Intra- and Inter-Item Associations Doubly Dissociate the Electrophysiological Correlates of Familiarity and Recollection

Theodor Jäger,[1] Axel Mecklinger,[1,*]
and Kerstin H. Kipp[1]
[1] Experimental Neuropsychology Unit
Department of Psychology
Saarland University
D-66123 Saarbruecken
Germany

Summary

Single-process models of recognition memory posit that recognizing is based on a unidimensional value of global memory strength. By contrast, dual-process models propose the existence of two independent processes subserving the explicit recognition of previously encountered episodes, namely "familiarity" and "recollection." Familiarity represents a noncontextual form of recognition that may only support the retrieval of associative information when the to-be-associated information can be unitized, such as when two photographs depicting the same person are memorized (intra-item associations). Conversely, recollection enables retrieving associations between arbitrarily linked information, such as associations between photographs of different persons (inter-item associations). By measuring event-related brain potentials (ERPs), we obtained a double dissociation of familiarity and recollection that strongly favors dual-process accounts of recognition memory: the electrophysiological correlate of familiarity was significantly larger for intra- than for inter-item associations. Conversely, the electrophysiological correlate of recollection was significantly larger for inter- than for intra-item associations.

Introduction

The brain's memory system provides humans the opportunity to "mentally travel back in time" via remembering previously encountered information or episodes (Tulving, 2002). "Recognition memory" refers to our ability to become consciously aware that something we encounter has already been experienced some time in the past. For cognitive neuroscientists, this ability is not a trivial phenomenon, as there is a continuing debate about the underlying neurocognitive processes of recognition experiences. Single-process models (Donaldson, 1996; Gillund and Shiffrin, 1984), which posit that recognition is based on a unidimensional scalar value of global memory strength, stand in contrast to dual-process models that advance the idea of two independent processes subserving recognition memory, namely, "familiarity" and "recollection" (Jacoby, 1991; Mandler, 1980; Yonelinas, 2002). Familiarity is tied to explicit recognition memory; it is suggested to represent a fast-acting memory process whereby a previously encountered item is perceived as "reminding us of something" without prompting retrieval of further contextual information. By contrast, recollection refers to the conscious and effortful retrieval of an item plus further contextual details, such as the spatio-temporal context of the episode or other related information.

A considerable body of literature suggests that the processes of familiarity and recollection can indeed be dissociated (Jacoby, 1991; Yonelinas, 2002). Moreover, functional neuroimaging (Davachi et al., 2003; Henke et al., 1997; Henson et al., 1999, 2005; Ranganath et al., 2003; Yonelinas et al., 2001, 2005) as well as patient studies (Aggleton and Shaw, 1996; Düzel et al., 2001; Quamme et al., 2004; Yonelinas et al., 2002) have provided evidence that the two putative processes underlying recognition memory may be functionally and neuroanatomically dissociable, although the topic remains highly controversial in these fields (Manns et al., 2003; Wais et al., 2006). Recently, Norman and O'Reilly (2003); cf. also (O'Reilly and Norman, 2002) have put forward an integrative neural-network model of recognition memory that was formulated on the basis of dual-process models (Aggleton and Brown, 1999; Eichenbaum, 1997). According to their framework, the hippocampus establishes associations between nonoverlapping medial temporal lobe cortex (MTLC) representations in memory and manages to subsequently retrieve the complete studied pattern in response to a partial cue. Thus, the hippocampus is believed to be intimately involved in the encoding and recollection of (arbitrary) "inter-item associations" (Achim and Lepage, 2005; Donaldson and Rugg, 1998, 1999). However, the recollection mechanism is suggested to break down when the overlap among the to-be-associated information is too high, since the hippocampus cannot establish pattern-separated representations in this case (Schacter et al., 1998). By contrast, it is assumed that MTLC (i.e., perirhinal, entorhinal, and parahippocampal cortices) supports familiarity judgments based on the relative sharpness of item representations. MTLC is thought to assign overlapping representations to similar stimuli, which enables MTLC to extract the shared structure of items and statistical regularities of the environment. Through a sharpening process, a smaller number of neurons are proposed to become specifically tuned to represent a particular stimulus over time whereas other neurons are inhibited, which decreases total MTLC activity in response to a familiar item relative to a novel item and enables familiarity-based recognition judgments (Brown and Bashir, 2002; Grill-Spector et al., 2006; Henson et al., 2003; Li et al., 1993).

On the basis of this view on the neurocomputational mechanisms underlying familiarity and recollection (Norman and O'Reilly, 2003), it may be argued that the retrieval of inter-item associations (i.e., associations between nonoverlapping representations) is strongly dependent upon hippocampal recollection, whereas the retrieval of "intra-item associations" (i.e., associations between highly overlapping representations) may not be achieved by the hippocampus since the overlap

*Correspondence: mecklinger@mx.uni-saarland.de

among the to-be-associated information is too high in this case (Schacter et al., 1998). By contrast, intra-item associations may be retrieved by the MTLC itself; some recent studies suggest that familiarity can support associative memory under certain circumstances, that is, when the to-be-associated information can be "unitized" or represented as a unified whole (Eichenbaum and Bunsey, 1995; Mayes et al., 2004; Opitz and Cornell, 2006; Quamme, 2004; Yonelinas et al., 1999). Importantly, this unitization process might occur in circumstances where representations of to-be-encoded items are highly overlapping.

In the present study, we directly tested these hypotheses by contrasting an "inter-item condition" with an "intra-item condition" in an associative recognition memory task. In the inter-item condition, participants studied pairs of faces representing two different persons. Thus, the necessity to establish and retrieve such arbitrary inter-item associations between faces may strongly engage hippocampal recollection. By contrast, in the intra-item condition, pairs of two physically different but still very similar faces that were perceived as depicting the same person were encoded. Hence, in this condition, MTLC is expected to assign highly overlapping representations to each photograph of a given pair. Therefore, the sharpening process that emerges across repeated exposures and produces the MTLC familiarity signal is hypothesized to occur more strongly when two subsequent photographs representing the same person are studied (intra-item condition) relative to when photographs of two different persons are encoded (inter-item condition). Furthermore, given that the encoding of two photographs showing the same person leads to successful unitization processes, the retrieval of such intra-item associations may be largely supported by familiarity without relying on recollection. Regarding the role of hippocampal recollection across the two conditions, it may be expected that where arbitrarily paired information has to be encoded and retrieved (i.e., in the inter-item condition), recollection should be intimately involved. By contrast, recollection should break down when the overlap of to-be-associated information is too high (i.e., in the intra-item condition).

On the basis of the preceding arguments, we expected a double dissociation of recollection and familiarity during the test phase of our associative recognition memory paradigm: recollection should be greater in the inter- relative to the intra-item condition, whereas familiarity should be greater in the intra- relative to the inter-item condition. Moreover, we hypothesized that in the intra-item condition familiarity supports the retrieval of associations between faces, whereas in the inter-item condition recollection should subserve associative retrieval. In consequence, we expected smaller contributions of familiarity and recollection in the respective conditions for unsuccessful versus successful retrieval of associative information. To test these hypotheses, we measured event-related brain potentials (ERPs) during an associative recognition task, since ERPs have been suggested to provide spatio-temporally dissociable indices of familiarity and recollection (Curran, 2000; Curran et al., 2006; Friedman and Johnson, 2000; Mecklinger, 2000; Rugg and Yonelinas, 2003; Woodruff et al., 2006): an early "frontal old/new effect" between 300 and 500 ms

is thought to reflect familiarity and a somewhat later "parietal old/new" effect between 400 and 700 ms is believed to be linked to recollection. However, note that the mapping of familiarity and recollection on these spatio-temporally distinct ERP components is not without counterarguments (Finnigan et al., 2002; Voss and Paller, 2006; Yovel and Paller, 2004). Moreover, as scalp-recorded ERPs do not have the spatial resolution to accurately identify their neuronal generators, it remains an open question whether the early frontal and the late parietal old/new effects are solely generated by MTLC and hippocampus, particularly in the light of findings suggesting important roles of frontal and parietal cortices for episodic memory retrieval (Aggleton and Brown, 1999; Wagner et al., 2005). Nevertheless, given the increasing evidence from neuroimaging and neuropsychological studies linking familiarity to MTLC and recollection to the hippocampus, it is reasonable to assume that the early frontal and the late parietal old/new effect at least partly depend on MTLC and hippocampal contributions, respectively.

