

Fluent Conceptual Processing and Explicit Memory for Faces Are Electrophysiologically Distinct

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Implicit memory and explicit memory are fundamentally different manifestations of memory storage in the brain. Yet, conceptual fluency driven by previous experience could theoretically be responsible for both conceptual implicit memory and aspects of explicit memory. For example, contemplating the meaning of a word might serve to speed subsequent processing of that word and also make it seem familiar. We examined electrophysiological correlates of conceptual priming with 180 celebrity faces to determine whether or not they resemble electrophysiological correlates of explicit memory. Celebrity faces are ideal for this purpose because they carry with them preexisting conceptual information (i.e., biographical facts) that can selectively be brought to mind such that conceptual processing can be manipulated systematically. In our experiment, exposure to biographical information associated with only one-half of the celebrities yielded conceptual priming for those faces, whereas all faces were perceptually primed. Conceptual priming was indexed by positive brain potentials over frontal regions from ~250 to 500 ms. Explicit memory retrieval was associated with later brain potentials over posterior regions that were strikingly similar to potentials previously associated with pure familiarity for faces (when a face seems familiar in the absence of retrieval of any specific information about previous occurrence). Furthermore, the magnitude of conceptual priming was correlated across subjects with the amplitude of frontal but not posterior potentials, whereas the opposite was true for explicit memory. Distinct brain processes were thus associated with conceptual priming and conscious recognition of faces, thus providing a sharper focus on the border between implicit and explicit memory.

Key words: conceptual priming; face memory; familiarity; event-related potentials; ERPs; episodic memory

Introduction

Conceptual priming and familiarity are deceptively similar memory phenomena, but they nonetheless lie on different sides of the distinction between implicit memory and explicit memory. Both “recollection” (conscious remembering with retrieval of specific contextual details) and “familiarity” (recognition that is unsubstantiated by episodic recall) support “explicit memory” for complex facts and autobiographical episodes (also known as “declarative memory”). Also, both recollection and familiarity are generally impaired in amnesia (Knowlton and Squire, 1995; Yonelinas et al., 1998; Khoe et al., 2000; Yonelinas, 2002). In contrast, amnesia can leave intact a set of memory capabilities that operate independent of conscious remembering, known collectively as “implicit memory” (Schacter, 1987; Gabrieli, 1998). “Priming” refers to a class of implicit memory phenomena whereby exposure to a stimulus alters subsequent stimulus processing in a perceptual or conceptual manner (“perceptual priming” or “conceptual priming,” respectively), as usually measured

by faster or more accurate responses (Schacter and Buckner, 1998).

A close connection between priming and familiarity has been proposed whereby priming entails a greater tendency to endorse an item as familiar (Whittlesea and Williams, 1998; Verfaellie and Cermak, 1999; Rajaram and Geraci, 2000). Various findings suggest that perceptual priming does not promote familiarity (Hamann and Squire, 1997; Wagner et al., 1997; Stark and Squire, 2000). In contrast, the highly controversial notion that familiarity is driven by the same neural process that leads to conceptual priming remains a tenable possibility (Jacoby and Dallas, 1981; Johnston et al., 1985; Wagner et al., 1997; Verfaellie and Cermak, 1999; Rajaram and Geraci, 2000). Indeed, Jacoby (1991) argued that familiarity-based recognition relies heavily on conceptual processing fluency. Likewise, Yonelinas (2002) took the position that similarities between familiarity and conceptual priming suggest that they “may in fact rely on common mechanisms” (Yonelinas, 2002, p 483).

In amnesia, behavioral results often indicate that conceptual priming and explicit memory operate independently, in that patients exhibit preserved conceptual priming despite impaired recall of learning episodes (Graf et al., 1985; Vaidya et al., 1995; Keane et al., 1997; Levy et al., 2004). However, conceptual priming is not always intact in amnesia (Cermak et al., 1998), and results may depend on how conceptual priming is assessed, for example, whether identification or production is required (Gabrieli et al., 1999). Thus, results from memory-impaired patients

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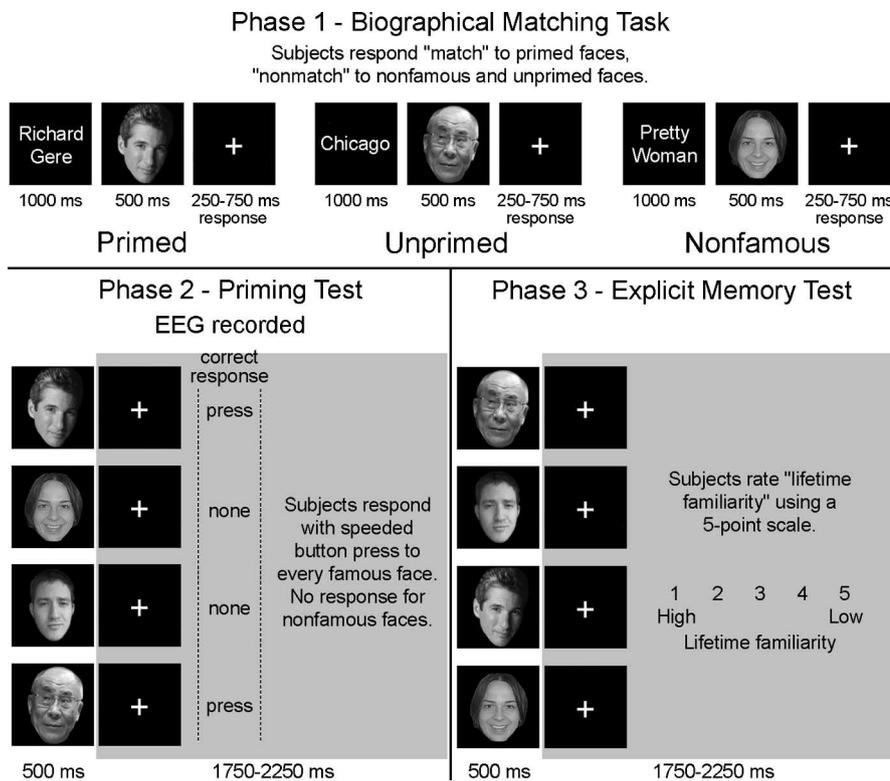


