The FN400 indexes familiarity-based recognition of faces

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Separate event-related brain potential (ERP) components have been hypothesized to index familiarity and recollection processes that support recognition memory. A 300- to 500-ms mid-frontal FN400 old/new difference has been related to familiarity, whereas a 500- to 800-ms parietal old/new difference has been related to recollection. Other recent work has cast doubt on the FN400 familiarity hypothesis, especially its application to familiarity-based recognition of conceptually impoverished stimuli such as novel faces. Here we show that FN400 old/new differences can be observed with novel faces, and as predicted by the familiarity hypothesis, these differences are observed regardless of whether or not recognition is accompanied by the recollection of specific details from the study episode. Furthermore, FN400 differentiation between hits and misses is more consistent with an explicit familiarity process than an implicit memory process.
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Dual-process theorists propose that recollection and familiarity are dissociable processes contributing to recognition memory (e.g., Hintzman and Curran, 1994; Jacoby, 1991; Mandler, 1980; Norman and O'Reilly, 2003; Rugg and Yonelinas, 2003; Yonelinas, 2002). Recollection is thought to involve processes by which specific details can be accurately recalled when something is recognized. Familiarity is thought to underlie a general sense that a stimulus has been previously encountered without the ability to remember specific details.

A wealth of evidence has supported the dual-process perspective (for reviews, see Rugg and Yonelinas, 2003; Yonelinas, 2002), including research measuring event-related brain potentials (for reviews see, Curran et al., 2006b; Friedman and Johnson, 2000; Mecklinger, 2000; Wilding and Sharpe, 2003). Familiarity has been associated with negative-going electrical activity recorded over frontal scalp locations between 300 and 500 ms, called the FN400 or mid-frontal old/new effect. Recollection has been associated with positive-going activity recorded over posterior parietal locations between 500 and 800 ms, often called the parietal old/new effect. For example, Curran (Curran, 2000; Curran and

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Cleary, 2003) performed a series of experiments in which subjects studied words or pictures. ERPs were recorded during recognition tests including studied items, non-studied lures that were similar to studied items (e.g., plurality-reversed words or orientation-reversed pictures), and new items. The FN400 discriminated between familiar (studied and similar lures) versus unfamiliar (new) items, whereas the parietal effect discriminated between recollected (hits to studied items) and non-recollected items (false alarms to similar lures or correctly rejected new items). Similar results have been obtained with semantically similar lures (Nessler et al., 2001, 2005).

A recent experiment by Yovel and Paller (2004) has cast some doubt on the proposed relationship between the FN400 and familiarity. The experiment used face stimuli to explore the "butcher-on-the-bus phenomenon," or the intuitive feeling experienced when a familiar person is encountered in an unfamiliar situation (such as seeing one's butcher on a bus). Twelve participants studied previously unfamiliar faces paired with occupations that were presented verbally by a male voice. Faces were monochromatic photographs with minimal background information, depicting young Caucasian adults without distinctive facial features such as facial hair or glasses (from Endl et al., 1998). During ten 24-item study lists, participants judged whether each face and occupation fit together or not. Each test list included 24 old/studied faces and 12 new/unstudied faces without occupations. First, participants gave standard old/new recognition judgments. If the participant responded "new," the trial ended. If they responded "old," they were presented with three subsequent choices: "occupation," "other specifics" and "no specifics." If the participant chose the "occupation" response, she or he said the occupation aloud. If the participant responded "other specifics," this meant that they recollected information from the study phase other than occupation. Participants responded "no specifics" if they knew the face was seen in the study phase, without recollection of occupation or other details. The latter responses were interpreted as indicative of familiarity-based responses.

Yovel and Paller's results were inconsistent with the hypothesis that FN400 old/new differences are related to familiarity: Rather than differentiating correctly classified old and new faces regardless of whether or not occupations or other details were recollected, the 300- to 500-ms FN400 old/new differences were only observed when occupations were recollected. Later, 500- to

700-ms amplitudes corresponding to the "parietal old/new effect" showed a graded pattern such that amplitudes when participants did not recollect any details fell in between amplitudes to new trials and trials in which occupations were recollected. Rather than indexing familiarity, the authors proposed that 300- to 500-ms old/new differences may be related to conceptual priming, as has been supported by subsequent research showing a positive correlation between FN400 effects and reaction time differences between old and new items on a conceptual priming task (Voss and Paller, 2006).