In the present associative recognition memory task, pairs of sequentially presented photographs depicting faces were studied (Figure 1). In the inter-item condition, the photograph-pairs showed two completely different persons. By contrast, in the intra-item condition the two photographs were highly similar and thus perceived as representing the same person. The photographs for this latter condition were drawn from morph-continua between pairs of faces. To ensure that participants formed associations between individual face stimuli, a two-step recognition memory procedure was employed in the subsequent test phase: first, a single test face had to be initially judged as "old" if it had been studied, or as "new" when it was a completely novel face. Second, after correct old responses, a forced-choice decision for two face stimuli that were both studied was required. Here, participants had to choose the photograph that was paired at the time of study with the previously presented single test face and to reject the photograph that was paired with another face at the time of study. ERPs were calculated for the single test faces and separated according to the success of subsequent associative (i.e., forced-choice) recognition judgments.

Additionally, we also investigated Dm effects, that is, differences in ERP activity at encoding that are correlated with the success of subsequent memory retrieval. Successful memory encoding is typically associated with widespread positive-going ERP deflections relative to unsuccessful encoding (Friedman and Johnson, 2000; Otten and Rugg, 2002; Paller and Wagner, 2002; Wagner et al., 1999). Capitalizing on these properties of the Dm effect, we contrasted the study phase ERPs for subsequent hits followed by successful versus unsuccessful associative judgments. This enabled us to examine whether there are dissociable neural correlates of inter- versus intra-item associations at the encoding stage.

Results

Behavioral Data
During the study phase, participants accurately judged the gender of both the first and the second face of
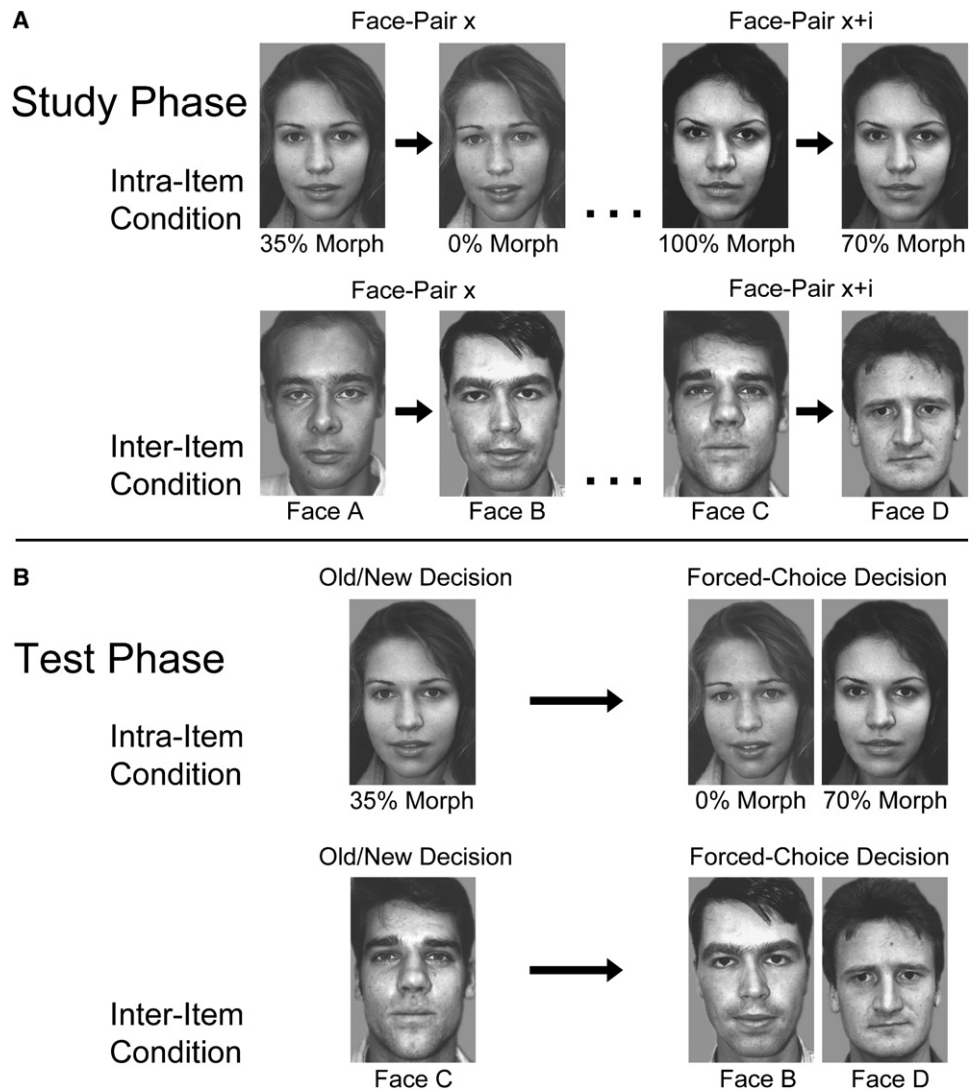
Figure 1. Illustration of the Study and the Test Phase of the Associative Recognition Memory Task

(A) In the study phase, pairs of morphed face stimuli were memorized. In the intra-item condition, 35% morphed and 0% morphed faces were memorized as pairs (presented in this order), and 100% morphed and 70% morphed faces from the same morph-continuum were memorized as pairs (presented in this order). In the inter-item condition, face-pairs depicting arbitrarily paired persons were memorized.

(B) In the test phase, a single test face initially had to be judged as "old" or "new." After correct old responses, a forced-choice judgment had to be made about which of two face stimuli—which were both studied—was paired with the single test face during the study phase. In the intra-item condition, an old single test face was always a 35% morphed face, which was followed by the 0% and 70% morphed faces that created the stimuli for the forced-choice judgment. In the inter-item condition, the procedure was identical, except that the face stimuli depicted arbitrarily paired persons.

each face-pair (97.2% and 99.2% correct judgments, respectively). Gender judgments generally occurred faster in the intra- than in the inter-item condition [$F(1,15)$ = 11.34, p = 0.0042 (Table 1)]. As expected, gender judgments were reliably faster for the second than for the first faces within the study face-pairs [$F(1,15)$ = 12.19, p = 0.0033]. This response speed enhancement was more pronounced in the intra-item condition [$F(1,15)$ = 24.15, p = 0.0002] for the interaction.

During the test phase, old/new discrimination as measured by Pr (a corrected recognition score calculated by subtracting the false alarm rate from the hit rate) was significantly better in the intra- than in the inter-item condition [$F(1,15)$ = 13.29, p = 0.0024]; however, response bias (Br, an index of the probability that an individual

responds that the item is old when he/she is uncertain about the old/new status of a particular item; see Snodgrass and Corwin, 1988) did not differ across conditions [$F(1,15)$ = 1.04, p = 0.3230]. While no condition effects were found for reaction times of hits [$F(1,15)$ = 0.82, p = 0.3794], correct rejections occurred significantly faster in the intra- relative to the inter-item condition [$F(1,15)$ = 19.62, p = 0.0005]. Forced-choice judgments were reliably above chance for both the intra-item condition [$t(15)$ = 10.75, p < 0.0001 (two-tailed)] and the inter-item condition [$t(15)$ = 3.49, p = 0.0033 (two-tailed)], with more accurate [$F(1,15)$ = 22.15, p = 0.0003] and faster [$F(1,15)$ = 29.46, p < 0.0001] responses in the intra-relative to the inter-item condition. In sum, old/new discrimination and associative recognition was reliably