Figure 1. Schematic representation of the experimental design in experiment 1, including timing parameters. The construction of phase 1 produced two classes of famous faces, primed and unprimed, that varied systematically in the degree to which associated conceptual knowledge was activated. The biographical information applied only to the primed faces (e.g., the 3 biographical cues depicted here apply to the primed celebrity). Brain potentials were recorded in phase 2 while speeded responses to each famous face were obtained. Deciding that a face is famous tends to entail access to relevant biographical facts, and we hypothesized that this response would be facilitated for faces to the extent that associated biographical information was activated in phase 1. Primed and unprimed faces were presumably subject to equivalent perceptual priming from viewing faces in phase 1. Conceptual priming was thus exhibited in phase 2 by faster and more accurate responses for primed compared with unprimed faces. An assessment of explicit memory in phase 3 revealed the extent to which each celebrity was known to each participant. Brain potential differences based on conceptual priming and explicit memory were thus contrasted for the same set of stimuli within the same task.

to date have not conclusively specified the functional relationship between these memory phenomena.

If conceptual priming and familiarity rely on common mechanisms, one might expect neural correlates of the two memory phenomena to coincide and overlap to a large extent. Therefore, we set out to examine neural correlates of conceptual priming and test the hypothesis that they match those of familiarity. A high degree of similarity would support the hypothesis of a close functional connection between the two, whereas a lack of similarity would imply that conceptual priming and familiarity reflect disparate memory phenomena.

We used direct measures of neural activity, averaged electroencephalographic (EEG) responses time-locked to particular events such as a class of stimuli. These event-related potentials (ERPs) were elicited in a novel behavioral paradigm that enabled us to identify neural correlates of conceptual priming and explicit memory for the same set of face stimuli with task requirements held constant.

Materials and Methods

Experiment 1

Subjects

Behavioral and ERP data were collected from 10 right-handed native English speakers (six females; age, 18–19 years). ERP data recorded from an additional three subjects were excluded because of excessive eye-

movement artifacts such that too few uncontaminated trials were available. The pattern of behavioral results for the 10 subjects contributing ERP data was identical to that for the entire group of 13 subjects. Behavioral data are thus reported for the entire group.

Materials

Facial stimuli consisted of 180 photographs of celebrities (actors, politicians, musicians, professional athletes, and television personalities) and 180 photographs of nonfamous individuals. The format of famous and nonfamous faces was similar and included only the head, in grayscale, on a black background. Famous and nonfamous faces were divided into two sets of 90 (mean percentage of females in each set, 50.3%).

Three biographical cues were compiled for each famous individual. The name was always used as a cue, as well as two other short identifying pieces of information. Additional cues most often included the title of a film or song, a television role, or a political office, and are given in supplemental Table 1 (available at www.jneurosci.org as supplemental material).

For each participant, one of the two sets of 90 famous faces was used for the condition designated the “primed” condition (see below). Participants were exposed to biographical cues for those 90 celebrities and did not see the biographical cues for the other 90 celebrities. The set of celebrities assigned to the primed condition was counterbalanced across ERP subjects.

Experimental design

The experiment comprised three distinct phases.

Biographical matching test (phase 1). Participants viewed faces belonging to three conditions: primed, unprimed, and nonfamous. The goal was for participants to think about person-specific information primarily for the primed

celebrities. Biographical information was shown on the screen just before each face. Participants indicated via button press whether each face matched the biographical cue that preceded it (Fig. 1). “Primed faces” were 90 celebrity photographs preceded by a matching biographical cue. “Unprimed faces” were 90 celebrity photographs preceded by a biographical cue for a randomly selected primed face. Each of 90 nonfamous faces was also preceded by a biographical cue for a randomly selected primed face. In the unprimed and nonfamous conditions, mismatching name cues did not necessarily match on gender. The priming phase was divided into three segments such that each of the 270 faces was presented once per segment, each time with a different biographical cue. The specific information pertaining to each primed celebrity appeared nine times (once per segment with the matching celebrity, once per segment with celebrity faces from the unprimed condition, and once per segment with nonfamous faces). Faces were shown in random order at a fast rate, as shown in Figure 1. This rapid presentation format, along with the task requirement to maintain information regarding a primed celebrity while evaluating each face and producing a response, functioned to limit the recall of information related to unprimed celebrities. This procedure thus provoked subjects to bring to mind a greater amount of conceptual information regarding primed than unprimed individuals, allowing us to obtain measures of conceptual priming in the next phase of the experiment.

