who were instructed to use a deep strategy elicited a more positive Left Parietal Positivity (later, at test) than the participants who were instructed to use a shallow strategy, whereas the FN400 did not differentiate strategy groups (see Rugg and Curran 2007, for a review). This suggests that the Left Parietal Positivity reflects the results of having deeply encoded an item.

Another approach to differentiating memory ERPs at both study and test has been dual-process theory of recognition memory. In dual-process theory, it is assumed that two distinct processes contribute to recognition memory at time of test: familiarity and recollection (Yonelinas 2002). The Remember/Know paradigm (Tulving 1985) has been widely used to test dual-process theory. Participants were asked to respond “remember” if they could retrieve the item and also its context (recollection) and “know” if they could only retrieve the item (familiar). Friedman and Johnson (2000) noted that the ERP during study trials was different for subsequent remember judgments than subsequent know judgments and subsequent misses, especially after 500 ms after the onset of the stimulus, within the range of the Slow Wave.

Alternatively, Smith (1993) suggested that the posterior Late Positive Component indexes encoding processes that lead to later recollection. Supporting this, Karis et al. (1984) found that when an item was both successfully free-recalled and recognized, the Late Positive Component was even more positive than when an item was later recognized but not recalled. Paller et al. (1988) also noted that the size of the Late Positive Component predicting recognition was smaller than the Late Positive Component predicting recall. Because recollection has been suggested to resemble recall (Yonelinas 2002), this raises the possibility that the Late Positive Component does indeed reflect encoding of some sort of context-laden information that can be accessed in a later recognition test.

With the Remember/Know procedure, Curran (2004) found a significant FN400 old/new contrast at retrieval, but there was no amplitude difference between remember and know responses. In contrast, the Left Parietal Positivity significantly differentiated between remember and know responses. This result was consistent with a possible mapping of the FN400 and Left Parietal Positivity onto familiarity and recollection, respectively.

In addition to the remember responses from the Remember/Know judgement, source memory is often thought of as a test of recollection. Source-memory judgments typically ask participants to make a second judgment about the target item (e.g., the item’s color, font, location). With this procedure, the Left Parietal Positivity waveform was found to be more positive for the correctly identified old responses with source than the correctly identified old responses without source (Guo et al. 2006; Woroch and Gonsalves 2010). These results are consistent with the proposal that the Left Parietal Positivity reflects recollection-based recognition judgments.

An alternative to dual-process theory, single-process theory, contends that recognition decisions are made based on a single memory-strength of the probe item (Yonelinas 2002; Wixted 2007). This is consistent with, for example, evidence that the FN400 tracks participants’ confidence judgments.

Further, Woroch and Gonsalves (2010) asked participants to perform old/new judgments with confidence ratings, followed by source judgments and confidence ratings of their source responses. The FN400 was sensitive to the confidence rating of the old/new judgement, whereas the Left Parietal Positivity was sensitive to the confidence rating of the source judgement. This is in line with the idea that not only the familiarity but recollection also is in fact a graded process that would relate to a participant's level of confidence (Wixted and Stretch 2004). However, this pattern also suggests that the Left Parietal Positivity might not relate to the old/new judgement itself, but rather, additional recollection- or source-retrieval that can follow the primary evidence (i.e., strength of familiarity) that is used to make the old/new judgement. Finally, Wixted (2007) pointed out that even if there are two different types of information that drive strength (such as familiarity and recollection), as long as those strengths are summated, and that summated strength used to make the old/new judgement, recognition behavior will be well characterized by a single-process theory model (one that assumes unequal variances).

A major alternative to the view that the FN400 reflects familiarity-based recognition is that the FN400 has the same source as the N400 (Voss and Federmeier 2011). The N400, mostly observed at central electrodes, is suggested to be sensitive to semantic processing (see Kutas and Federmeier 2011, for a review). First, the N400 habituates with repetition, suggesting an effect of priming (Neville et al. 1986; Paller and Kutas 1992; Rugg 1990; Young and Rugg 1992). Furthermore, with semantically related primes (semantic/conceptual priming), N400 amplitude for target is closer to baseline than with unrelated primes (Kutas and Federmeier 2011). Voss and Federmeier (2011) demonstrated that with semantic priming without recognition, the FN400 was elicited at same latency and electrodes as to the N400, suggesting that the FN400 could be functionally identical to the N400. The Left Parietal Positivity, on the other hand, was not affected by priming, suggesting that the Left Parietal Positivity is mainly related to memory retrieval. However, the conceptual-priming interpretation of FN400 has also been challenged (see target article and commentary in Voss et al. 2012).

Relating ERPs at encoding to ERPs at retrieval

In considering the debate between recognition memory theories, we came to suspect that the old/new judgement itself might be as simple as the single-process theory, whereas any more complicated judgement (remember/know, source judgment, etc.) might be (quite understandably) best understood with some version of dual-process theory. There is reason to suspect that Remember/Know, confidence and source judgments, whether done simultaneously or following old/new judgments, may change the way participants do the old/new discrimination (Yonelinas 2002). We thus selected the simplest and most conventional judgement (old versus new) to assess memory performance, to avoid inadvertently complicating the task. Despite the complexity of the debate about the cognitive correlates of encoding and retrieval ERP features, one can see parallels emerging: first, between the Late Positive Component and the FN400, and second, between the Slow Wave and the Left Parietal Positivity. In general, earlier deflections in ERPs seem to reflect shallower and more stimulus-driven processes (Luck 2005), so for this completely generic reason, we might hypothesize that the earlier subsequent memory effect ERPs should have something in common with the earlier old/new effect deflections, and likewise for the later ones. In addition, the Late Positive Component and FN400 have both been linked to shallow, contextually impoverished memory, and the Left Parietal Positivity and the Slow Wave have both been linked to deep levels of processing, elaborative encoding strategies and contextually rich memory.

Our aim, therefore, was to test this set of hypotheses linking subsequent memory effect and old/new effect ERP deflections using an individual-differences approach. We measured the magnitude of the subsequent memory effect and the old/new effect for each participant (from their difference waves), and then computed correlations between these ERP measures across participants. In addition to the old/new effect analysis, we also conducted a retrieval-success effect analysis (Dolcos et al. 2005), subtracting the retrieval ERP for hits and the retrieval ERP for misses. It is important to note that we correlated the difference waves, not the original ERPs. If we were simply correlating ERP amplitudes between study and test, one would expect, especially for the subsequent memory effect and retrieval-success analyses, that precisely the same responses would be present at study and test—namely, those that corresponded to stimulus processing. By starting with difference measures (hits–misses or hits–correct rejections), we are in fact avoiding such ERPs and confining our analyses to deflections that at least bear some relationship to memory. We are thus not asking whether the ERP deflections at study return at test. Rather, we are assuming that the memory-related ERPs reflect different processes (encoding processes during study and retrieval processes during test), and asking whether an ERP deflection at study reflects an encoding process that results in later improved memory outcome, as indexed by a different ERP deflection at test.