Table 1. Means, and SE, for Behavioral Performance and Reaction Times

	Inter-item condition	Intra-item condition
RT for gender judgment first study face	597 (23)	588 (17)
RT for gender judgment second study face	578 (32)	513 (25)
Old/new discrimination Pr	0.66 (0.04)	0.77 (0.02)
Response bias Br	0.38 (0.05)	0.44 (0.06)
RT for Hits	807 (36)	795 (33)
RT for correct rejections	852 (27)	816 (27)
Proportion of correct forced-choice judgments	0.58 (0.02)	0.71 (0.02)
RT for correct forced-choice judgments	1045 (24)	896 (21)

RT, reaction time. Means and SE of reaction times are reported in ms.
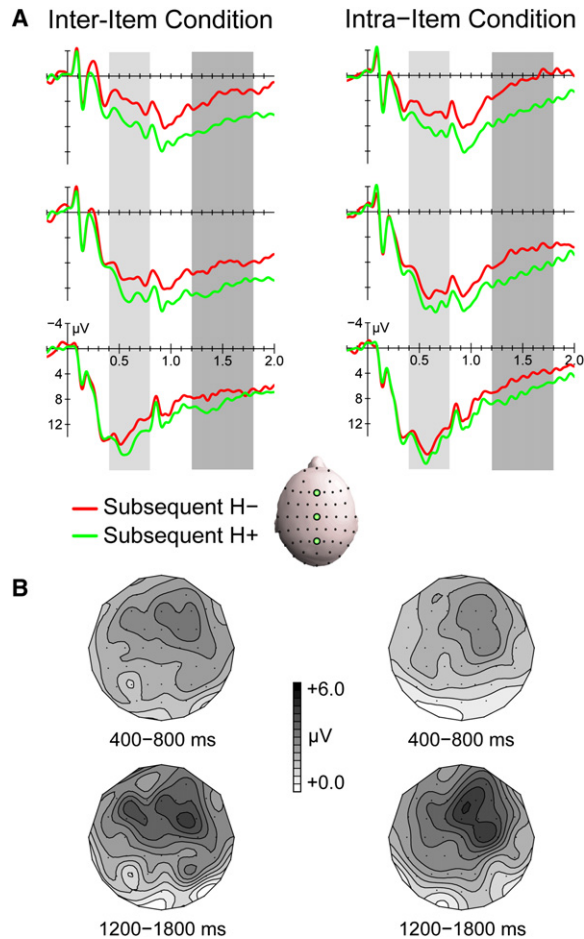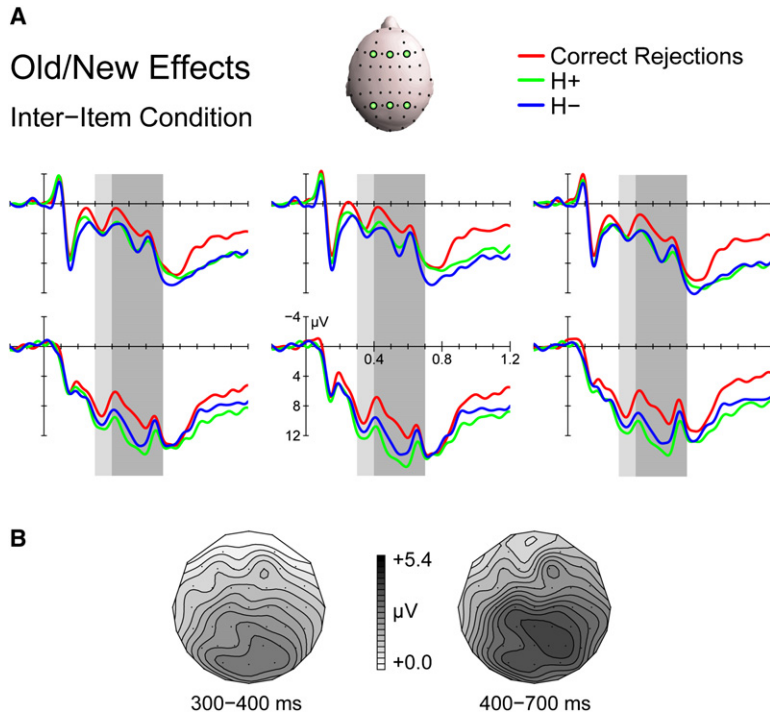

Figure 2. Study Phase ERPs

(A) ERPs depicting Dm effects for the second faces within study face-pairs. The ERPs (shown at electrodes Fz, Cz, and Pz) were formed for subsequent hits followed by correct forced-choice judgments (H+) and for subsequent hits followed by incorrect forced-choice judgments (H−). The two time windows used for statistical analyses are shaded.

(B) Topographical maps depicting Dm effects across conditions in the two time windows.

better in the intra-item condition. The following ERP analyses were performed to reveal whether familiarity and recollection differentially contributed to the two recognition memory conditions.

ERP Data

Study Phase ERPs

No reliable Dm effects were obtained for the first faces within the study face-pairs (see Supplemental Results for global and subsequent analyses of variance [ANOVAs]), suggesting that the processes leading to successful associative recognition were not initiated upon presentation of the first, but rather the second, faces within study face-pairs. In fact, large and reliable Dm effects were observed for the second faces in both conditions. In other words: ERPs to hits that were followed by correct forced-choice judgments (referred to as H+ in the following) were more positive-going than ERPs to hits followed by incorrect forced-choice judgments (referred to as H−). This effect started at approximately 400 ms after stimulus onset and lasted until the end of the recording epoch (Figure 2). Importantly, these Dm effects showed a similar fronto-central topography and magnitude in both conditions across the two time windows used for statistical evaluation. Results from the global and subsequent ANOVAs and from topographical analyses confirmed that Dm effects in both time windows were not dissociable for inter- versus intra-item associations.

Test Phase ERPs

ERPs and topographical maps illustrating the old/new effects elicited by the single test faces are depicted in Figure 3 and Figure 4. Most importantly, an early (300–400 ms) frontal old/new effect associated with H+ was obtained in the intra-item condition, but not in the inter-item condition. Conversely, a late (400–700 ms) parietal old/new effect associated with H+ was present in the inter-item condition, but not in the intra-item condition. Results from the global and subsequent ANOVAs confirmed the aforementioned results (see Supplemental Data).

Based on our a priori assumptions that an early frontal old/new effect indexing familiarity should be stronger in the intra-item condition than in the inter-item condition, and that a later parietal old/new effect indexing recollec-

tion should be stronger in the inter-item condition than in the intra-item condition, the early frontal and the late parietal old/new differences (i.e., amplitude differences between H+ and correct rejections at the respective locations) were submitted to a Condition × Time Window ANOVA, which revealed a significant crossover Condition × Time Window interaction [$F(1,15) = 72.21$, p < 0.0001 (Figure 5)]. This interaction reflected the fact that the early frontal (F3, Fz, F4) old/new effect was substantially greater in the intra- than in the inter-item condition [$t(15) = 5.13$, p < 0.0001 (one-tailed)], whereas the late parietal (P3, Pz, P4) old/new effect was substantially greater in the inter- than in the intra-item condition [$t(15) = −7.24$, p < 0.0001 (one-tailed)]. Moreover, as can be seen in the Supplemental Results, the early frontal old/new effect in the intra-item condition was significantly greater for H+ than for H−, indicating that the early frontal old/new effect was partly contingent upon successful associative recognition. The late parietal old/new effect in the inter-item condition was

A

Old/New Effects
Inter−Item Condition

B

300−400 ms   400−700 ms

Figure 3. Test Phase ERPs for the Inter-Item Condition

(A) ERPs depicting old/new effects for the inter-item condition. The ERPs (shown at frontal [F3, Fz, F4] and parietal [P3, Pz, P4] electrodes) were formed for correct rejections, hits followed by correct forced-choice judgments (H+), and hits followed by incorrect forced-choice judgments (H−). The two time windows used for statistical analyses of the electrophysiological correlates of familiarity (300–400 ms) and recollection (400–700 ms) are shaded.