Conceptual priming test (phase 2). Approximately 5 min after phase 1, each of the 270 faces was shown again along with 90 nonfamous faces never seen before (to equate the number of famous and nonfamous

faces). Subjects made a speeded go/no-go response by pressing a button as quickly as possible after each famous face (not pressing any button in response to nonfamous faces). Faces were presented in random order. Given that deciding whether a face is famous entails accessing pertinent conceptual information, we expected that responses to famous faces that were recently conceptually primed would be facilitated relative to those that were not.

Explicit memory test (phase 3). The assessment of explicit memory followed phase 1 by ~25 min. Stimuli and presentation parameters were identical to those in phase 2, except that stimuli were presented in a different random order. For each famous and nonfamous face, subjects made a rating using a five-point scale in which “1” corresponded to “very familiar” and “5” corresponded to “not familiar at all.” This test can be said to measure “lifetime familiarity,” as assessed in a recent study of explicit memory (Diana et al., 2005), in that subjects were instructed to quickly make a gut-level memory assessment for which the source of the memory was irrelevant (i.e., it could include their experiences before the experiment or experiences during the experiment). This probe was designed to determine the extent to which each famous face was known to each participant while potentially remaining sensitive to the influence of previous phases of the experiment, thus yielding a behavioral index of the relative amount of explicit memory of any type occurring in response to each face. Given that ERP measures are potentially sensitive to any type of retrieval that takes place, this somewhat general measure of explicit memory (including both episodic and semantic retrieval) is useful for also being sensitive to these multiple influences of memory on face processing.

ERP data acquisition

EEG recordings were made during phase 2 from 59 scalp sites using tin electrodes embedded in an elastic cap at locations designed to provide fairly even coverage across the scalp. Four channels were used for monitoring horizontal and vertical eye movements, and trials contaminated by electro-ocular artifacts were excluded from ERP analyses. Impedance was lowered to 5 k Ω or less. EEG signals were collected with a bandpass of 0.05–200 Hz, sampled at a rate of 1000 Hz, and rereferenced off-line to average mastoids. Each averaging epoch lasted 1200 ms, including 100 ms before stimulus onset. Baseline correction was performed by subtracting the mean amplitude over the prestimulus interval from every poststimulus time point.

ERP analysis

ERPs elicited by famous faces during phase 2 were averaged in two different ways: (1) ERPs were computed as a function of conceptual priming based on the presentation of biographical information during phase 1 (i.e., primed vs unprimed conditions); and (2) ERPs were computed as a function of subsequent ratings during phase 3, with faces endorsed with a high familiarity rating (1 or 2 on the five-point scale) operationally defined as high in explicit memory retrieval (HEM) and those endorsed with a low rating (3, 4, or 5) defined as low in explicit memory retrieval (LEM). Responses to famous faces that were not endorsed as famous in phase 2 (10% on average) were excluded from both analyses.

ERP waveforms included data from 10 subjects for the primed/unprimed contrast and data from 8 subjects for the HEM/LEM contrast. Two subjects were excluded from the latter analysis because nearly all celebrities were endorsed with high ratings during phase 3, such that there were too few trials (<20) in the LEM condition. Data from a total of eight subjects were suitable for comparisons of primed and unprimed faces matched in explicit memory and of HEM and LEM faces matched in priming.

Formal statistical comparisons were performed on ERP waveforms derived from two different electro-ocular artifact identification procedures. Our standard approach was to reject trials with artifacts in the –100 to 1100 ms range (23% of trials, on average; SEM, 0.04%). Formal statistical comparisons focused on the first 750 ms after stimulus onset, whereas many of the artifacts occurred after this interval. Therefore, a supplementary analysis identified artifacts within the first 750 ms of each trial, such that only 9% of trials were rejected. This supplementary analysis yielded an identical pattern of results as the main analysis (i.e., the

same null hypotheses were rejected, but with different levels of significance), and so statistical results from the main analysis are emphasized and artifact-free ERP waveforms for the entire epoch are presented.

Significant differences in ERP measurements were evaluated using repeated-measures ANOVA ($\alpha = 0.05$) with Geisser–Greenhouse corrections when necessary. *Post hoc* pairwise comparisons were reported only if significant after Bonferroni’s correction. Time-course analyses were conducted using consecutive 5 ms averaging windows with uncorrected pairwise comparisons between corresponding windows from each condition. For presentation purposes only, waveforms were smoothed with a 55 Hz low-pass, zero-phase-shift Butterworth filter.

Experiments 2 and 3

Behavioral data were collected from six subjects in experiment 2 (three females; age, 18–20 years) and six subjects in experiment 3 (four females; age, 18–19 years). Except for the following modifications, experiments 2 and 3 (behavioral control experiments) were conducted exactly as described above. In both experiments, EEG recordings were not made. Also, in both experiments there were changes for the unprimed condition in phase 1. In experiment 2, meaningless strings of characters (consonants and punctuation) preceded unprimed faces. Subjects responded to each face using one of three buttons to indicate whether the preceding information matched, did not match, or was neutral (meaningless character strings). “Neutral” responses were made by pressing the appropriate response button three times while counting backward from three, such that recall of information related to unprimed celebrities was minimized by taxing working memory, as accomplished in experiment 1 using biographical information. In phase 1 of experiment 3, an appropriate gender description (“male” or “female”) preceded every unprimed face. One-half of the nonfamous faces were preceded by an inappropriate gender description instead of a celebrity fact. Subjects responded “match” (all primed and unprimed faces) or “nonmatch” (only nonfamous faces). All gender responses were made three times while counting backward, such that working memory during unprimed faces was taxed to a similar extent in all three experiments.