Given the theoretical importance of Yovel and Paller's (2004) experiment, it is critical to determine the replicability and generalizability of the results. The present experiment followed Yovel and Paller's design in most respects except for two key differences. First, we sought to maximize familiarity-based discrimination of old and new items. Most familiarity-based models of recognition memory suggest that familiarity reflects an assessment of the global similarity between a test item and all previously studied information (Dennis and Humphreys, 2001; Gillund and Shiffrin, 1984; Hintzman, 1988; Norman and O'Reilly, 2003; Shiffrin and Steyvers, 1997). Thus, familiarity does not provide a sufficiently accurate basis for discriminating studied items from similar lures (e.g., Hintzman and Curran, 1994, 1995; Hintzman et al., 1992). Indeed, previous research has shown that the FN400 differentiates old items from dissimilar lures, but does not differentiate old items from similar lures (Curran, 2000; Curran and Cleary, 2003; Nessler and Mecklinger, 2003; Nessler et al., 2001). Thus, rather than using relatively homogeneous faces with a high degree of inter-item similarity like those of Yovel and Paller (e.g., monochromatic, young, Caucasian, no facial hair or glasses), we chose a more heterogeneous set including color photographs of people who varied in ethnicity (or race), age, facial hair and glasses. We surmised that a more heterogeneous face set would reduce the similarity between old and new items, and thereby increase familiarity-based discrimination. Second, we noticed that Yovel and Paller's subjects showed a markedly conservative response bias such that correct rejection rates (88%) were much higher than hit rates (65%)—possibly caused by requiring follow-up responses to "old" judgments, but not to "new" judgments. Participants may have been biased to choose the easier and quicker of the two alternatives. To obtain more hits for ERP analyses, we sought to reduce this response bias by requiring follow-up responses after both "old" and "new" judgments. In particular, subjects were asked to give confidence ratings and to guess the person's occupation on a randomly selected third of faces judged "new."

If the FN400 is not related to familiarity, then Yovel and Paller's results should be replicated under the present conditions that maximize the ability for familiarity to contribute to face recognition. Specifically, the 300- to 500-ms FN400 old/new difference should be observed only when comparing trials with occupation recollection to new trials. If the FN400 is related to familiarity, then FN400 old/new differences should be similar for words recognized with or without occupation recollection.

Method

Participants

Thirty-three right-handed students at the University of Colorado participated in the experiment for payment of $15 per hour. All participants gave informed consent. Data from nine participants were discarded because of excessive eye-movement artifacts ($n=2$), low trial counts (less than 20 trials/condition, $n=4$), low accuracy ($n=1$) or an excessive number of bad channels ($n=2$). Of the remaining 24 subjects included in the analyses (mean age=21 years; range=18–27 years), 14 were female.

Stimuli

Stimuli were 360 faces and 240 occupations. Face stimuli were taken from the color FERET database of photographs (Phillips et al., 2000). Face stimuli consisted of 126 Caucasian women, 54 non-Caucasian women, 111 Caucasian men and 69 non-Caucasian men. The racial and ethnic groups of non-Caucasian faces included African American, Asian, Southeast Asian, Middle Eastern, Pacific Islander, Hispanic and Native American. The photographs depicted 24 individuals wearing glasses, 29 men with moustaches and 25 men with beards. Face stimuli were shown in color, including shoulders with clothing and some jewelry on the women. The occupations were mostly the same as those used by Yovel and Paller, but we replaced some unusual occupations (e.g., drug dealer) with ones that were more typical, as well as replacing some that were too confusable (e.g., civil engineer and electrical engineer; see Supplementary Materials). The occupations were presented directly below the faces in white on a black background on an LCD computer monitor. All face stimuli subtended a visual angle of 2.46° horizontally, 3.84° vertically.

Design

The experiment consisted of 10 blocks and lasted approximately 136 min. In each block, participants studied 24 unique face–occupation pairings. Approximately 0.5 min later, the participants were tested with those 24 faces plus 12 new faces. For each subject separately, faces were randomly assigned to old (studied) or new (non-studied) conditions and old faces were randomly paired with occupations. Responses were registered using a four key response pad. EEG was collected only during each test phase.

Procedure

Participants completed a short practice to familiarize them with the various procedures of the experiment. A Geodesic Sensor Net was then applied.