(B) Topographical maps depicting old/new effects, which were formed by subtracting ERPs of correct rejections from ERPs of H+, reveal a strong late (400–700 ms) parietal old/new effect for the inter-item condition.

significantly greater for H+ than for H−, while the old/new effect was also reliable for H−. Topographic analyses confirmed that the early, frontally focused old/new effect in the intra-item condition was topographically dissociable from the late, parietally distributed old/new effect in the inter-item condition (Figures 3 and 4).

In sum, this pattern reflects a double dissociation of the early frontal and the late parietal old/new effect. As behavioral performance differed across conditions, it is important to note that such double (rather than single) dissociations cannot simply be byproducts of differential task difficulty or task performance across conditions. Nevertheless, in a post-hoc analysis we aimed at further strengthening the obtained double dissociation by matching behavioral performance across conditions. For this purpose, we selected participants whose intra-item forced-choice accuracy was below the median (n = 8) and contrasted their ERPs with participants whose inter-item forced-choice accuracy was equal or above the median (n = 9). Importantly, forced-choice accuracy

A

Old/New Effects
Intra−Item Condition
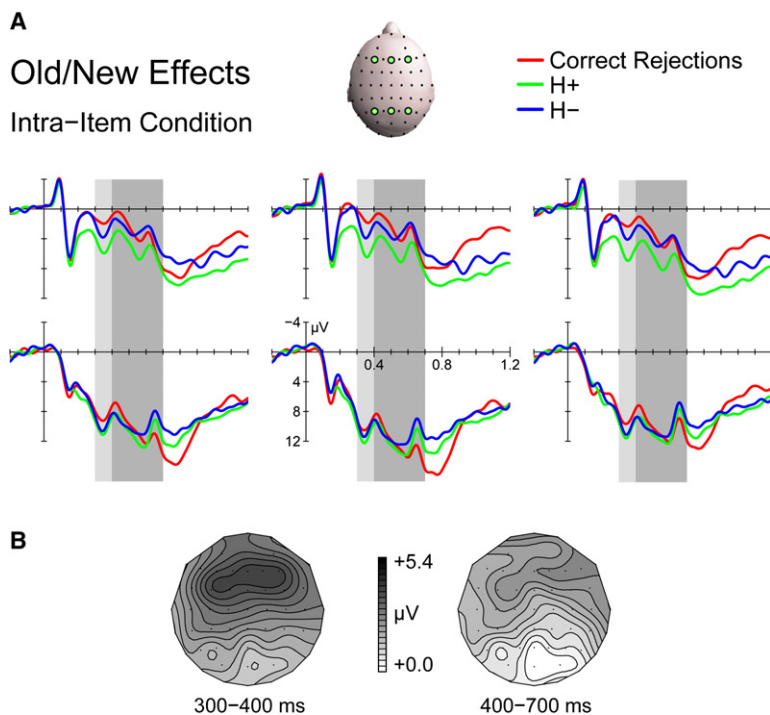
B

300−400 ms   400−700 ms

Figure 4. Test Phase ERPs for the Intra-Item Condition

(A) ERPs depicting old/new effects for the intra-item condition. The ERPs (shown at frontal [F3, Fz, F4] and parietal [P3, Pz, P4] electrodes) were formed for correct rejections, hits followed by correct forced-choice judgments (H+), and hits followed by incorrect forced-choice judgments (H−). The two time windows used for statistical analyses of the electrophysiological correlates of familiarity (300–400 ms) and recollection (400–700 ms) are shaded.

(B) Topographical maps depicting old/new effects, which were formed by subtracting ERPs of correct rejections from ERPs of H+, reveal a strong early (300–400 ms) frontal old/new effect for the intra-item condition.
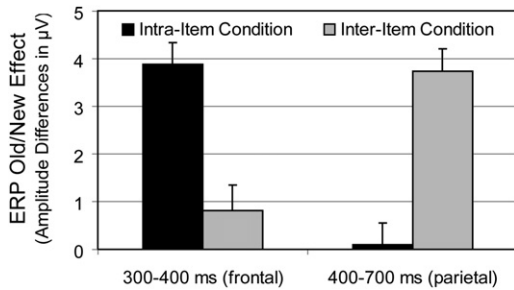
Figure 5. ERP Old/New Effects Across Conditions

Old/new effects (plus standard error [SE]), which represent amplitude differences between correct rejections and hits followed by correct forced-choice judgments (H+), are shown separately for the inter-item condition and the intra-item condition at frontal electrodes (F4, Fz, F3) in an early (300–400 ms) time window and at parietal electrodes (P4, Pz, P3) in a late (400–700 ms) time window.

was now matched across conditions [intra-item condition: $M = 0.65$; inter-item condition: $M = 0.63$; $t(15) = 0.76$, p = 0.4620]. Despite reduced statistical power, independent-samples t tests confirmed that the group formed for the intra-item condition exhibited a significantly greater early frontal old/new effect associated with H+ than the group formed for the inter-item condition [$t(15) = 2.56$, p = 0.0110 (one-tailed)]. Conversely, the group formed for the inter-item condition exhibited a significantly greater late parietal old/new effect associated with H+ than the group formed for the intra-item condition [$t(15) = 2.92$, p = 0.0053 (one-tailed)]. The same analysis was repeated by matching Pr values instead of forced-choice accuracy, resulting in two groups (n = 7 and n = 9) with similar Pr values [intra-item condition: $M = 0.69$; inter-item condition: $M = 0.74$; $t(14) = 1.15$, p = 0.2680]. Again, the group formed for the intra-item condition exhibited a significantly greater early frontal old/new effect associated with H+ than the group formed for the inter-item condition [$t(14) = 3.64$, p = 0.0014 (one-tailed)], whereas the group formed for the inter-item condition exhibited a significantly greater late parietal old/new effect associated with H+ than the group formed for the intra-item condition [$t(14) = 3.79$, p = 0.0010 (one-tailed)].

As apparent from Figure 4, at around 800 ms there was a positive and parietally focused ERP deflection for correct rejections in the intra-item condition. Since correct rejections occurred significantly faster in the intra-item condition, this late positive ERP deflection may be related to the confidence with which novel faces were rejected. However, its late onset (at around 700 ms) suggests that it was well beyond the time interval used for statistical analysis of the late parietal old/new effect. Because of this, the late positive deflection did not confound the aforementioned analysis of retrieval-related ERP effects.

In addition to the aforementioned old/new effects, the ERPs of both conditions indicated that there were very early and frontally pronounced old/new differences between 200 and 300 ms that appeared to differ between conditions (Figures 3 and 4). A post-hoc analysis on these early old/new differences (see Supplemental Results) revealed reliable old/new differences in both conditions in the 200–300 ms time window. However, these effects differed across conditions, in that at frontal locations there was a significant old/new difference for H+, but not for H−, in the intra-item condition, whereas both H+ and H− were associated with old/new differences in the inter-item condition.

Discussion

In the present study, we compared two types of associative encoding: a condition in which face-pairs depicting two different, arbitrarily paired persons were memorized (inter-item condition) and a condition in which participants encoded pairs of physically different photographs that were perceived as representing the same person (intra-item condition). Besides these differences in face similarity within face-pairs, task requirements were kept constant across conditions. On the basis of Norman and O'Reilly's (2003) neurocomputational model of recognition memory, we hypothesized that the two conditions differ in the relative contributions of familiarity and recollection during the retrieval phase of the associative recognition memory task, which tested memory for the particular face pairings. Specifically, a double dissociation of familiarity and recollection was expected, such that familiarity should be greater in the intra- than in the inter-item condition, whereas recollection should be greater in the inter- than in the intra-item condition.