Results

Behavior

Conceptual priming was found both in speed and accuracy of button-press responses in phase 2. A high proportion of the celebrity faces were endorsed as famous during the priming test (90%; SE, 1.85%). On average, reaction times (RT) on correct trials were 32 ms faster for primed faces than for unprimed faces ($t_{(12)} = 3.08$; $p = 0.01$; mean RTs, 620 and 652 ms, respectively). Every subject exhibited RT priming (range, 4–71 ms). In addition, all subjects achieved higher accuracy for primed than unprimed faces ($t_{(12)} = 4.96$; $p < 0.001$; mean hit rate, 93 and 86%, respectively). Subjects responded incorrectly to nonfamous faces very infrequently, and these false alarms occurred equally often for nonfamous faces presented for the first time during phase 2 (mean, 5.7%) and nonfamous faces repeated from phase 1 (mean, 5.7%). Behavioral responding for these two types of nonfamous faces also did not differ in phase 3 ($t_{(12)} = 1.41$; $p = 0.18$) and so are considered together in all other analyses.

In related priming studies, Dobbins et al. (2004) showed that response learning can contribute to priming effects. Here, a relative facilitation for responding “yes” in phase 2 for primed compared with unprimed faces could theoretically have resulted because of the fact that primed faces received match responses in phase 1 whereas unprimed faces received nonmatch responses. Results from experiments 2 and 3 ruled out this possibility, because the same magnitude of priming was observed using different response requirements in these two behavioral control experiments. In both designs, primed and unprimed faces received the same response in phase 1, and RT priming paralleling that in experiment 1 was observed (experiment 2: mean priming, 29 ms;