We used a verbal recognition-memory procedure that is consistent with prior procedures used in subsequent memory effect and old/new effect studies, and obtained both a large number of trials per participant (225 studied words and an equal number of unstudied items as lure probes) and a large sample size (64 participants). Because we wanted there to be sufficient individual variability in study and test, we did not instruct participants to study in any specific way. In addition to the commonly adopted old/new effect analysis, we also consider a retrieval-success effect analysis, in the hope of addressing brain activity that is more closely linked to successful (versus unsuccessful) recognition-memory performance. Because the retrieval-success effect analysis compares hits vs misses at test, as does the subsequent memory effect at study, we expected the subsequent to correlate more with the retrieval-success measures than with the old/new effect measures.

Methods

Participants

Seventy-nine (11 self-reported left-handed,[1] 68 self-reported right-handed; 30 female) undergraduate students who in an introductory psychology course at the University of Alberta, aged 18–28 (mean = 20, SD = 2.29) participated for course credit. Data from 15 participants were excluded from analyses: 7 were excluded from analyses due to low rates of misses (<11 trials, <5 %), 6 due to excessive amounts of artifacts in the EEG and 2 who presumably reversed the response-key mapping (accuracy <50 %). All participants were required to have English as their first language and had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board.

Materials

The stimuli were nouns drawn from the Toronto Word Pool (Friendly et al. 1982) composed of 4–8 letters. Kucera-Francis frequency was between 1 and 712 per million. Study items and test probes were presented in the center of the computer screen using Times New Roman 17 point font with the E–Prime presentation software version 2.0 (Psychology Software Tools).

Procedure

The session took place in an electrically shielded, sound-attenuated chamber. The study phase instructed participants to study each word displayed one at a time. Each study set comprised 25 words, presented one word at a time. Each word was presented for 1,500 ms with jittered uniform–random intertrial interval between 300 and 500 ms. The end-of-list distractor task, included to reduce recency effects that can contribute nuisance variability to the memory measure, consisted of 5 equations of the form of $A(+\text{ or }-)B(+\text{ or }-)C =$, where A, B and C were randomly selected digits between 1 and 9, and the addition and subtraction operation were randomly selected in the equation. The participant was asked to type the correct answer. Each equation remained in the center of the screen until the participant made a response. In the recognition judgement phase, which immediately followed the distractor task, 50 words were presented, with half (25 words) from the study phase (targets or "old" items) and half (25 words) were never presented for study (lures or "new" items), drawn at random, without replacement from the word pool. Each probe was a single word that remained on the screen until the participant made an old/new response by pressing key 1 for old (judged to be a target) and 2 for new (judged to be a lure). Nine blocks of study/test were presented for a total of 225 study trials and 450 probe trials (Fig. 1). For each trial, response time (RT) and accuracy were recorded.

EEG recording and analyses

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1,000 and sampled at 250 Hz. Impedances were kept below 50 kΩ and EEG was initially referenced to the vertex electrode (Cz). Data were analyzed by custom MATLAB scripts in conjunction with the open-source EEGLAB toolbox (Delorme and Makeig 2004, http://sccn.ucsd.edu/eeglab). Signal was average re-referenced and digitally bandpass filtered between 0.5 and 30 Hz. Artifacts were corrected via independent component analysis, implemented in EEGLAB. Trials for which voltage deviated 300 μV from baseline were rejected. As a result, a mean of 19 (range 0–53 per subject) trials out of a total of 225 during the study phase were rejected and a mean of 34 (range 1–81 per subject) trials out of a total of 450 during the recognition-test phase were rejected. Trials were referenced to a 100 ms pre-stimulus baseline. Based on the participants' responses during the test phase, trials were separated into subsequently remembered items (subsequent memory effect hits) and subsequently forgotten items (subsequent memory effect misses). Electrodes and time windows were selected to be consistent with previous measurements of our ERP features of interest. The two subsequent memory effect components were analyzed at electrode Pz in the time window of 400–700 ms latency post-stimulus for the Late Positive Component. Due to the longer time window of the Slow Wave (700–1,200 ms) and variability in time windows in which the Slow Wave has been reported in the literature, we separated the Slow Wave into 700–900 ms (Slow Wave-Early) and 900–1,200 ms (Slow Wave-Late) post-stimulus. The two old/new effect components were analyzed in the time window of 300–500 ms post-stimulus for the FN400 at electrode Fz and 500–800 ms post-stimulus for the Left Parietal Positivity at electrode P3. The same time windows and electrodes were

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[1] When we excluded these 11 participants from the analyses, the pattern of results was not affected.

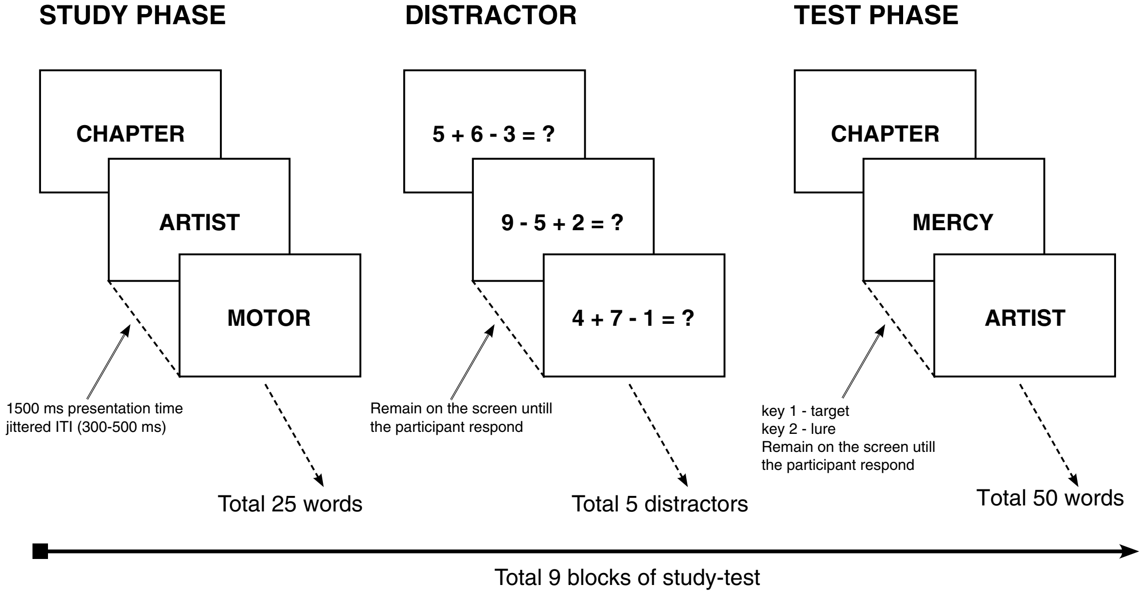

Fig. 1 The procedure of the experiment. Each *box* illustrates the computer screen at a particular stage in the task (text has been enlarged relative to the screen size to improve clarity of the figure). There were 9 blocks of study–distractor–test