Our pattern of findings was largely consistent with this hypothesis: first, the putative electrophysiological correlate of familiarity, namely the early frontal old/new effect, was significantly greater in the intra- than in the inter-item condition (Figure 5). Given that the MTLC is part of a neural network that contributes to the early frontal old/new effect, this effect may result from more pronounced sharpening processes within MTLC accompanying the sequential processing of two highly similar faces (intra-item condition) relative to two dissimilar faces (inter-item condition). In other words, seeing a particular person repeatedly in physically different photographs may result in a sharper representation of that person because some MTLC neurons are specifically tuned to represent the statistical regularities of the item across repeated exposures. The sharpening process proposed to result from competitive self-organization (arising from Hebbian learning and inhibitory competition) was arguably enhanced in the intra- relative to the inter-item condition, resulting in unitized representations and greater familiarity signals in the intra-item condition (Norman and O'Reilly, 2003). This stronger familiarity signal might have been responsible for better old/new discrimination in the intra-item condition.

Second, the finding that the putative electrophysiological correlate of recollection, namely the late parietal old/new effect, was relatively strong in the inter-item condition, but virtually absent in the intra-item condition (with a significant difference between conditions; Figure 5), is consistent with the hypothesis that the retrieval of arbitrarily associated, nonoverlapping information requires some form of hippocampal recollection (Achim and Lepage, 2005; Norman and O'Reilly, 2003). The hippocampus is proposed to establish pattern-separated representations of to-be-associated information in region CA3 that are linked to each other and to a copy of

the MTLC input pattern via region CA1 (Norman and O'Reilly, 2003). By contrast, hippocampal recollection is suggested to break down when the overlap of the to-be-associated information is too high, as might have been the case in the intra-item condition where indeed no significant parietal old/new effect was observed.

This question then arises: which process might have supported associative recognition in the intra-item condition, if not hippocampal recollection? Several authors have proposed that not only recollection, but also familiarity, may support associative recognition memory in cases where the to-be-associated information can be encoded as a unitized whole (Eichenbaum and Bunsey, 1995; Mayes et al., 2004; Opitz and Cornell, 2006; Quamme, 2004; Yonelinas et al., 1999). In the present study, we assumed that the encoding of two different photographs representing the same person results in such unitization processes: the MTLC representations of the two photographs are merged or unitized into a global (highly overlapping) representation of that person. Thus, due to successful unitization processes, MTLC may have been able to retrieve the associations between (parts of) highly similar faces directly and without the detour through the hippocampal recollection mechanism. This is also consistent with the proposal that MTLC (i.e., perirhinal cortex) allows distinguishing representations of complex and highly similar objects that are represented in inferotemporal area TE (Buckley and Gaffan, 2006). While we can only speculate on the particular binding mechanisms involved in both tasks, one possibility is that in the inter-item condition, associations between two faces as a whole had to be formed, whereas the intra-item condition promoted associations between the single features of the individual faces. Importantly, our finding that the early frontal old/new effect was significantly greater for correct relative to incorrect associative judgments in the intra-item condition provides direct evidence for the view that familiarity supports the retrieval of associative information in circumstances where unitization can occur. On the basis of these findings, we suggest to extend the Norman and O'Reilly (2003) model, offering the possibility that MTLC can subserve associative retrieval under circumstances in which the to-be-associated materials contain highly overlapping features that allow unitization into a coherent whole (Mayes et al., 2004).

By contrast, in replication of previous ERP studies on associative recognition (Donaldson and Rugg, 1998, 1999) and consistent with behavioral studies revealing a predominant role of recollection in associative recognition memory tasks (Yonelinas, 2002), a significant late parietal, but no early frontal, old/new effect was found in the inter-item condition in which associative recognition relied on the successful establishment of associations between unrelated faces. This finding is compatible with the view that recollection is intimately involved in the retrieval of arbitrarily associated information, whereas familiarity is not supportive of the associative recognition of unrelated items (Quamme, 2004). Again, the result that the late parietal old/new effect was significantly greater for correct relative to incorrect associative judgments in the inter-item condition is direct evidence that in addition to item (face) memory, the successful retrieval of associations between faces exerts an

influence on the recollection process (note that compared to the intra-item condition, fewer participants performed reliably above chance in inter-item forced-choice judgments; hence, it is not surprising that the difference between H+ and H−, though statistically reliable, was relatively small in the inter-item condition). The fact that associative recognition was worse in the inter- than in the intra-item condition may result from the hippocampal recollection mechanism being more effortful and more prone to errors than the MTLC familiarity mechanism. Another possible explanation for better associative recognition performance in the intra-item condition may be that successful unitizations of faces in the intra-item condition resulted in facilitated rejection of nontarget faces in the forced-choice task, since they were not part of the unitized representations activated by the single test faces.

On the basis of our findings, we suggest that recognition of items that are part of unitized or "generalized" representations (such as the faces in the intra-item condition) is mainly based on familiarity, whereas recognition of items that were not generalized or unitized with other items (such as the faces in the inter-item condition) is mainly based on recollection. This could be the case because unitization processes occurring across repeated exposures might result in generalized item representations that are not strongly linked to a specific episodic context and thus represent some kind of semantic memory that facilitates familiarity-based recognition without the recollection of specific episodes. By contrast, items that are only encountered in unique episodes are likely to be stored in memory traces that consist of connections between items and specific episodic information, which enables conscious retrieval of the items and the episodes in which they were experienced. This view is supported by our finding that an early frontal, but no significant late parietal, old/new effect supported recognition in the intra-item condition, whereas a significant late parietal, but no early frontal, old/new effect accompanied recognition in the inter-item condition. In other words, the task characteristics of the inter-item condition seem to have boosted recollection-related retrieval processes while familiarity-based recognition only played a negligible role.

Our data also revealed old/new differences that arose earlier than the ERP correlate of familiarity (cf. Tsivilis et al., 2001). Specifically, between 200 and 300 ms, both conditions were associated with frontally pronounced, more positive-going waveforms for hits relative to correct rejections. Although the functional significance of these early effects is unclear, a tentative interpretation might be that they reflect perceptual priming or implicit memory processes elicited by the presentation of previously encountered material. Interestingly, these processes seemed to support associative judgments in the intra- but not in the inter-item condition, since only in the former condition was there a significant difference between H+ and H−. Hence, it remains to be investigated whether a perceptual priming account can explain this finding, as it is unclear why perceptual priming should occur for successful (H+) but not for unsuccessful (H−) associative judgments in the intra-item condition. This pattern could only be accommodated by perceptual priming if it is assumed that the greater

familiarity level for H+ items is associated with more pronounced perceptual priming for H+ relative to H− items. To conclude, further studies are warranted to disclose the functional significance of such very early frontally pronounced old/new effects.

A second issue addressed in the present study was whether there are dissociable electrophysiological correlates of inter- versus intra-item associations at the encoding stage. Consistent with other studies that have compared Dm effects for different qualities of hit responses (i.e., "remember" versus "know" responses; Duarte et al., 2004; Friedman and Trott, 2000; Mangels et al., 2001; Smith, 1993; Yovel and Paller, 2004), we investigated whether Dm effects emerge in encoding activity that leads to successful associative retrieval. We found reliable Dm effects for successful associative recognition of face-pairs elicited by the second faces within the study face-pairs (Figure 2). The Dm effects were widespread, positive-going ERP deflections with a maximum over fronto-central sites emerging approximately 400 ms after stimulus onset and sustaining until the end of the recording epoch. Together with the finding that there were no reliable Dm effects during presentation of the first faces within the study face-pairs, this pattern clearly suggests that the Dm effects reflected brain activity specifically tied to the encoding of associations between faces. However, despite the fact that the retrieval of both types of associations could be electrophysiologically dissociated, at the encoding stage there were no differential Dm effects for inter- versus intra-item associations, indicating that highly similar encoding-related control processes in pursuit of successful memory performance were initiated in both conditions.

Although our findings are largely consistent with the expected pattern for the electrophysiological correlates of familiarity and recollection, our data are open to alternative interpretations. A first issue is that the dissociation of the early frontal from the late parietal old/new effect may be a byproduct of condition differences in task difficulty or task performance. However, this seems to be unlikely because double (rather than single) dissociations cannot be accounted for by differences in task difficulty. Moreover, our post-hoc analyses using groups with matched behavioral performance confirmed the double dissociation of the early frontal and the late parietal old/new effect. Given this, it seems unlikely that differences in behavioral performance have confounded the present findings.