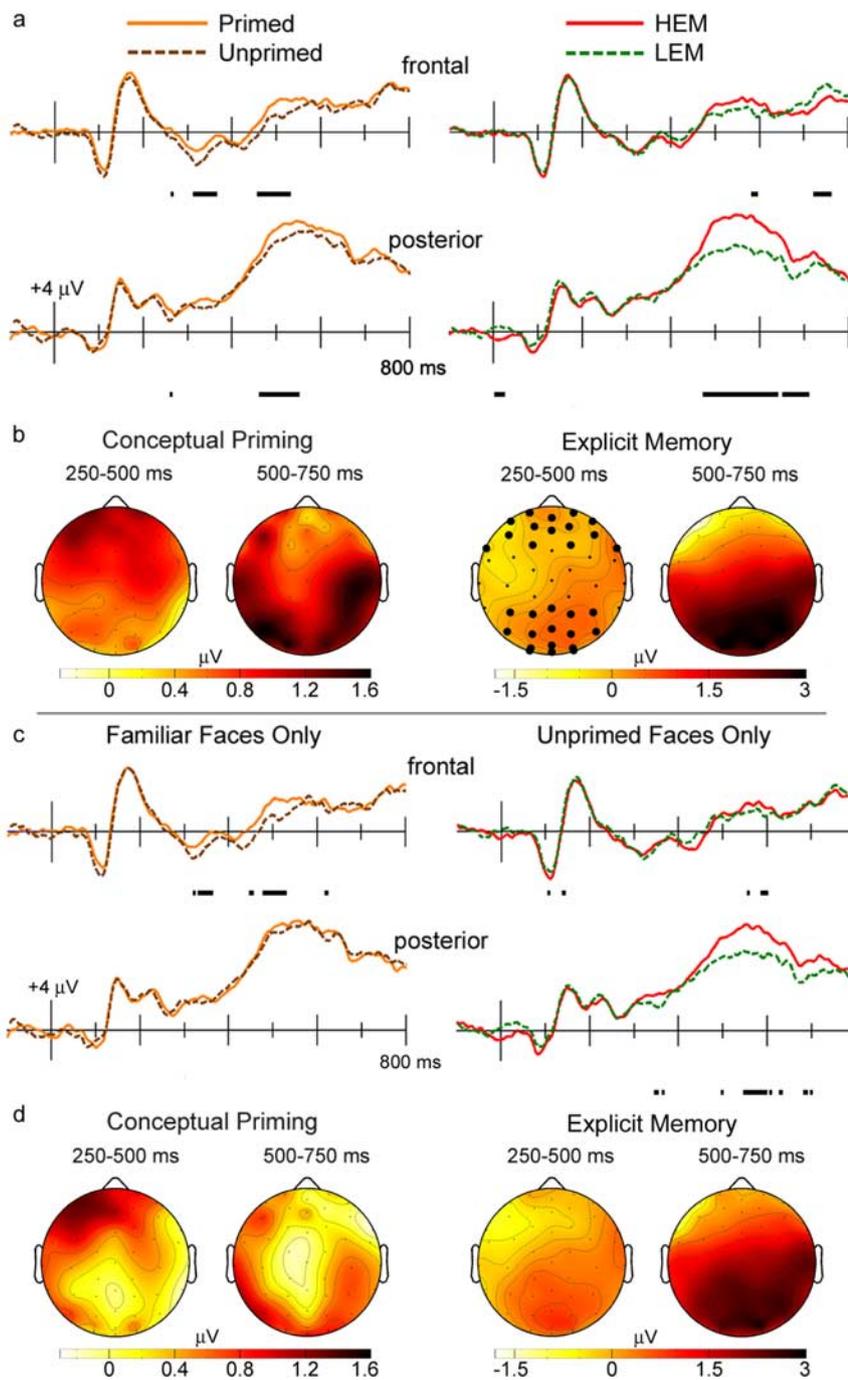


Figure 2. ERPs elicited by famous faces during the priming test. *a*, ERPs for primed and unprimed conditions ($n = 10$) and HEM and LEM conditions ($n = 8$) at frontal (slightly posterior to Fz) and parietal (Pz) midline locations. Significant pairwise differences for 5 ms windows are indicated by black bars below each axis. The assignment of famous faces to primed and unprimed conditions was counterbalanced across subjects, such that reliable differences cannot be attributed to the specific faces used in each condition. *b*, Topographic maps of mean ERP differences between primed versus unprimed and HEM versus LEM conditions averaged over two time intervals. The three electrode regions for formal analyses are indicated in the explicit memory 250–500 ms map: frontal and posterior regions by large dots (16 and 18 electrodes, respectively); middle region by small dots (18 electrodes). *c*, ERPs from the same two locations as in *a* for the primed/unprimed contrast for HEM faces only ($n = 8$) and for the HEM/LEM contrast for unprimed faces only ($n = 8$). *d*, Topographic maps of mean ERP differences for the corresponding two contrasts from *c* averaged over two time intervals.

$t_{(5)} = 2.48$; $p = 0.0557$; experiment 3: mean priming, 27 ms; $t_{(5)} = 3.33$; $p = 0.021$).

Presentation of biographical information in phase 1 also influenced explicit memory performance in phase 3; small differences in mean explicit memory ratings on the five-point scale

were observed (2.09 vs 2.37 for primed and unprimed faces, respectively; $t_{(12)} = 5.63$; $p = 0.001$). Nonfamous faces engaged very little explicit retrieval compared with celebrities (4.52 vs 2.23 for nonfamous and famous faces, respectively; $t_{(12)} = 17.7$; $p < 0.001$). The priming manipulation in phase 1 can thus be said to have influenced both implicit and explicit memory; nevertheless, neural correlates of conceptual priming and explicit memory can be derived selectively by virtue of analyses that take both types of behavioral memory measures into account.

An additional analysis established the feasibility of planned ERP comparisons. An ERP contrast between priming and explicit memory would only be meaningful to the extent that primed faces were not all rated as highly familiar and unprimed faces were not all rated as less familiar. Indeed, large numbers of both primed and unprimed faces were included in the HEM condition (an average of 56% primed faces and 44% unprimed faces) and likewise for the LEM condition (an average of 42% primed faces and 58% unprimed faces).

ERPs during phase 2

ERPs were found to be more positive for primed than unprimed famous faces from ~250 to 550 ms and more positive for HEM than LEM faces from ~450 to 750 ms (Fig. 2*a*). ERPs were formally analyzed over two consecutive time intervals, 250–500 and 500–750 ms, and over three regions, defined by averaging waveforms from anterior, middle, and posterior scalp locations (Fig. 2*b*). Differences in ERP amplitudes were analyzed using repeated-measures ANOVA with factors: condition (primed/unprimed or HEM/LEM), region (frontal/middle/posterior), and time interval (early, 250–500 ms; late, 500–750 ms). Comparing primed and unprimed faces yielded a significant main effect of condition ($F_{(1,9)} = 10.04$; $p = 0.01$) and a three-way interaction ($F_{(1,31,11,77)} = 12.12$; $p = 0.003$). Comparing HEM and LEM faces also yielded a significant main effect of condition ($F_{(1,7)} = 6.03$; $p = 0.044$) and a three-way interaction ($F_{(1,09,7,63)} = 13.93$; $p = 0.006$). *Post hoc* pairwise comparisons between conditions, run separately for each region and interval and corrected for multiple comparisons, revealed significant differences between primed and unprimed famous faces early in the frontal region ($t_{(9)} = 3.81$; $p = 0.004$) and late in middle ($t_{(9)} = 3.92$; $p = 0.003$) and posterior ($t_{(9)} = 3.86$; $p = 0.004$) regions. In contrast, HEM/LEM differences were significant late in middle ($t_{(7)} = 5.61$; $p < 0.001$) and posterior ($t_{(7)} = 5.89$; $p < 0.001$) regions.

Figure 2*b* shows topographies of ERP differences between conditions averaged over the same two time intervals. Priming differences appeared in the early interval as a relative positivity maximal over frontal locations and in the late interval as a positivity over posterior locations. Explicit memory differences appeared as a positivity localized to posterior locations and maximal in the late interval. A direct test of the differential sensitivity of the early frontal positivity to the two manipulations was conducted. Frontal amplitude differences over the 250–500 ms interval were significantly greater for the priming contrast compared with the explicit memory contrast (mean difference, 1.26 vs $-0.05 \mu\text{V}$, respectively; $F_{(1,16)} = 4.64$; $p = 0.04$).

Given that exactly this kind of early frontal ERP difference has been hypothesized to reflect conceptual priming (Yovel and Paller, 2004), we analyzed correlations between each subject's RT measure of conceptual priming and the amplitude of the early frontal positivity in the primed/unprimed contrast. ERPs were measured in each subject by selecting the electrode showing the greatest priming difference at 250–500 ms within the frontal region. An extremely strong correlation was found between this ERP measure and the magnitude of priming ($r^2_{(8)} = 0.77$; $p < 0.001$). In contrast, the maximum amplitude difference in the late interval (measured at the location showing the largest difference at middle and posterior regions during this interval) was not correlated with priming magnitude ($r^2_{(8)} = 0.03$; $p = 0.64$).