Table 1 Accuracy (percentage) and response time (ms) values, reported along with their standard deviations across subjects in parentheses

Condition	Accuracy (%)	Response time (ms)
Hits (old)	79.9 (10.6)	971 (195)
Misses (old)	20.1 (10.6)	1,369 (440)
Correct rejections (new)	87.0 (11.6)	1,095 (269)
False alarms (new)	13.0 (11.6)	1,537 (554)

used for the retrieval-success effect analyses. The selection of analysis electrodes and time window was based on previous ERP studies. Additionally, statistical analyses were carried out using PASW Statistics 18 for Mac, Release version 18.0.0 (SPSS, Inc., 2009, Chicago, IL, www.spss.com) on the mean voltage differences at the corresponding electrodes and time windows.

Results

Behavior

Accuracy and RT are summarized in Table 1. Reassuringly, accuracy was not near ceiling or floor, which would have made our analyses difficult. Standard deviations of both accuracies and RTs are large; thus, there is good reason to expect that there is meaningful variability across participants that could support our planned correlation analyses.

ERPs

We first analyzed ERPs during study and test separately to check whether we could replicate the classic ERP components of interest.

Encoding stage

Three subsequent memory effect components, the Late Positive Component, the Slow Wave-Early and the Slow Wave-Late, were analyzed at electrode Pz (Fig. 2). Paired-samples, two-tailed t tests comparing mean voltage between subsequent hits and subsequent misses were significant at all time intervals of interest at Pz [Late Positive Component: $t(63) = 2.63$, $p < 0.05$; Slow Wave-Early: $t(63) = 2.98$, $p < 0.05$; Slow Wave-Late: $t(63) = 2.24$, $p < 0.05$], where subsequent hits were more positive than subsequent misses. Thus, we replicated these classic subsequent memory effect components (Paller and Wagner 2002).

Retrieval stage

We first analyzed the retrieval ERPs in the usual manner, taking the old/new effect approach. We compared the ERP for correct old trials (hits) with the ERP for correct new trials (CRs). Two components can be seen: the FN400 (Fig. 3a) and the Left Parietal Positivity (Fig. 3b). Paired-samples t tests on mean voltage confirmed both old/new effect components [FN400 at electrode Fz: $t(63) = 4.52$, $p < 0.01$; Left Parietal Positivity at electrode

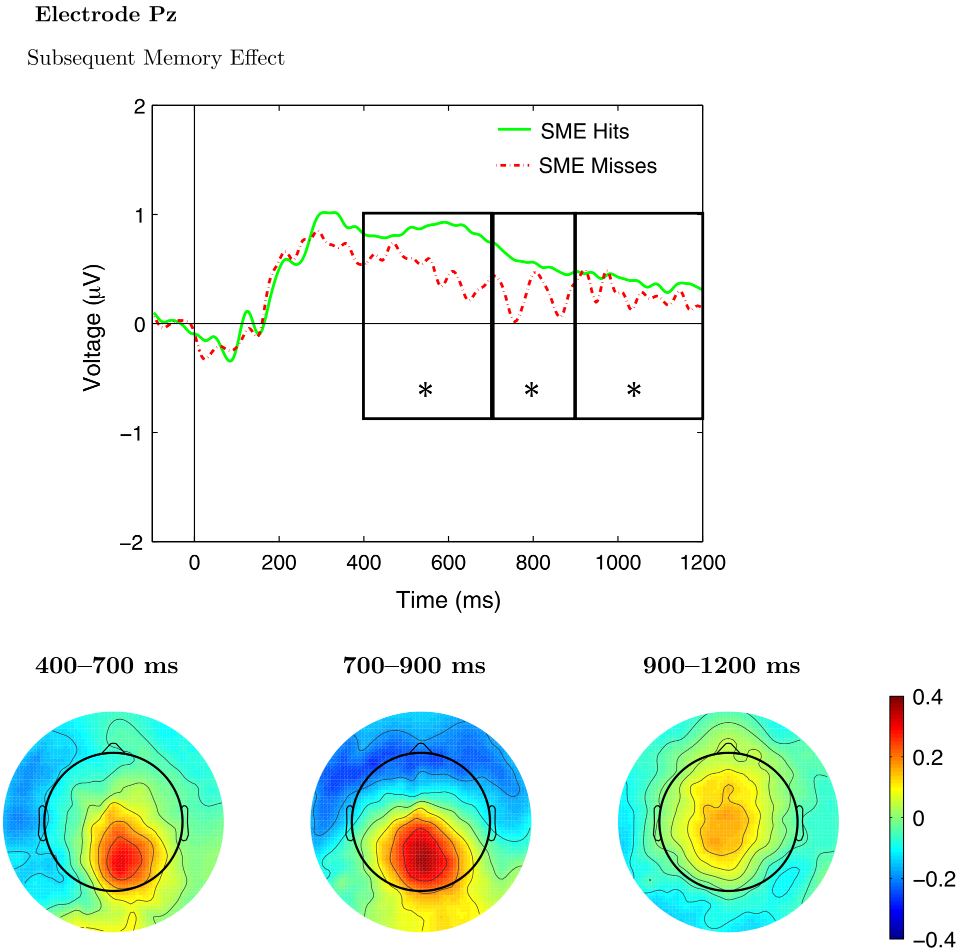

Fig. 2 Grand-average subsequent memory effect ERPs at Pz. Encoding ERPs for subsequently remembered trials (SME hits) is contrasted with subsequently forgotten (SME misses) trials. Topographic maps are *spline plots*, where *color* reflects mean voltage (µV) over the corresponding time window

P3: $t(63) = 5.76$, $p < 0.01$], consistent with prior findings (Rugg and Curran 2007).

In addition to the old/new effect analysis, we conducted a retrieval-success effect analysis, comparing the ERP for hits to the ERP for misses. Figure 3 shows that the FN400 (c) and Left Parietal Positivity (d) were also readily observable in the retrieval-success effect analysis and were significant [FN400 at electrode Fz: $t(63) = 5.08$, $p < 0.01$; Left Parietal Positivity electrode P3 [$t(63) = 3.88$, $p < 0.01$]. To foreshadow the correlation analyses, note that our sensitivity was greater for the FN400 in the retrieval-success effect analysis, but was greater for the Left Parietal Positivity in the old/new effect analysis. One can see a high degree of resemblance between the timecourses and topographies of the retrieval-success effect and old/new effects in Fig. 3; as we suggested in the "Introduction," this may be part of the reason previous researchers have not drawn a large distinction between these two approaches.