A second issue is that there might have been condition differences in encoding- and retrieval-related strategy application that influenced the pattern of ERP findings. Although this possibility cannot be completely ruled out, at least two results argue against this interpretation. First, we found no condition differences for the obtained Dm effects. Given that the Dm effects reflected the application of strategic encoding operations targeted at forming associations between face stimuli, this result indicates that there were no differences between conditions with regard to encoding-related strategy application. Second, differential strategy applications may likely lead to condition differences in the time course of behavioral performance. Specifically, a mnemonic strategy engaged in one but not the other condition may selectively improve performance in the former condition across the time course of the task. To examine this possibility, we conducted ANOVAs on an ensemble of behavioral measures using the additional factor of Time-on-Task (first versus second half of the task). Here, we found no reliable Condition × Time-on-Task interactions (all F values < 0.80), indicating that there were no condition differences in encoding- or retrieval-related strategies.

A third issue concerns the functional interpretation of the observed ERP effects. Some authors have interpreted the early frontal old/new effect as resulting from conceptual priming (Voss and Paller, 2006). However, we believe that at least two arguments support the view that the early old/new effect reflects familiarity rather than conceptual priming. First, it is questionable whether conceptual priming can be elicited by unfamiliar faces at all, given that they do not carry with them preexisting semantic knowledge (cf. Bruce and Young, 1986; Curran et al., 2006; Voss and Paller, 2006). Second, assuming that conceptual priming can indeed be evoked by unfamiliar faces, the most important challenge for a conceptual priming account is the fact that H+ elicited a significantly greater early frontal old/new effect than H− in the intra-item condition. Here, a conceptual priming account would predict a similar early frontal old/new effect across H+ and H− because conceptual priming should occur to a similar degree, irrespective of the success of associative judgments.

Another issue is whether the late parietal old/new effect may simply reflect the strength of memory traces. However, the fact that this effect was stronger in the more difficult inter-item condition (as indicated by lower recognition memory performance) strongly speaks against this alternative hypothesis, because the general strength of memory traces was arguably greater in the intra-item condition. Our data rather suggest that the late parietal old/new effect depends on the retrieval of specific types of associations, that is, associations between arbitrarily paired, nonoverlapping information.

A final issue to be addressed is that although the two faces of the forced-choice judgment in the intra-item condition were equal in morph-degrees away from the previously presented test face, the two faces may nevertheless not have been *perceived* as equally similar to the previously presented test face as a result from unitization (or other) processes occurring during the encoding phase. By this means, the test phase of the intra-item condition may have been a simple identity matching task. Although it cannot be completely ruled out that identity matching was one of the mechanisms contributing to forced-choice judgments in the intra-item condition, we believe that at least three results speak against the possibility that the task could be performed solely on the basis of identity matching without relying on associative representations. First, in the post-experiment interview no participant explained that for the forced-choice judgment he/she could simply choose the photograph that depicted the same person as the previously presented single test face. Second, if one adopted the assumption that the intra-item condition consisted of a pure identity matching task, the obtained performance in the forced-choice decision would have been surprisingly low (i.e., 71%). Third, the fact that the early frontal old/new effect was significantly larger for successfully

associated (H+) compared with unsuccessfully associated (H−) face-pairs is hard to explain under the assumption that the forced-choice judgment consisted of a pure identity matching task. This pattern could only be explained if it is assumed that single faces that were accompanied by high levels of item familiarity were associated with higher probabilities of correct identity matching compared to low-familiarity faces. In this case, the greater familiarity signal for H+ relative to H− in the intra-item condition could simply reflect differences in item-level familiarity rather than mirroring how well participants encoded and retrieved intra-item associations. However, as it cannot easily be explained why differences in item-level familiarity should be associated with a differential success in identity matching, we believe that our findings favor the view that the obtained early frontal old/new effect partly reflected associative recognition memory processes rather than differences in item-level familiarity alone.

In conclusion, the present findings have shed new light on the controversy concerning the neurocognitive mechanisms underlying (associative) recognition memory. To the best of our knowledge, a double dissociation of familiarity and recollection within the same experiment has never been reported before, except in a recent study by Woodruff et al. (2006). These authors found that words recognized on the basis of familiarity (operationally defined as the confidence level with which an old response was given) in the absence of recollection elicited an early frontal, but no late parietal, ERP old/new effect. The former effect also varied with the strength of the familiarity signal that participants experienced during recognition of the single words. By contrast, words that were reported to be accompanied by the recollection of specific contextual details relative to highly familiar words elicited a later parietal old/new effect that was insensitive to familiarity, indicating that the late parietal old/new effect is specific for recollection. The data of the present study extend this finding and provide strong evidence for dual-process accounts by doubly dissociating the putative electrophysiological correlates of familiarity and recollection in a manner consistent with the proposed functional characteristics of these memory processes as per Norman and O'Reilly's (2003) dual-process model. Hence, our findings reveal further and compelling evidence for this neurocomputational model. Moreover, the present results extend our knowledge on the dual processes supporting human recognition memory, since our data indicate that familiarity and recollection may subserve distinct types of associative retrieval: while recollection seems to enable retrieval of associations between arbitrarily paired, nonoverlapping items, familiarity may support associative recognition judgments in situations where the to-be-associated items can be unitized. Finally, our findings revealed common neural activity in the encoding phase that supported the formation of intra- and inter-item associations in episodic memory.

Experimental Procedures

Participants
Sixteen healthy, right-handed students with normal or corrected-to-normal vision from Saarland University (mean age = 22.31, stan-dard deviation [SD] = 2.33, range = 19–26; eight females) provided informed consent to participate in the study in return for cash payment. Data from one additional participant were discarded due to pulse artifacts on the left mastoid recording.

Face Stimuli
The face stimuli were 552 gray-scale photographs of unfamiliar faces taken from a picture database (Jäger et al., 2005) (see Supplemental Experimental Procedures). Among others, the picture database contained pairs of morphed faces, that is, sets of two different faces that were gradually transformed into each other, resulting in intermediate morphed faces along the morph-continua. Of the available morph-continua, we selected the 0%, 35%, 70%, and 100% morphed faces, which were then used for the intra-item condition. Every morph-continuum was rated in a pilot study for similarity on physical and identity dimensions (Jäger et al., 2005), and we selected 60 morph-continua (i.e., 240 face stimuli) in which neighboring morph-degrees were rated as clearly physically discriminable but still representing the same person to a high degree. Additionally, we selected 312 further unmodified face stimuli from the same picture database for the inter-item condition and the new faces of both conditions.

Associative Recognition Memory Task
Participants performed 24 blocks of an associative recognition memory task, with each block consisting of a study and a test phase (Figure 1). In 12 blocks, participants encoded face-pairs representing two different but gender-matched persons (i.e., inter-item condition). In the other 12 blocks, participants encoded face-pairs consisting of faces that were judged to represent the same person to a high degree (i.e., intra-item condition; see Supplemental Experimental Procedures). This was achieved by creating face-pairs consisting of a 35% and a 0% morphed face and face-pairs consisting of a 100% and a 70% morphed face. Participants were told that they would be presented with study-test blocks in which two photographs have to be memorized that either show two different persons or the same person twice on physically different pictures. Intra- and inter-item blocks were pseudorandomly intermixed.