In a complementary analysis, we found that explicit memory was related to late posterior ERP differences but not to the early frontal positivity. The mean difference in familiarity rating was computed between primed and unprimed conditions. This behavioral measure of the influence of the priming manipulation on explicit memory was marginally correlated with the maximum primed/unprimed amplitude difference in the late interval at middle and posterior regions ($r^2_{(8)} = 0.44$; $p = 0.052$), whereas it was not correlated with the early frontal positivity ($r^2_{(8)} = 0.04$; $p = 0.61$).

ERP correlates of conceptual priming and explicit memory clearly differed in topography (Fig. 2*b*). This impression was substantiated by a significant condition-by-region interaction ($F_{(2,48)} = 5.14$; $p = 0.001$) in a comparison between ERPs averaged over each of the three regions and subjected to amplitude normalization using the root-mean-square procedure (McCarthy and Wood, 1985).

The time course of these effects was analyzed using consecutive 5 ms intervals for data from the frontal and posterior electrode locations shown in Figure 2*a*. Differences pertaining to priming were reliable at the frontal electrode primarily from 300 to 350 ms and again from 425 to 475 ms and at the posterior electrode from 425 to 475 ms. Differences pertaining to explicit memory were significant at the posterior electrode from ~ 425 to 710 ms. Therefore, the relatively large time intervals chosen for formal analyses effectively captured the between-condition differences.

Given that priming magnitude and familiarity ratings were not entirely independent, another analysis focused on differences attributable to either the priming manipulation or explicit memory with the other variable held constant. To this end, sets of primed and unprimed famous faces were identified that were matched in explicit memory [i.e., all highly familiar, rated with 1 or 2 on the five-point scale; 74% (SE, 0.05%) of primed faces and 64% (SE, 0.06%) of unprimed faces were given such ratings]. Similarly, subsets of HEM and LEM famous faces were identified that were all unprimed. ERPs to primed and unprimed faces matched in explicit memory and to HEM and LEM faces matched

in priming were thus computed (Fig. 2*c,d*). The difference between explicit-memory-matched primed and unprimed faces was a relative frontal positivity for primed from 300 to 550 ms. In contrast, the ERP difference between priming-matched HEM and LEM faces was a relative posterior positivity for HEM from 450 to 750 ms. Pairwise comparisons indicated that the priming difference was significant early in the frontal region ($t_{(7)} = 4.36$; $p = 0.0033$), whereas the explicit-memory difference was significant late in middle ($t_{(7)} = 4.98$; $p = 0.0016$) and posterior ($t_{(7)} = 4.31$; $p = 0.0035$) regions.

The procedures used here to elicit conceptual priming succeeded because subjects were already knowledgeable about the biographical information presented. However, some of the biographical cues were not person specific, in that they could apply to several different celebrities, and some were not known to some subjects. Nonetheless, the significant results found using both behavioral and electrophysiological measures confirm that the procedure in phase 1 successfully prompted differential processing of conceptual information associated with primed versus unprimed celebrities. Moreover, ERP priming effects could also be observed when short-lag priming was produced using conceptually related famous faces or names (Schweinberger, 1996), but priming at the delays used here entails different memory processing than when the primed information remains at the focus of attention when the target item appears.

Because ERPs associated with conceptual priming in experiment 1 were maximal over frontal electrodes, special consideration of possible electro-ocular artifacts is warranted. If this frontal ERP positivity was based on residual artifact, a relative negativity for the same contrast would be expected at electrodes positioned below each eye. Instead, ERPs at these electrodes were slightly more positive for primed compared with unprimed faces in the interval from 250 to 500 ms (0.41 and 0.22 μV at left and right electrodes, respectively). Thus, frontal ERP correlates of conceptual priming can be attributed to brain activity rather than to electro-ocular artifact.

ERP correlates of episodic familiarity

ERP correlates of explicit memory identified by the HEM/LEM contrast could index a combination of explicit memory processes, including recollection or familiarity for phase 1 episodes, retrieval of semantic information acquired before the experiment, and recollection or familiarity for relevant pre-experimental episodes. Accordingly, we cannot determine how much of the HEM/LEM contrast reflects pure familiarity. Neural responses to famous faces may generally include retrieval beyond familiarity to the extent that people tend to recall biographical information when seeing the face. Indeed, when people view well known celebrities, as in phase 2, recall of pre-experimental information may be virtually impossible to exclude. With nonfamous faces, however, pure familiarity experiences can be identified using variants of the "remember"/"know" procedure (Tulving, 1985; Gardiner and Java, 1991), in which subjects introspect about their memory experiences to determine whether episodic information is recollected.