In sum, the two encoding-related ERP deflections and the two retrieval-related ERP deflections (in both the old/new effect and retrieval-success effect analyses) were present and statistically robust, setting the stage for the correlation analyses comparing them to one another.

Relationship between encoding and retrieval ERPs

We now turn to our main hypotheses regarding the relationship among these study—and test-phase deflections. For each participant, the subsequent memory effect measure was the average ERP voltage difference between hits and misses during study at Pz, during the respective time windows. Likewise, the old/new effect measures were the voltage difference between hits and CRs during retrieval at the corresponding electrodes and time windows of interest, and the retrieval-success effect measures were the same as the old/new effect measures, but computed as hits–misses during test.

Correlations between ERP components within-phase

In order to understand the relationship between ERP components during encoding and retrieval, we first need to evaluate the relationship between two components from the same memory stage. If the components in the same memory stage are highly correlated, it will be more difficult to make interpretations from the across-phase correlation than if the components are independent. During encoding, the Late Positive Component was positively correlated

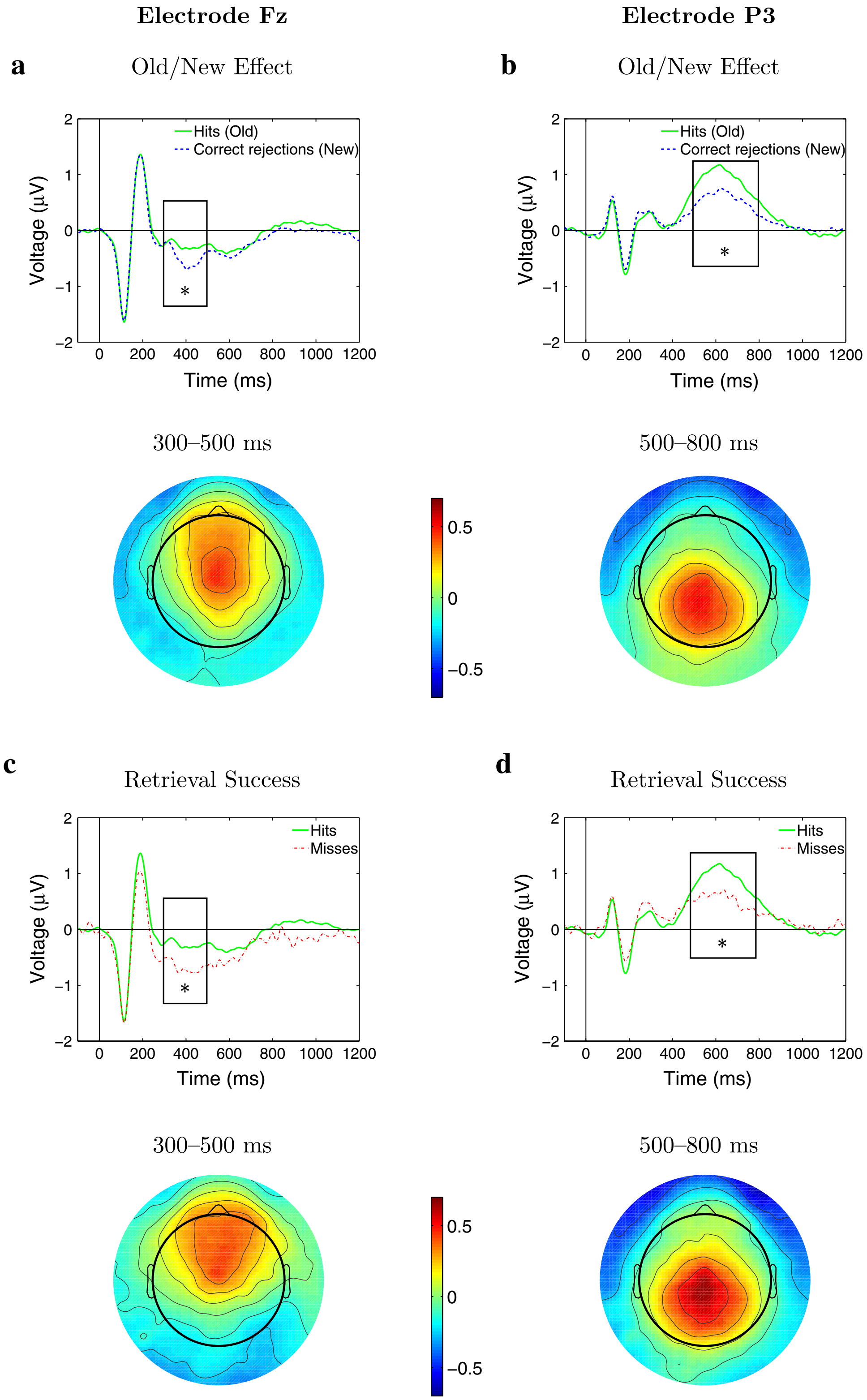

Fig. 3 Grand-average ERPs and topographic distribution across participants during the test phase, applying the old/new effect approach (**a**, **b**) and the retrieval-success approach (**c**, **d**). The old/new effect contrasts ERPs for correctly identified old items (hits) with ERPs for correctly identified new items (correct rejections), at Electrode Fz (**a**), showing the FN400 and at Electrode P3 (**b**), showing the Left Parietal Positivity. Retrieval success contrasts ERPs for correctly identified old items (hits) with ERPs for incorrectly identified old items (misses), again shown at both Electrode Fz (**c**) for the FN400 and at Electrode P3 (**d**) for the Left Parietal Positivity. Topographic maps are spline plots, where color reflects mean voltage (µV) over the corresponding time window

with Slow Wave-Early ($r(62) = 0.74$, $p < 0.05$), as well as with Slow Wave-Late ($r(62) = 0.55$, $p < 0.05$); Slow Wave-Early and Slow Wave-Late were correlated as well ($r(62) = 0.72$, $p < 0.05$). Therefore, if two subsequent memory effect components correlate with a given retrieval ERP component, additional follow-up analyses (partial correlation) will be carried out to clarify the findings. During retrieval, on the other hand, the FN400 old/new effect was

Table 2 Pearson correlation ($df = 62$) between encoding ERPs (subsequent memory effect) and retrieval ERPs (old/new effect) across participants

	LPC	SW-early	SW-late
FN400	0.10	−0.01	−0.27*
Left Parietal Positivity	(0.25*)	0.35*	0.06

() Indicates that this significant correlation become nonsignificant after the partial correlation analysis

* $p < 0.05$

Table 3 Pearson correlation ($df = 62$) between encoding ERPs (subsequent memory effect) and retrieval ERPs (retrieval-success effect) across participants

	LPC	SW-early	SW-late
FN400	0.51*	(0.43*)	0.13
Left Parietal Positivity	0.14	0.15	−0.22†

() indicates that this significant correlation become nonsignificant after the partial correlation analysis

* $p < 0.05$; † $p < 0.1$

not significantly correlated with the Left Parietal Positivity old/new effect ($p > 0.1$) and likewise for the retrieval-success effect analysis ($p > 0.1$).