In each study phase (Figure 1A), a total of ten face-pairs had to be memorized. Photographs of each face-pair were presented sequentially. Every novel face-pair was announced by "next pair" (1500 ms), after which a fixation cross appeared on the screen (1000 ms); then, the first face of a given face-pair was presented (700 ms), followed by a fixation cross (1500 ms). Then, the second face of the face-pair was presented (700 ms), again followed by a fixation cross (1500 ms) and finally a blank screen (200 ms). Thereafter, the next study trial started. In the inter-item condition, ten face-pairs were encoded that depicted two arbitrarily paired, but gender-matched, persons. In the intra-item condition, there were ten face-pairs of which five face-pairs were a 35% and a 0% morphed face (presented in this order), whereas the other five face-pairs were a 100% and a 70% morphed face (presented in this order). Participants were instructed to memorize the particular pairings of photographs for a subsequent associative recognition memory test. Additionally, participants were required to judge the gender of each face stimulus by a button press in order to reduce the likelihood that participants engage in strategic encoding operations. After the study phase, a distractor task was performed for 20 s in which participants had to count aloud backward in steps of 6, 7, 8, or 9 from a randomly presented number between 100 and 200.

In each test phase (Figure 1B), five old (i.e., studied) and three new (i.e., unstudied) trials were intermixed. First, a fixation cross was presented (1000 ms), followed by a single test face (500 ms) that had to be judged as old or new. The single test faces that should have been endorsed as new were completely novel faces. The single test faces that should have been judged as old were faces that were presented as the first faces within the study face-pairs. In the intra-item condition, the studied single test faces were always the 35% morphed faces. After the single test face, a fixation cross stayed on the screen (1500 ms). In the case of a correct old response, two faces that were both studied were next presented side by side. Participants indicated by a forced-choice judgment which of the two faces was paired with the previously presented single test face by pressing the left or right key, respectively. Photographs used in the

forced-choice task were always the second faces within the studied face-pairs. (Note that in the post-experiment interviews only one participant stated having noticed that the single test faces were always the first faces within study face-pairs and that faces of the forced-choice task were always the second faces within study face-pairs.) For the forced-choice judgment, the faces stayed on the screen until either a response was made or 1500 ms had elapsed. In the intra-item condition, the target photograph of the forced-choice task was always the 0% morphed face, while the nontarget photograph was always the 70% morphed face of the same morph-continuum. Hence, both target and nontarget faces differed by a morph-degree of 35% along the morph-continuum from the initially presented single test face, which was a 35% morphed face. Because of this, forced-choice decisions could not be made solely on the basis of differences in face similarity (Figure 1B). Faces initially paired with the nontarget faces of the forced-choice task during the study phase were excluded from the test phase. When the single test face was an unstudied face and correctly endorsed as new, two gray rectangles appeared on the screen in the same size as the face stimuli of the forced-choice judgment, and participants had to press a key (left or right) to continue. In the case of a wrong old/new response to the single test face (i.e., misses or false alarms), two gray rectangles including the word "wrong" were presented, and again a button had to be pressed (left or right). Before the next test trial started, a blank screen was presented for 2000 ms.

Before starting the experiment, participants performed 4 practice blocks of the associative recognition memory task using faces that did not appear during the 24 subsequent blocks. In the study and the test phase, responses were given on a response box, and the mapping of response type to response keys was counterbalanced across participants for both the study phase and the test phase.

Electrophysiological Methods
Scalp electroencephalogram (EEG) was recorded from an array of 59 silver/silver-chloride electrodes embedded in an elastic cap, and amplified from DC to 1000 Hz at a sampling rate of 500 Hz (see Supplemental Experimental Procedures). EEG was acquired referenced to the left mastoid and was off-line re-referenced to linked mastoids. Further off-line data processing included a digital low-pass filter set to 30 Hz. Continuous EEG data was separated into 2200 ms epochs, commencing 200 ms prior to stimulus onset (baseline).

Data Analyses
Statistical analyses of behavioral data included measures of old/new discrimination (Pr), response bias (Br), the proportion of correct forced-choice judgments, and response times. For both the behavioral data and the EEG data, trials were excluded from further analyses whenever an old/new response occurred beyond 2000 ms. Selection of the time windows for ERP analyses was based on previous studies and on visual inspection of the waveforms. As Dm effects have been shown to reflect early as well as late ERP modulations (Mecklinger and Müller, 1996), the ERP data in the study phase were quantified by measuring the mean amplitudes in an early (400–800 ms) and a late (1200–1800 ms) time window. The ERP data in the test phase were quantified by measuring the mean amplitudes in two consecutive time windows (300–400 ms and 400–700 ms), which was done to tap the early frontal old/new effect (the putative correlate of familiarity [300–400 ms]) and the late parietal old/new effect (the putative correlate of recollection [400–700 ms]).

Behavioral and ERP data were analyzed using repeated measures analyses of variance (ANOVAs) with an α level of $\alpha = 0.05$. The Greenhouse-Geisser correction for nonsphericity was used whenever appropriate and epsilon-corrected p values are reported together with uncorrected degrees of freedom. ERP Dm effects were computed as amplitude differences between hits associated with correct forced-choice judgments and hits associated with incorrect forced-choice judgments. These ERP Dm effects, which were computed for both the first and second faces of each study face-pair, were analyzed using global Condition (inter-item condition, intra-item condition) × Response Type (subsequent H+, subsequent H−) × Time Window (400–800 ms, 1200–1800 ms) × Anterior-Posterior (anterior-frontal [Fp1, Fpz, Fp2], frontal [F3, Fz, F4], central [C3, Cz, C4], parietal [P3, Pz, P4], occipital [O1, Oz, O2]) × Lateral (left [Fp1, F3, C3, P3, O1], middle [Fpz, Fz, Cz, Pz, Oz], right [Fp2, F4, C4, P4, O2])

ANOVAs. Test phase ERPs capturing the early frontal and the late parietal old/new effects were analyzed using a global Condition × Response Type (correct rejection, H+, H−) × Time Window (300–400 ms, 400–700 ms) × Anterior-Posterior × Lateral ANOVA using the same electrode montage as for Dm effects. For reasons of clarity, only significant main effects or interactions involving the factors of Condition and/or Response Type are reported. Planned single comparisons were performed using paired-samples t tests (two-tailed, but one-tailed where directional hypotheses were tested).

Supplemental Data
The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/52/3/535/DC1/.

References

Achim, A.M., and Lepage, M. (2005). Neural correlates of memory for items and for associations: An event-related functional magnetic resonance imaging study. J. Cogn. Neurosci. *17*, 652–667.

Aggleton, J.P., and Brown, M.W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. Behav. Brain Sci. *22*, 425–489.

Aggleton, J.P., and Shaw, C. (1996). Amnesia and recognition memory: A re-analysis of psychometric data. Neuropsychologia *34*, 51–62.

Brown, M.W., and Bashir, Z.I. (2002). Evidence concerning how neurons of the perirhinal cortex may effect familiarity discrimination. Philos. Trans. R. Soc. Lond. B Biol. Sci. *357*, 1083–1095.

Bruce, V., and Young, A. (1986). Understanding face recognition. Br. J. Psychol. *77*, 305–327.

Buckley, M.J., and Gaffan, D. (2006). Perirhinal cortical contributions to object perception. Trends Cogn. Sci. *10*, 100–107.

Curran, T. (2000). Brain potentials of recollection and familiarity. Mem. Cognit. *28*, 923–938.

Curran, T., Tepe, K., and Piatt, C. (2006). Event-related potential explorations of dual processes in recognition memory. In Handbook of Binding and Memory: Perspectives From Cognitive Neuroscience, H.D. Zimmer, A. Mecklinger, and U. Lindenberger, eds. (Oxford: Oxford University Press), pp. 467–492.

Davachi, L., Mitchell, J.P., and Wagner, A.D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. Proc. Natl. Acad. Sci. USA *100*, 2157–2162.

Donaldson, W. (1996). The role of decision processes in remembering and knowing. Mem. Cognit. *24*, 523–533.

Donaldson, D.I., and Rugg, M.D. (1998). Recognition memory for new associations: Electrophysiological evidence for the role of recollection. Neuropsychologia *36*, 377–395.

Donaldson, D.I., and Rugg, M.D. (1999). Event-related potential studies of associative recognition and recall: Electrophysiological evidence for context dependent retrieval processes. Brain Res. Cogn. Brain Res. *8*, 1–16.