In a previous experiment (Yovel and Paller, 2004), we succeeded in characterizing neural correlates of pure familiarity with faces. Subjects first viewed novel faces presented with unique person-specific information (an occupation) in a study phase. Faces presented for recognition judgments in a test phase were endorsed with episodic recollection (remembering the face along with contextual or episodic information) or with episodic familiarity (endorsing the face as old but failing to remember the as-

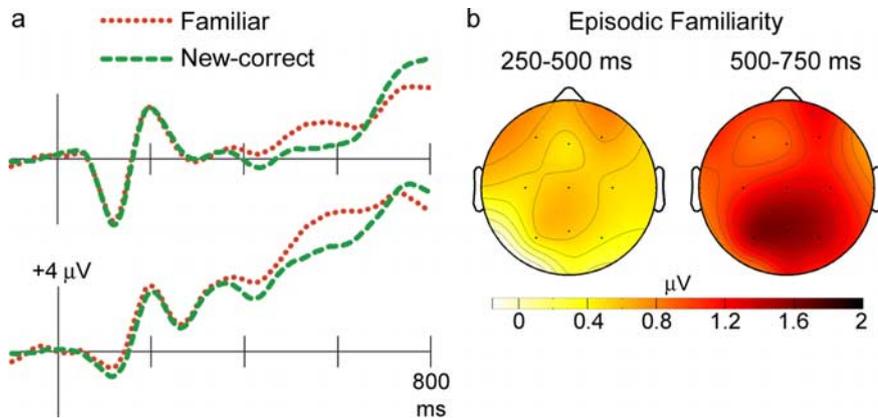


Figure 3. ERPs elicited by nonfamous faces to produce neural correlates of pure familiarity, shown in the same format as in Figure 2. Results were reported in detail by Yovel and Paller (2004). *a*, ERPs for faces recognized with pure familiarity and new faces at electrode locations matching those displayed in Figure 2 (top, Fz; bottom, Pz). *b*, Topographic maps of mean ERP differences based on the ERPs in *a* and averaged over two time intervals. These results show that neural correlates of pure familiarity bear a strong similarity to neural correlates of explicit memory for famous faces (Fig. 2, right).

sociated occupation and failing to recollect any specific episodic information). Figure 3 shows ERP waveforms and difference topographies associated with this experience of recognizing faces with pure familiarity, using the same format as in Figure 2 so as to allow a direct juxtaposition between the ERP results of Yovel and Paller (2004) and ERP results from the present experiment. Importantly, ERP correlates of pure familiarity were nearly identical in timing and topography to ERP correlates of explicit memory, as observed in the HEM/LEM contrast and, to a lesser extent, in the primed/unprimed contrast of the present experiment (Fig. 2). Notably, the ERP correlate of episodic familiarity (Fig. 3) did not include any sign of the early frontal component associated with conceptual priming in the present experiment.

Discussion

We characterized neural correlates of an implicit memory phenomenon, conceptual priming, using famous faces in a novel behavioral paradigm. Distinct ERPs were associated with conceptual priming versus explicit memory. Because these two contrasts were derived from the same data, the possibility that observed differences merely reflect confounding task differences can be dismissed. Direct neural comparisons between conceptual priming and explicit memory, as achieved in the current experiment, have not been made before. This electrophysiological analysis, together with previous ERP findings, thus provided valid insights into the two types of memory.

Priming was observed in every individual tested in the form of faster and more accurate responses to primed than to unprimed famous faces. Perceptual priming was presumably matched between the primed and unprimed conditions, given that each face appeared three times in phase 1. Moreover, possible differences in attentional focus or elaborative processing between primed and unprimed faces would not influence perceptual priming, given our previous demonstration of equivalent perceptual priming under such contrasts (Paller et al., 1999). The priming effects thus belong soundly in the category of conceptual priming.

The frontal positivity found in the priming contrast at 250–500 ms was taken as an ERP correlate of conceptual priming (the effect can also be considered an amplitude reduction in frontal N400 potentials). In contrast, explicit memory was associated with a posterior positivity at 500–750 ms. Given that late posterior potentials were also apparent in the primed/unprimed com-

parison (albeit with smaller amplitudes), one might ask whether the posterior potentials are actually the electrophysiological correlates of conceptual priming. Several arguments suggest not. First, given that the priming manipulation influenced explicit memory, as shown behaviorally in phase 3, a greater degree of explicit retrieval was likely engaged in phase 2 for some primed faces compared with unprimed faces. The primed/unprimed and HEM/LEM contrasts could thus be expected to share ERP correlates of explicit retrieval (i.e., the late posterior positivity). Second, RT indices of conceptual priming correlated with early frontal amplitude differences but not with late posterior amplitude differences. The extent to which the priming manipulation influenced episodic memory was correlated with late posterior amplitude differences and not with early frontal amplitude differences.

Furthermore, an analysis of the primed/unprimed contrast restricted to the most well known celebrities yielded only the early frontal effect. We thus conclude that conceptual priming and explicit memory occurred in conjunction with distinct electrical signals.

The explicit memory test used did not provide a process-pure measure of familiarity but rather was meant to index memory for celebrity faces from any source, whether or not the source was also retrieved. If, instead, subjects had been directed to one source only, phase 1 experiences, behavioral measures would have more specifically reflected episodic memory, but this tactic would be problematic because neural measures would likely be contaminated by recall of portions of the extensive pre-experimental knowledge available concerning these celebrities. Fortunately, evidence already available (Fig. 3) showed that pure familiarity experiences provoked by repeated faces were associated with late posterior potentials (Yovel and Paller, 2004). In general, late posterior potentials of the sort elicited in association with explicit memory in the present experiment have been ubiquitously related to episodic memory (Friedman and Johnson, 2000; Mecklinger, 2000; Paller, 2000; Rugg and Allan, 2000). Explicit memory for faces is apparently associated with late, posterior potentials both (1) when retrieval induced by famous faces includes episodic and semantic knowledge (Fig. 2) and (2) when retrieval induced by nonfamous faces is restricted so as to support pure-familiarity experiences (Fig. 3).