Correlations between ERP components across-phase

To directly test our hypotheses, we correlated each component measure (from the corresponding difference wave) of the subsequent memory effect with each component measure from the old/new effect across participants and reported in Table 2. Contradicting our prediction, the FN400 was not correlated with Late Positive Component; neither was it correlated with the Slow Wave-Early. The FN400 was significantly, but negatively, correlated with the Slow Wave-Late, consistent with the notion that the FN400 and the Slow Wave-Late reflect distinct, mildly mutually exclusive memory strategies.

Consistent with our prediction, the Left Parietal Positivity was positively correlated with the Slow Wave-Early, but was also unexpectedly correlated with the Late Positive Component. Because the subsequent memory effect components are not independent, follow-up analysis is needed for further clarification. Partial correlation, controlling for the Late Positive Component, indicated a positive correlation between the Slow Wave-Early and the Left Parietal Positivity (old/new effect), $r(61) = 0.26, p < 0.05$; in contrast, partial correlation, controlling for the Slow Wave-Early, found no significant correlation between the Late Positive Component and the Left Parietal Positivity (old/new effect), $r(61) = -0.02, p > 0.1$. This suggests that the positive correlation between the Late Positive Component and the Left Parietal Positivity (old/new effect) was mediated by Slow Wave-Early.

As a complementary, but arguably more direct comparison of encoding and retrieval ERPs, we next correlated the subsequent memory effect measures with the retrieval-success effect measures, which we report in Table 3. The FN400 was significantly positively correlated with the Late Positive Component, matching our prediction, as well as with the Slow Wave-Early, which was unexpected. The Left Parietal Positivity was not correlated with either the Late Positive Component or the Slow Wave-Early, and, surprisingly, trended toward negatively correlating with the Slow Wave-Late. As before, due to the dependence of the subsequent memory measures, follow-up analyses are required. Again, a partial correlation analysis was applied to explain the relationship between the FN400 (retrieval-success effect) and two subsequent memory effect components. Partial correlation, controlling for the Slow Wave-Early, indicated a positive correlation between the Late Positive Component and the FN400 (retrieval-success effect), $r(61) = 0.35, p < 0.05$; in contrast, partial correlation, controlling for the Late Positive Component, found no significant correlation between the Slow Wave-Early and the FN400 (retrieval-success effect), $r(61) = 0.08, p > 0.1$. This suggests that the positive correlation between the Slow Wave-Early and the FN400 (retrieval-success effect) was mediated by the Late Positive Component. Finally, to check our selection of time windows, we computed the correlation values for all pairwise timepoints ("Appendix"). Inspection of the plotted (Figure 6) shows that our pattern of correlations was fairly robust to the precise choice of time windows.

In sum, our predicted correlation pattern was found, but only when using the retrieval-success effect measure of the FN400 and the old/new effect measure of the Left Parietal Positivity (Fig. 4).

Relationship between memory-related ERPs and behavioral measures

Because EEG measures are observational, one can always ask whether a given ERP feature is relevant for memory performance or not. In the case of memory-related ERPs, we examine the differences between remembered and not-remembered trials (subsequent memory effect at encoding and retrieval-success effect at retrieval). The assumption is that these ERP-differences could reflect some processes related to memory function. However, if ERP measures could also be shown to explain variance in memory performance across subjects, that would provide additional convergent evidence that would strengthen the argument for behavioral relevance. To test this possible behavioral relevance, we correlated, across subjects, each difference-wave

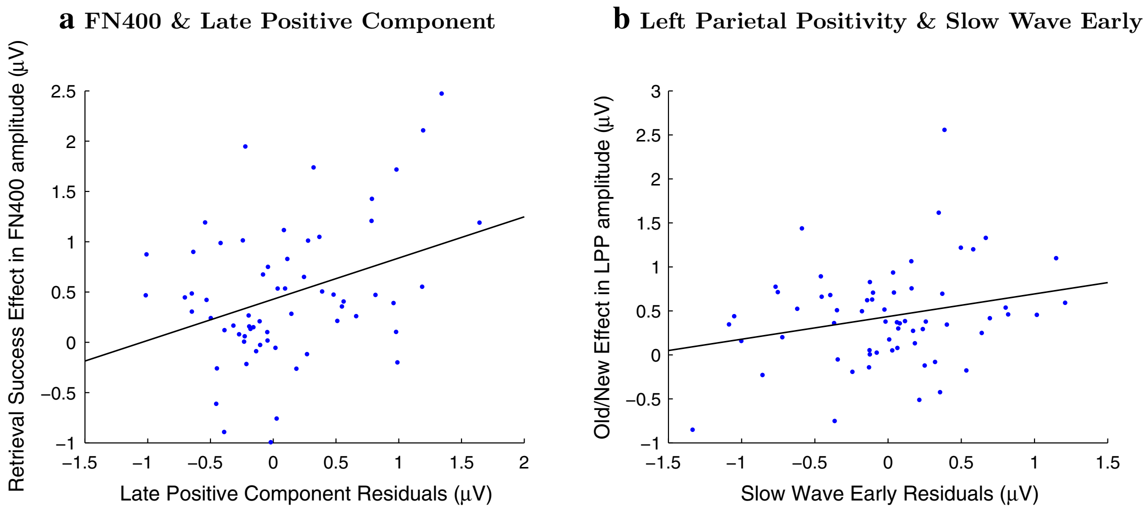

Fig. 4 Across-subjects *scatter plots* illustrating relationships between pairs of ERPs across memory stages; **a** showing FN400 Retrieval-Success Effect (difference wave of hits–misses) at test positively correlating with the residual of the Late Positivity Component (difference wave of hits–misses) after controlling for Slow Wave-Early at study; **b** showing the Left Parietal Positivity Old/New effect (difference wave of hits-correct rejections) at test correlating with Slow Wave-Early (difference wave of hits–misses) controlling for Late Positivity Component at study