Each study trial began with a 1000-ms gray fixation cross at eye level on a black background followed by a 2000-ms face–occupation presentation. Occupation names appeared visually below targets—a minor departure from Yovel and Paller's auditory presentation of occupations. To enhance encoding, participants were asked to judge the fit of each face/occupation pair. Participants pressed one of two keys on each trial according to whether they believed the face and occupation fit together or not. Participants were also told to try to remember the face–occupation pairings because they would appear on a subsequent memory test.

During the test phase, the faces appeared without occupations and participants were asked to judge whether they believed the face had appeared in the study phase or not (i.e., "old" or "new"). Each test trial consisted of a pre-stimulus fixation varying between 1250 and 1750 ms, a face that appeared for 1000 ms, followed by another fixation until the subject made a response. We chose a

1000-ms presentation, rather than 500 ms (Yovel and Paller, 2004), to remove possible offset potentials from the recording epoch. Subjects were instructed to withhold their response until the face disappeared to lessen response-related ERP effects. If an "old" response was detected, the fixation cross was replaced after a 600-ms delay and the participant was asked, "Do you: (1) Remember the person's occupation (occupation), (2) Remember specific details about the person (other specific details) or (3) Not remember any specific details (no specific details)?" If an "occupation" response was detected, this signified that the associated occupation could be recalled, and it was then spoken aloud. If an "other specifics" response was detected, this signified that details of the study-phase episode (other than occupation) could be recalled, but no verbal response was given. If a "no specifics" response was detected, this signified that no details from the study-phase episode could be remembered, and no verbal response was given. If a "new" response was detected, the fixation cross was replaced after a 600-ms delay with the following choices for the next response: "very confident" (high) or "not confident" (low). After this response, the participants were then asked to generate an occupation for the face for randomly selected trials following 33% of "new" responses. This additional requirement made the "new" condition more equitable with the "old" condition in regards to difficulty and time commitment. The experimenter then initiated the next trial after EEG artifacts had subsided. Throughout each test block, participants were instructed to refrain from blinking insofar as they were able.

To motivate participants to perform adequately on the task, they received one point for correctly identifying each face as either "old" or "new." They were told that the highest scoring participant would receive a $25 bonus once all participants had completed the experiment.

EEG/ERP methods

Scalp voltages were collected during each test list with a 128-channel Geodesic Sensor Net™ connected to an AC-coupled, 128 channel, high-input impedance amplifier (200 MΩ, Net Amps™, Electrical Geodesics Inc., Eugene, OR). Amplified analog voltages (0.1–100 Hz bandpass, −3 dB) were digitized at 250 Hz. Individual sensors were adjusted until impedances were less than 50 kΩ. ERPs were baseline corrected to a 100-ms pre-stimulus recording interval and digitally low-pass filtered at 40 Hz. Trials were discarded from analysis if they contained eye movements (EOG over 70 μV), or more than 20% of channels were bad (average amplitude over 100 μV or transit amplitude over 50 μV). EEG was measured with respect to a vertex reference (Cz). An average-referenced transformation was used for the primary analyses to more accurately estimate the scalp topography of the measured electrical fields and to minimize the effects of reference-site activity (Dien, 1998). Subsidiary analyses used an average-mastoid reference to facilitate comparison with Yovel and Paller (2004).

Results

Yovel and Paller's (2004) primary analyses focused on correct rejections, familiar hits ("no specific details"), and hits associated with recollection of the correct occupation. They reported that ERPs were similar for correct rejection and misses but did not formally report misses. We include misses here because they are potentially relevant for differentiating processes related to familiarity vs. priming, which is particularly relevant to the FN400 interpretation.[1] Other conditions were considered in the Supplementary Materials. For analysis of variance (ANOVA) involving both reaction time (RT) and ERPs, all p values associated with more than 1 degree of freedom have been corrected according to the conservative Geisser–Greenhouse procedure for sphericity violations (Winer, 1971).

Behavioral results

Accuracy

Responses reflecting accurate recognition memory ("hit rates") averaged 81% for old faces (range 67–94%). Correct rejections of new stimuli averaged 90% (68–99%). When participants correctly identified faces as old, they recalled occupations 30% (15–60%) of the time, identified "other specific details" 34% (0–68%) of the time, and reported "no details" 36% (9–79%) of the time. The accuracy of verbally reported occupations was 96% (84–100%).

Reaction time

Reaction times (RT) were slowed artificially by the requirement to withhold responses until the test face disappeared (1 sec after face onset), so RTs are unlikely to accurately reflect decision times. However, we observed RT differences among the four primary conditions used for ERP analyses: occupation hits (MN=1582 ms), familiar hits (1658 ms), misses (1615 ms) and correct rejections (1429 ms), $F(3, 23)=5.65$, MSE=42315, $p<0.01$. Pairwise comparisons indicated that correct rejections were faster than all other responses involving old faces (all $p<0.02$), but none of the responses to old faces differed among themselves.