ERP recordings provide a temporal resolution ideal for examining rapid processing responsible for memory, but they are chiefly sensitive to synchronized postsynaptic potentials generated by neurons situated in a geometric orientation suitable for producing electrical potentials at the scalp. Functional magnetic resonance imaging (fMRI) is subject to different sorts of bias. In fMRI investigations of conceptual priming, frontal and inferior temporal cortices have been implicated, although none of these studies used facial stimuli (Thompson-Schill et al., 1999; Buckner et al., 2000; Wagner et al., 2000). One study contrasted brain networks associated with conceptual priming versus explicit memory with words (Donaldson et al., 2001). Because the explicit-memory network did not include as a subset the network associated with conceptual priming, results were used to argue that explicit retrieval did not depend on a contribution from

implicit memory. Given that separate tasks were used (abstract/concrete judgments vs old/new recognition), the pattern of activations could conceivably reflect different task demands per se. Nonetheless, the argument that conceptual priming and explicit memory operate independently is strengthened by the current results, which were not subject to this limitation.

The present results also converge with dissociations observed in amnesia when conceptual priming is spared despite severely impaired explicit memory for learning episodes (Graf et al., 1985; Vaidya et al., 1995; Keane et al., 1997; Levy et al., 2004). Here, the neural signature of conceptual priming did not appear to precede ERP correlates of explicit memory for faces (Fig. 2) or of pure familiarity for faces (Fig. 3). Together, these findings from patients and healthy individuals are consistent with the hypothesis that conceptual priming and explicit memory rely on distinct neural processes.

The present results also have implications for understanding recollection and familiarity. Medial temporal structures have been differentially related to recollection and familiarity in animals (Brown and Aggleton, 2001; Fortin et al., 2004), and similar distinctions have been supported using fMRI in humans. Hippocampal and parahippocampal activity seems critical for recollection, whereas familiarity is associated with perirhinal activity (Brewer et al., 1998; Eldridge et al., 2000; Yonelinas et al., 2001; Davachi et al., 2003; Henson et al., 2003; Ranganath et al., 2004). However, fMRI data have not conclusively shown that mutually exclusive neural processes are responsible for recollection and familiarity.

In ERP studies, late positive potentials with a posterior topography are consistently found in association with recollection, whereas ERP analyses of familiarity are more controversial. Some findings suggest that neural correlates of recollection and familiarity differ quantitatively, with similar timing and topographic characteristics (Smith, 1993; Trott et al., 1999; Yovel and Paller, 2004). Results from several other ERP experiments, however, have been taken as support for the notion that familiarity relies on mechanisms independent from recollection. In these studies (Düzel et al., 1997; Rugg et al., 1998; Tendolcar et al., 1999; Curran, 2000; Mecklinger, 2000; Tsivilis et al., 2001; Curran and Cleary, 2003), familiarity for verbal items was putatively associated with reduced frontal negativity at 300–500 ms. When words or namable pictures are used to assess neural correlates of familiarity, stimulus repetition inevitably results in conceptual priming in addition to episodic memory [e.g., words altered in plurality from study to test are not just familiar, as assumed by Curran (2000), but are also conceptually primed]. It is thus crucial in such studies to disentangle familiarity and conceptual priming before claims regarding neural correlates of either type of memory can be confirmed. Indeed, we propose that putative neural correlates of familiarity appearing as reduced frontal negativities may actually reflect conceptual priming.

Results presented here provide additional evidence against the hypothesis that reductions in frontal N400 potentials reflect familiarity. By disentangling explicit memory and conceptual priming for faces, we showed that reductions in frontal N400 potentials were strongly associated with conceptual priming. This outcome is in accord with the previous proposal (Olichney et al., 2000) that preserved N400 reductions with word repetition in amnesic patients reflected spared conceptual priming. With nonfamous faces, pure familiarity was indexed by posterior positive potentials and recollection by similar but larger potentials, and neither by reductions in N400 amplitude (Yovel and Paller, 2004). In another experiment, divided attention reduced behav-

ioral measures of recollection and familiarity for words as well as late posterior ERP effects, whereas no influence of divided attention on frontal N400 amplitudes was found (Curran, 2004). Given these arguments, previous hypotheses linking frontal N400 effects to familiarity should be reconsidered in light of our alternative interpretation.

In conclusion, a pervasive challenge for characterizing implicit or explicit memory processes independently is that these phenomena tend to co-occur. Explicit retrieval often occurs, even if unintentionally, during implicit memory tests (Schacter and Buckner, 1998), thus posing difficulties for the identification of valid neural correlates of memory functions. Our use of behavioral measures of both types of memory allowed us to isolate electrophysiological signals corresponding to conceptual priming and explicit memory, and striking temporal and topographic differences were observed. These findings thus constitute a neural dissociation between conceptual priming and explicit memory. In addition, these distinct electrophysiological correlates of memory are consistent with two more speculations: (1) that neural processing responsible for priming in the conceptual domain occurs before that supporting explicit memory; and (2) that this fluent conceptual processing does not make a significant contribution to explicit memory, at least in some situations. The venerable distinction between implicit memory and explicit memory, which came to prominence because of neuropsychological analyses of amnesic patients, receives additional support from our analyses of ERP recordings in healthy brains precisely where support is currently needed, at the controversial border between conceptual priming and familiarity.

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