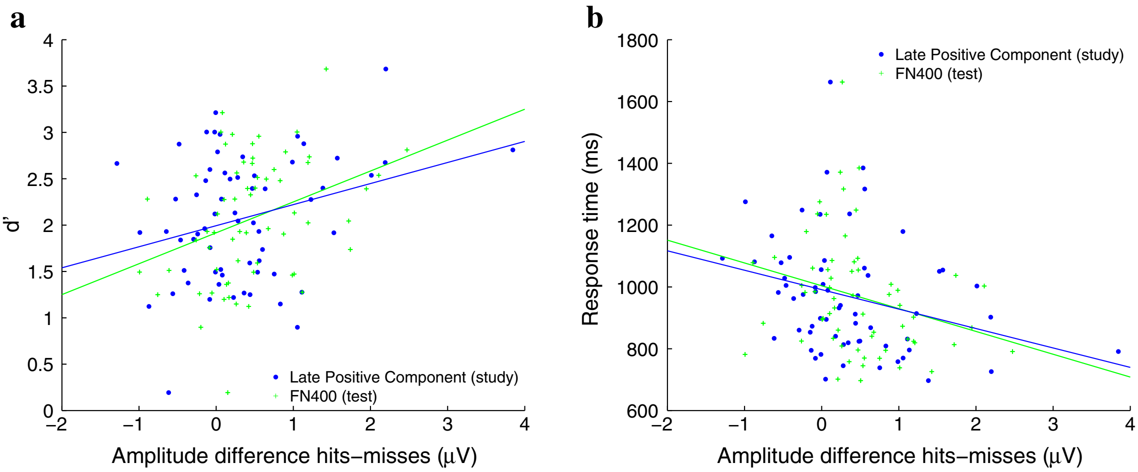

Fig. 5 Across-subjects scatter plots illustrating relationships between ERPs and behavioral measures **a** showing a positive correlation of d′ with the Late Positive Component amplitude difference between hits and misses at study (*blue bullet*), and also with FN400 amplitude difference between hits and misses at test (*green plus*); **b** showing a negative correlation of response time with the Late Positive Component amplitude difference between hits and misses at study (*blue bullet*), and FN400 amplitude difference between hits and misses at test (*green plus*) (color figure online)

measure of the subsequent memory effect, old/new effect and retrieval-success effect each with d′ and response time of hits. Of the encoding ERPs, the Late Positive Component correlated positively with d′ [$r(62) = 0.29$, $p < 0.05$] and negatively with response time [$r(62) = -0.28$, $p < 0.05$]. The correlations between the Slow Wave and both d′ and response time were not significant. Of the retrieval ERPs, we found no significant correlations using the old/new effect measure; however, with the retrieval-success effect measure, FN400 correlated positively with d′ ($r(62) = 0.34$, $p < 0.05$) and negatively with response time ($r(62) = -0.26$, $p < 0.05$) (Fig. 5). The Left Parietal Positivity was not correlated with either behavioral measure.

As reported in the previous section, we found a significant correlation between the Late Positive Component and the FN400 (retrieval-success effect). To further understand the relationship between the ERPs and behavior, we carried out partial correlations. While controlling for d′, the Late Positive Component and the FN400 remained significantly correlated ($r(62) = 0.47$, $p < 0.05$). However, when controlling for either the Late Positive Component or the FN400, the correlations between d′ and the other ERP measure were no longer significant. The same pattern emerged with a partial correlation controlling for response time. The Late Positive Component remained significantly correlated with the FN400 ($r(62) = 0.48$, $p < 0.05$), but the correlation with response time no longer stayed significant when controlling for either ERP measure. This correlation pattern suggests that some of the shared variance between the ERP components drives memory outcome, but the two ERP components also share variance that is untapped by the old/new memory test.

Discussion

Introducing an alternative approach to memory ERP research, we exploited individual variability by correlating memory-related ERPs at study with those at test, across participants. This analysis provides a new way of testing hypotheses about the cognitive significance of memory-related ERP deflections: namely, one can ask whether two ERP deflections reflect common or distinct processes (i.e., explain common or independent portions of the variance) and can ask whether a given ERP deflection explains individual variability in memory performance. This approach provides new insights that can inform previous interpretations of memory-related ERP deflections, as we elaborate below.

Our chief goal was to test whether a commonly reported pair of study-related ERP deflections mapped onto a commonly reported pair of test-related ERP deflections, as might be inferred from the current literature. At first blush, we found support for this pattern; the Late Positive Component and the FN400 were positively correlated (using the retrieval-success effect analysis), and the Slow Wave and the Left Parietal Positivity were positively correlated (using the old/new effect analysis), after partial correlation analyses took into account the statistical dependence of the subsequent memory effect components. This pattern of results echoes prior findings that the Late Positive Component and the FN400 correspond to "shallow" encoding processes, whereas the Slow Wave and the Left Parietal Positivity correspond to "deep" encoding processes (Fabiani et al. 1990; Rugg and Curran 2007).

The Late Positive Component and the FN400 (retrieval-success effect) correlated with d′ and response time, which strengthens the notion that these two early ERP features are relevant to memory performance. However, the Slow Wave and Left Parietal Positivity correlated only when the old/new analysis was used (not retrieval success); this and their nonsignificant correlation with behavioral measures weaken the evidence for these late ERP features contributing directly to old/new recognition-memory.

Although some researchers have functionally distinguished the Late Positive Component from the Slow Wave, measures of these subsequent memory effect components are highly correlated. This is evident in many published subsequent memory effect ERP figures: it is often not clear when the Late Positive Component ends and the Slow Wave begins (Figure 2), leading one to wonder whether at least some of the variance in the Slow Wave should really be viewed as a continuation of the voltage shift due to the Late Positive Component. However, the fact that the retrieval ERPs correlated differentially with the Late Positive Component and the Slow Wave suggests that, although they may overlap, they are at least partly functionally distinct.

When we correlated the Left Parietal Positivity (retrieval-success effect) with the two Slow Wave windows, we only found a trend toward a negative correlation between Left Parietal Positivity and Slow Wave-Late. It is not clear why Left Parietal Positivity and Slow Wave-Late were negatively correlated; however, it may be that although Slow Wave-Late and Left Parietal Positivity were both suggested to reflect "deeper" processing, they could have different neural sources, possibly reflecting slightly mutually exclusive, deep strategies. Finally, the dependence of the Slow Wave-Early correlation with the Left Parietal Positivity on the old/new analysis suggests that the cognitive process tapped by the Slow Wave-Early affects how, at test, lure items will be processed, which we discuss below.

At retrieval, we applied both the old/new effect approach (comparing hits with correct rejections) and the retrieval-success effect approach (comparing hits with misses). Both approaches have been used to investigate ERP signals related to memory retrieval, but they could be quite different. The old/new effect discriminates old from new items (which were, by definition, never presented during study), whereas the retrieval-success effect discriminates remembered from not-remembered items (all having been presented during study). The conventional ERPs and topographies look similar using these two approaches (Figure 3), which may explain why there has not been much debate about the relative merits of each method. However, correlations are sensitive not to mean values, but to variability around the means, and our correlation results suggest that the subtle difference between old/new effect and retrieval-success effect may be cognitively relevant.