Duarte, A., Ranganath, C., Winward, L., Hayward, D., and Knight, R.T. (2004). Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. Brain Res. Cogn. Brain Res. *18*, 255–272.

Düzel, E., Vargha-Khadem, F., Heinze, H.J., and Mishkin, M. (2001). Brain activity evidence for recognition without recollection after

early hippocampal damage. Proc. Natl. Acad. Sci. USA *98*, 8101–8106.

Eichenbaum, H. (1997). Declarative memory: Insights from cognitive neurobiology. Annu. Rev. Psychol. *48*, 547–572.

Eichenbaum, H., and Bunsey, M. (1995). On the binding of associations in memory: Clues from studies on the role of the hippocampal region in paired-associated learning. Curr. Dir. Psychol. Sci. *4*, 19–23.

Finnigan, S., Humphreys, M.S., Dennis, S., and Geffen, G. (2002). ERP 'old/new' effects: Memory strength and decisional factor(s). Neuropsychologia *40*, 2288–2304.

Friedman, D., and Johnson, R., Jr. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. Microsc. Res. Tech. *51*, 6–28.

Friedman, D., and Trott, C. (2000). An event-related potential study of encoding in young and older adults. Neuropsychologia *38*, 542–557.

Gillund, G., and Shiffrin, R.M. (1984). A retrieval model for both recognition and recall. Psychol. Rev. *91*, 1–67.

Grill-Spector, K., Henson, R., and Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. Trends Cogn. Sci. *10*, 14–23.

Henke, K., Buck, A., Weber, B., and Wieser, H.G. (1997). Human hippocampus establishes associations in memory. Hippocampus *7*, 249–256.

Henson, R.N.A., Rugg, M.D., Shallice, T., Josephs, O., and Dolan, R.J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. J. Neurosci. *19*, 3962–3972.

Henson, R.N.A., Cansino, S., Herron, J.E., Robb, W.G., and Rugg, M.D. (2003). A familiarity signal in human anterior medial temporal cortex? Hippocampus *13*, 164–174.

Henson, R.N.A., Hornberger, M., and Rugg, M.D. (2005). Further dissociating the proceses involved in recognition memory: An fMRI study. J. Cogn. Neurosci. *17*, 1058–1073.

Jacoby, L.L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. J. Mem. Lang. *30*, 513–541.

Jäger, T., Seiler, K.H., and Mecklinger, A. (2005). Picture database of morphed faces (MoFa): Technical report. Psydoc Online (http://psydok.sulb.uni-saarland.de/volltexte/2005/505/).

Li, L., Miller, E.K., and Desimone, R. (1993). The representation of stimulus familiarity in anterior inferior temporal cortex. J. Neurophysiol. *69*, 1918–1929.

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. Psychol. Rev. *87*, 252–271.

Mangels, J.A., Picton, T.W., and Craik, F.I.M. (2001). Attention and successful episodic encoding: An event-related potential study. Brain Res. Cogn. Brain Res. *11*, 77–95.

Manns, J.R., Hopkins, R.O., Reed, J.M., Kitchener, E.G., and Squire, L.R. (2003). Recognition memory and the human hippocampus. Neuron *37*, 171–180.

Mayes, A.R., Holdstock, J.S., Isaac, C.L., Montaldi, D., Grigor, J., Gummer, A., Cariga, P., Downes, J.J., Tsivilis, D., Gaffan, D., et al. (2004). Associative recognition in a patient with selective hippocampal lesions and relatively normal item recognition. Hippocampus *14*, 763–784.

Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. Psychophysiology *37*, 565–582.

Mecklinger, A., and Müller, N. (1996). Dissociations in the processing of "what" and "where" information in working memory: An event-related potential analysis. J. Cogn. Neurosci. *8*, 453–473.

Norman, K.A., and O'Reilly, R.C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. Psychol. Rev. *110*, 611–646.

Opitz, B., and Cornell, S. (2006). Contribution of familiarity and recollection to associative recognition memory: Insights from event-related potentials (ERP). J. Cogn. Neurosci. *8*, 453–473.

O'Reilly, R.C., and Norman, K.A. (2002). Hippocampal and neocortical contributions to memory: Advances in the complementary learning systems framework. Trends Cogn. Sci. *6*, 505–510.

Otten, L.J., and Rugg, M.D. (2002). The birth of a memory. Trends Neurosci. *25*, 279–281.

Paller, K.A., and Wagner, A.D. (2002). Observing the transformation of experience into memory. Trends Cogn. Sci. *6*, 93–102.

Quamme, J.R. (2004). The role of unitization in the representation of associations in human memory. Ph.D. thesis at University of California at Davis, Davis, California.

Quamme, J.R., Yonelinas, A.P., Widaman, K.F., Kroll, N.E.A., and Sauvé, M.J. (2004). Recall and recognition in mild hypoxia: Using covariance structural modeling to test competing theories of explicit memory. Neuropsychologia *42*, 672–691.

Ranganath, C., Yonelinas, A.P., Cohen, M.X., Dy, C.J., Tom, S.M., and D'Esposito, M. (2003). Dissociable correlates of recollection and familiarity within the medial temporal lobes. Neuropsychologia *42*, 2–13.

Rugg, M.D., and Yonelinas, A.P. (2003). Human recognition memory: A cognitive neuroscience perspective. Trends Cogn. Sci. *7*, 313–319.

Schacter, D.L., Norman, K.A., and Koutstaal, W. (1998). The cognitive neuroscience of constructive memory. Annu. Rev. Psychol. *49*, 289–318.

Smith, M.E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. J. Cogn. Neurosci. *5*, 1–13.

Snodgrass, J.G., and Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. J. Exp. Psychol. General *117*, 34–50.

Tsivilis, D., Otten, L.J., and Rugg, M.D. (2001). Context effects on the neural correlates of recognition memory: An electrophysiological study. Neuron *31*, 497–505.

Tulving, E. (2002). Episodic memory: From mind to brain. Annu. Rev. Psychol. *53*, 1–25.

Voss, J.L., and Paller, K.A. (2006). Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. J. Neurosci. *26*, 926–933.

Wagner, A.D., Koutstaal, W., and Schacter, D.L. (1999). When encoding yields remembering: Insights from event-related neuroimaging. Philos. Trans. R. Soc. Lond. B Biol. Sci. *354*, 1307–1324.

Wagner, A.D., Shannon, B.J., Kahn, I., and Buckner, R.L. (2005). Parietal lobe contributions to episodic memory retrieval. Trends Cogn. Sci. *9*, 445–453.

Wais, P.E., Wixted, J.T., Hopkins, R.O., and Squire, L.R. (2006). The hippocampus supports both the recollection and the familiarity components of recognition memory. Neuron *49*, 459–466.

Woodruff, C.C., Hayama, H.R., and Rugg, M.D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. Brain Res. *1100*, 125–135.

Yonelinas, A.P. (2002). The nature of recollection and familiarity: A review of 30 years of research. J. Mem. Lang. *46*, 441–517.

Yonelinas, A.P., Kroll, N.E.A., Dobbins, I.G., and Soltani, M. (1999). Recognition memory for faces: When familiarity supports associative recognition judgments. Psychon. Bull. Rev. *6*, 654–661.

Yonelinas, A.P., Hopfinger, J.B., Buonocore, M.H., Kroll, N.E.A., and Baynes, K. (2001). Hippocampal, parahippocampal and occipital-temporal contributions to associative and item recognition memory: An fMRI study. Neuroreport *12*, 359–363.

Yonelinas, A.P., Kroll, N.E.A., Quamme, J.R., Lazzara, M.M., Sauve, M.J., Widaman, K.F., and Knight, R.T. (2002). Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. Nat. Neurosci. *5*, 1236–1241.

Yonelinas, A.P., Otten, L.J., Shaw, K.N., and Rugg, M.D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. J. Neurosci. *25*, 3002–3008.

Yovel, G., and Paller, K.A. (2004). The neural basis of the butcher-on-the-bus phenomenon: When a face seems familiar but is not remembered. Neuroimage *21*, 789–800.