ERP results

Initial analysis focused on spatial regions of interest (ROIs) based upon our previous research (Curran, 2000, 2004; Curran and Cleary, 2003; Curran and Dien, 2003; Curran and Friedman, 2004; Curran et al., 2002, 2006a, 2007). The FN400 was analyzed over two anterior, superior channels groups located near the standard F3 and F4 sites. These are labeled left and right anterior/superior regions (LAS and RAS, respectively, see Fig. 1). The parietal old/new effect was analyzed over two posterior, superior channels groups that included the standard P3/P4 locations in addition to more anterior channels. These are labeled left and right posterior/superior regions (LPS and RPS, respectively, see Fig. 1). ERP waveforms created by averaging the ERPs within each region and across subjects are shown in Fig. 2. The number of correct, artifact-free trials entered into each ERP/subject averaged 99 for correct rejections, 63 for familiar hits, 44 for occupation hits and 42 for misses. Following Yovel and Paller (2004), the FN400 was analyzed from 300 to 500 ms whereas the parietal effects were analyzed from 500 to 700 ms.

FN400 results (300–500 ms)

If the FN400 is related to familiarity, then it should be more negative for correct rejections than hits, as is normally observed, and it should not differ between occupation hits and familiar

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[1] False alarm rates were not high enough to obtain sufficient observations for ERP analyses.
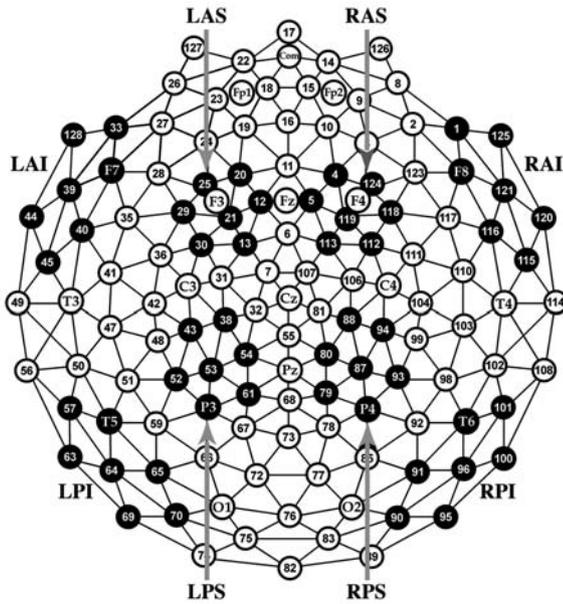
Fig. 1. Geodesic sensor net layout. Electrode sites are numbered along with selected 10–10 positions. Black clusters are regions included in the topographic analyses. L=left, R=right, A=anterior, P=posterior, I=inferior, S=superior.

Table 1
Amplitude means and (standard errors)

Latency (ms)	Correct rejection	Miss	Familiarity hit	Occupation hit
300–500	−3.2 (0.4)	−2.6 (0.4)	−2.0 (0.5)	−1.8 (0.4)
500–700	2.2 (0.5)	1.3 (0.5)	1.9 (0.5)	3.3 (0.5)

Note. 300–500 ms amplitudes were calculated from the average of left and right anterior, superior regions (LAS and RAS). 500–700 ms amplitudes were calculated from the average of left and right posterior, superior regions (LPS and RPS).

hits. The FN400 to misses should represent an intermediate level of familiarity, falling in between hits and correct rejections. Differences between hits and misses should be larger than differences between correct rejections and misses because the latter two familiarity distributions should have more overlap (both falling to the left of the new/old criterion) than hits and misses (falling on opposite sides of the new/old criterion). If the FN400 is related to implicit priming, on the other hand, it might be expected to differentiate old and new items regardless of

explicit recognition accuracy, so hits and misses would be similar and both would differ from correct rejections (e.g., Rugg et al., 1998).