The FN400 correlated with the Late Positive Component only when the retrieval-success effect measure was used, suggesting that it is tightly linked to effective judgments of studied items (namely, study processes tapped by the Late Positive Component), but reflects little about how the response to lure items is influenced by what happens at study. We found support in our dataset that the FN400 correlated with memory performance measures, d′ and response time. Moreover, this FN400–memory performance measure correlation was significant only using the retrieval success contrast of FN400. This is in line with the view that the FN400 reflects the strength of the probe item in the single-process model or the familiarity strength in a dual-process model of recognition memory. Our findings are compatible with the view that the FN400 and the N400 are related, in that they both reflect semantic processing, because of evidence that the Late Positive Component reflects some semantic processing (Kutas and Federmeier 2011). Our findings are also compatible with the view that the FN400 indexes the memory strength or confidence (Finnigan et al. 2002; Woroch and Gonsalves 2010).

The coupling of the Late Positive Component to the FN400, however, means that whatever interpretation is ultimately favored for the FN400 may also apply to the Late Positive Component. Our Left Parietal Positivity correlated positively with the Slow Wave-Early (when controlling for the Late Positive Component) when the old/new effect analysis was used, but no significant correlation was found using the retrieval-success effect measure. This suggests that the Left Parietal Positivity does not reflect recognition success as a consequence of encoding processes per se (as measured by our subsequent memory effect components). This finding is reminiscent of numerous sources of evidence that parietal-lobe contributions to memory retrieval are more closely linked to metamemory processes, such as judgments of recollection, than to veridical recognition itself (Ally et al. 2008; Cabeza et al. 2008; Wagner et al. 2005; Woroch and Gonsalves 2010). Our findings thus suggests that the Left Parietal Positivity could be used to discriminate old from new items (targets from lures), based on what happened during study (as indexed by the Slow Wave-Early). This at first seems paradoxical, because new items were not available to the participant during study. However, there are precedents for this kind of result. The latency of the Left Parietal Positivity increased with increasing hit rate but also increased with increasing correct rejection rate across participants (Johnson et al. 1985). We did not find any significant correlation between behavioral measures with the amplitude of the Left Parietal Positivity; however, it is possible that latency carries different information than amplitude.

Finnigan et al. (2002) argued that the Left Parietal Positivity facilitates the discrimination of old and new items. There is in fact a class of models of recognition memory that embody the assumption that strengths of new items could be influenced by study processes; a prominent and well-tested model, Retrieving Effectively from Memory (REM; Shiffrin and Steyvers 2008), is an example. In REM, when an item is studied, episodic traces are formed and test items are later compared to those memory traces to determine the old/new judgment. In addition, in REM, the more target items are studied, the more unstudied items, when presented as lure probes, will have *less* similarity to memory for the list. This prediction of a strength-based mirror effect was then observed in behavioral data (Criss 2006, 2009) and further supported by neuroimaging evidence (Criss et al. 2013). The Slow Wave-Early during encoding might thus contribute to memory in a manner that reduces the memory match for unstudied items. Likewise, the Left Parietal Positivity may reflect a portion of recognition-test activity that is sensitive to the reduced memory match for unstudied items.

As brought up in the introduction, there has been an ongoing debate about whether old/new recognition judgments are based on one continuous-valued source of information or two qualitatively different sources, termed single-process theory and dual-process theory, respectively (see Yonelinas 2002, for a review). ERPs have been rallied in support of both models (Rugg and Curran 2007; Rugg and Yonelinas 2003). In the old/new effect, the FN400 and Left Parietal Positivity have been thought to index familiarity and recollection, respectively. Paller and Kutas (1992) first suggested that the Left Parietal Positivity could index recollection, followed up by Allan et al. (1998) and Wilding et al. (1995) who suggested that the Left Parietal Positivity would also index a recall-like process. Our results cannot select between single-process theory and dual-process theory. That said, we did replicate those Left Parietal Positivity, retrieval ERP feature that has been linked to recollection and source judgment. The standard dual-process theory argument would be that the Left Parietal Positivity reflects recollection, and recollection drives the old/new recognition judgement. However, if the Left Parietal Positivity truly reflected information derived from study that led to better recognition memory, then one would expect the retrieval-success effect-measured Left Parietal Positivity to correlate with one of the later ERP components of the subsequent memory effect (Slow Wave) and also with behavioral memory outcomes. Therefore, we see only two interpretations with respect to the debate between single-process theory and dual-process theory: (1) Dual-process theory is correct, and recollection was present in our task (but failed to explain individual-difference effects in behavior), or (2) single-process theory is correct, and the recollection-related processes simply do not drive the old/new judgement in our task. Rather, the recollection-related ERP features may index cognitive processes that would drive remember/know judgments or source judgments in some future task.

Many memory ERP papers have looked at both ERPs at encoding and ERPs at retrieval (e.g., Chen et al. 2011; Cycowicz and Friedman 1999; Evans and Federmeier 2007; Friedman 1990a, b; Friedman and Trott 2000; Guo et al. 2006; Smith 1993; Weyerts et al. 1997), but they did not directly test for relationships of ERPs across phases. This is very likely due to insufficient power for the correlation analysis. Many ERP studies have relatively smaller sample size (typically 15–30 participants) than our sample ($N = 64$ included participants), which delivered us sufficient power to support the between-subject, across-phase correlations. Our findings show that across-phase correlations can add precision to our understanding of the cognitive processes tapped by study- and test-related ERPs, in the spirit of memory research, by following memory from encoding to retrieval. By directly relating ERPs between encoding and retrieval, we obtained a more nuanced understanding of the electrophysiological mechanisms of memory. We deliberately took a heavily a priori approach to focus our current work on clarifying the four most highly replicated memory ERP components related to recognition memory at study and test. Clearly, there are numerous other ERP components that have been reported during study and test phases of memory tasks, and similar approach could be useful in elucidating the cognitive processes tapped by them as well. The proportion of variance accounted for by our correlation results, while significant, is not large, which suggests (not surprisingly) multiple processes are involved in both encoding and retrieval stages. Even where positive correlations were observed, the correspondence between encoding and retrieval ERPs is certainly not complete.

When we designed the study, we wanted to use the simplest form of the recognition task (old/new judgment) and give participants no specific instructions as to how to study the words. This approach enabled us to exploit spontaneously occurring individual variability to relate study and test ERPs. Future studies could build on our findings and investigate how ERPs at study and test combine to produce memory as measured by remember/know judgments, source memory and so on. In addition, because we wanted to test hypotheses about highly replicated memory-relevant ERP signals, here we looked only at specific electrodes and time windows derived from prior studies. Our approach may be subject to a confirmation bias. Indeed, as we point out already, the correlations explain only a small (albeit significant) proportion of the covariance due to individual variability. This study, thus, lays the groundwork for future exploratory approaches that build on the pairwise correlation analyses here, which have the potential to discover previously overlooked or under-reported ERP signals that are relevant for old/new recognition memory.

Conclusion: implications for interpretating the cognitive meaning of memory-related ERPs

As we expressed in the introduction, our approach is complementary to other published approaches. Far from replacing standard, within-phase ERP analyses, our approach leads to findings that provide new constraints on how we can understand the cognitive significance of ERP features. For example, in the introduction, we described the ongoing debate about whether the FN400 reflects familiarity or conceptual priming (Voss and Federmeier 2011). Our findings cannot resolve that debate, but they do suggest that the cognitive function of the FN400 is linked to that of the Late Positive Component and should be investigated together. If definitive evidence were found that the FN400 reflected conceptual priming, that would suggest that the Late Positive Component also reflects encoding processes that lead to conceptual priming. If the FN400 reflects a combination of conceptual priming and familiarity effects, then the Late Positive Component may also reflect this same combination. Furthermore, the coupling of the FN400 with the Late Positive Component suggests that one might even be able to pinpoint the cognitive function of the FN400 by studying the functions of the Late Positive Component.

As for the late ERP features, our findings suggest that they may be less instrumental in driving old/new recognition than previously thought. Rather, the coupling of the Slow Wave and the Late Parietal Positivity might jointly drive more complex memory judgments, such as remember/know, source judgments or association memory.

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Appendix: Robustness to the selection of time windows

One of the trickiest challenges in ERP research is the selection of time windows of analysis. We wanted to test our hypotheses in a manner that would speak directly to the ERP components that have reported previously, and thus designed our time windows in a way that would minimize our visual-inspection bias by referring to time windows during which the ERP components of interest have been previously reported. However, one can still worry that our results were sensitive to the precise choice of time window, particularly because the time windows used in previous research have varied. To assess the robustness of the correlation results, we plotted the full matrix, timepoint-by-timepoint, of correlation values in Fig. 6. Although there are patches of significance outside the windows of interest, the general impression one gets from these figures is that the pattern of results we obtained are relatively robust to the selection of time windows. This

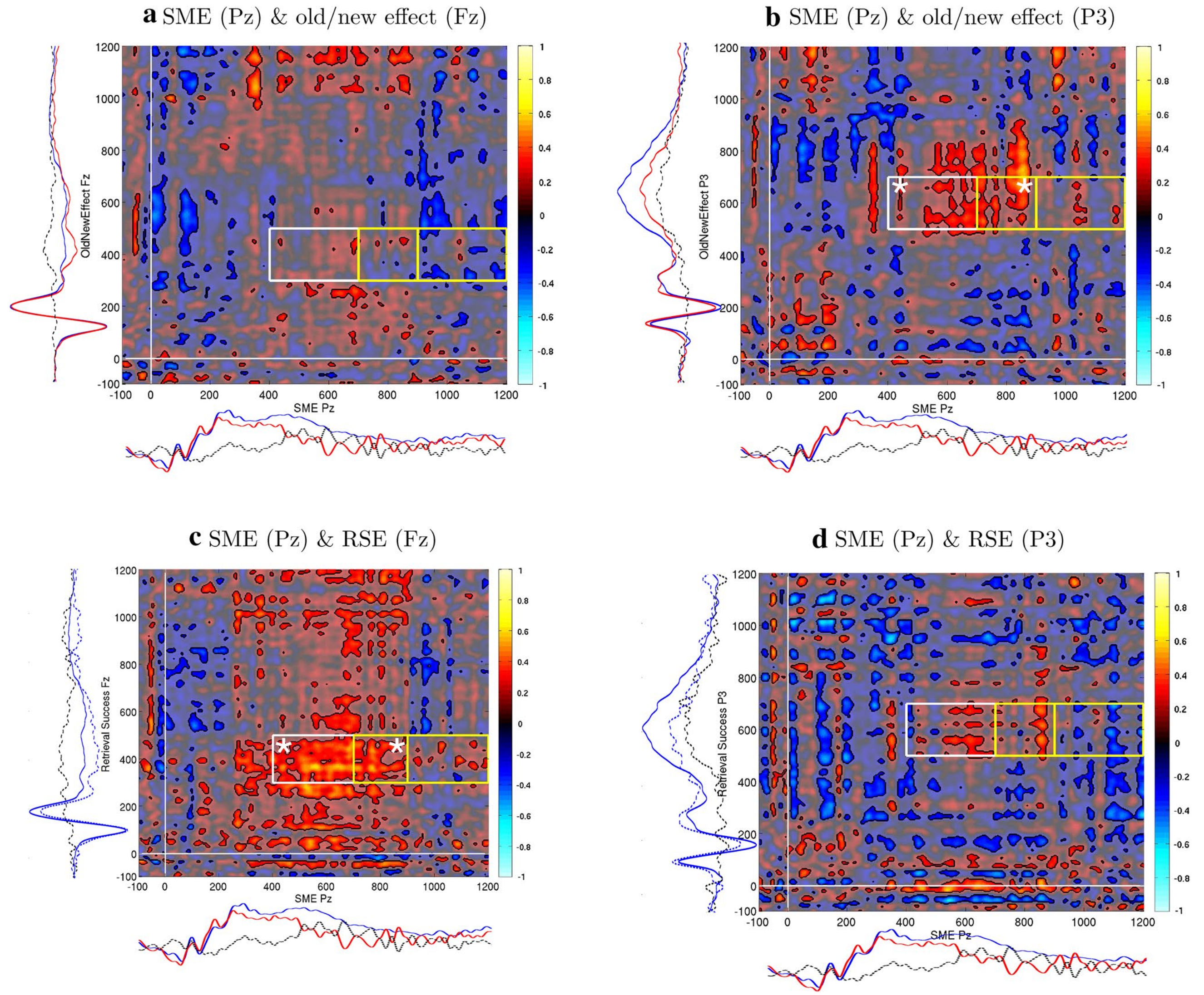

Fig. 6 Correlation between encoding and retrieval ERPs across all participants, for all combinations of encoding and retrieval times. The *horizontal axis* represents the timecourse at electrode Pz during the encoding stage (subsequent memory effect). The *vertical axis* represents the timecourse at electrode Fz (FN400) or P3 (Left Parietal Positivity) during the retrieval stage (old/new effect or retrieval-success effect), with the 100 ms pre-stimulus baseline, and 1,200 ms post-stimulus time. The subsequent memory effect (encoding hits–misses) is correlated with the old/new effect (hits–correct rejections; *panels* **a** and **b**), or retrieval-success effect (hits–misses; *panels* **c** and **d**) at every pair of time samples. The *white line marks* the onset of the stimulus, and the semi-transparent white screen masks out any nonsignificant points ($p > 0.05$, pointwise). The *boxes* on the figure indicate the time windows selected for the main correlation analyses, where the *white box* marks the time window selected for Late Positive Component and *yellow boxes* mark the time window selected for Slow Wave-Early and Slow Wave-Late. *Asterisks* denotes significance ($p < 0.05$) when the corresponding time windows were averaged across. The *insets* are the corresponding ERPs of interest, with the *black, dashed plot* being the ERP difference wave from which were derived the voltage values that went into the correlation calculations

applies both to the old/new effect analysis (panels a and b) and to the retrieval-success effect analysis (panels c and d).

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