Mean LAS and RAS amplitude between 300 and 500 ms was the dependent measure. A condition (occupation hit, familiar hit, correct rejection, miss) × hemisphere ANOVA indicated differences between conditions, $F(3,69)=7.06$, MSE=2.66, $p<0.001$ (see top of Fig. 2 and Table 1). Pairwise comparisons confirmed that the difference in amplitudes between familiar hits and correct rejections was significant, $F(1,23)=13.61$, $p<0.001$, as was the difference in amplitudes between the occupation hits and correction rejections, $F(1,23)=19.01$, $p<0.001$. Amplitudes for hits associated with familiarity versus occupation recollection did not differ significantly, $F(1,23)=0.45$. Misses were more negative than occupation hits ($F(1,23)=6.53$, $p<0.05$), marginally more negative than familiar hits ($F(1,23)=3.69$, $p=0.06$) and not different from correct rejections ($F(1,23)=2.47$, $p=0.12$).

Because the pattern of FN400 results was qualitatively different from those reported by Yovel and Paller (2004), we wanted to verify that disparities could not be attributed to analytic approach. Therefore, following Yovel and Paller (2004), we re-referenced the ERPs to the average of the two mastoid
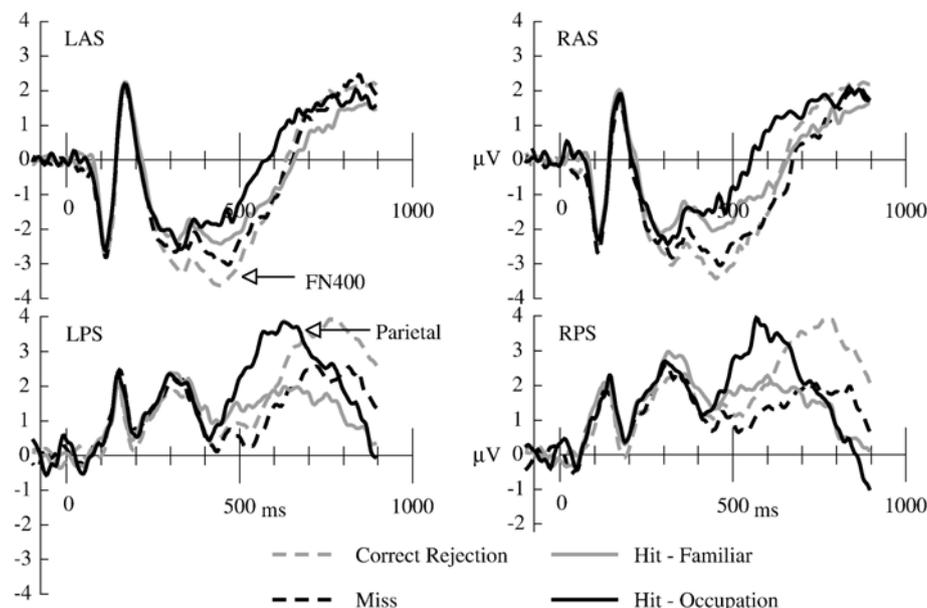

Fig. 2. Average-referenced, grand averaged ERPs in each of the 4 regions depicted in Fig. 1. L=left, R=right, A=anterior, P=posterior, I=inferior, S=superior.
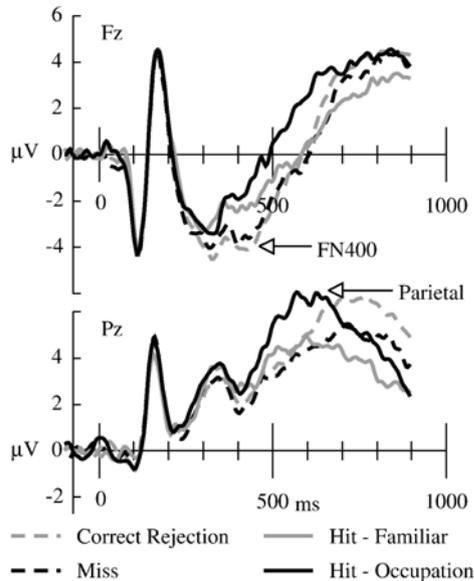
Fig. 3. Mastoid-referenced, grand averaged ERPs from frontal (Fz) and parietal (Cz) sensor locations.

electrodes (57 and 101) and focused on a standard series of mid-line channels (see Fig. 3). Mean mastoid-referenced amplitudes between 300 and 500 ms were analyzed in a condition (occupation-hit, familiar-hit, correct rejection, miss) × channel (Fpz [16], Fz [6], Cz [62], Pz [62], Oz [76]) ANOVA. All effects were significant: condition ($F[3, 69] = 5.20$, MSE=6.18, $p < 0.01$), channel ($F[4, 92] = 12.44$, MSE=41.81, $p < 0.001$) and condition × channel ($F[12, 276] = 4.21$, MSE=1.43, $p < 0.001$). The condition × channel interaction captured the fact that condition effects were larger over frontal than posterior electrodes. Pairwise comparisons focusing on the Fz location, where differences were largest, indicated that amplitudes to correct rejections (MN=−3.84 μV) were more negative than both familiar hits (MN=−2.35 μV; $F = 18.72$, $p < 0.01$) and occupation hits (MN=−1.92 μV; $F = 30.99$, $p < 0.001$), but the two categories of hits did not significantly differ ($F = 1.54$). Misses (MN=−3.40 μV) were more negative than occupation hits ($F(1,23) = 18.46$, $p < 0.001$), more negative than familiar hits ($F(1,23) = 9.34$, $p < 0.05$) and not different from correct rejections ($F(1,23) = 1.61$).

Overall, the pattern of FN400 differences is consistent with the hypothesis that this component is related to familiarity: occupation hits=familiar hits>misses=correct rejections. The analysis of mastoid-referenced mid-line channels was entirely consistent with our initial average-referenced analysis of the LAS and RAS ROIs, except that the difference between familiar hits and misses was significant with the mastoid reference ($p < 0.05$), but only marginally significant for the average reference ($p = 0.06$).

Parietal results (500–700 ms)

Mean LPS and RPS amplitude between 500 and 700 ms was the dependent measure. A condition (occupation hit, familiarity hit, correct rejection, miss) × hemisphere ANOVA indicated that the 500- to 700-ms effect varied significantly by condition, $F(3,69) =$

9.48, MSE=3.62, $p < 0.001$ (see bottom of Fig. 2 and Table 1).[2] Pairwise comparisons revealed that the difference between occupation hits and correct rejections was significant, $F(1,23) = 10.72$, $p < 0.01$, as was the difference between the occupation hits and familiar hits, $F(1,23) = 13.10$, $p < 0.002$. The difference between the correct rejections and the familiar hits was not significant $F(1,23) < 1$. Amplitudes for misses were lower than for occupation hits ($F(1, 23) = 26.88$, $p < 0.001$) and correct rejections ($F(1, 23) = 4.99$, $p < 0.05$) but were not different from familiar hits ($F(1, 23) = 2.28$).

Range normalized difference scores

To consider the broader topography of the results, we computed mean amplitude within each of the 8 electrode clusters depicted in Fig. 1 (following, Curran, 2000, 2004; Curran and Cleary, 2003; Curran et al., 2002, 2006a). Separate difference scores were intended to be associated with recognition with recollection (occupation hits minus correct rejections, OH-CR; Fig. 4B) and without recollection (familiar hits minus correct rejections, FH-CR; Fig. 4A). The difference scores were scaled using a range normalization method (McCarthy and Wood, 1985).[3] Qualitatively different scalp topographies might reflect either (a) different neuronal sources or (b) the same source with different relative strengths (see also Alain et al., 1999; Picton et al., 2000). Thus, condition × location interactions are consistent with separate sources, but do not necessarily demand separate sources. Furthermore, we chose this approach to maintain consistency with Yovel and Paller (2004) who also considered scalp topography with rescaled amplitudes.

The range-normalized difference scores were analyzed in a time (300–500, 500–700) × condition (FH-CR, OH-CR) × hemisphere × anterior/posterior (AP) × inferior/superior (IS) ANOVA. As is the purpose of rescaling, the condition main effect was removed, $F < 1$. Although many time and/or location effects were significant, we will only report interactions with condition that are of primary interest. The time × condition × IS interaction, $F(1,23) = 6.39$, MSE=1.03, $p = 0.02$, captured the observation that all old/new effects were characterized by positive superior differences together with negative inferior differences, except for the 500–700 FH-CR difference which was relatively flat across superior and inferior regions. This merely reflects the absence of significant old/new effects associated with familiar hits in the later time period (Fig. 4A, right). The time × condition × AP interaction, $F(1,23) = 8.15$, MSE=0.68, $p = 0.009$, indicated that posterior parietal old/new differences were largest from 500 to 700 ms when occupation was recollected (Fig. 4B, right).

Discussion

As predicted by the hypothesis that 300- to 500-ms mid-frontal FN400 old/new effects are related to familiarity, we found that the FN400 did not differ according to subject's ability to recollect occupations that had been previously associated with correctly recognized faces. Critically, FN400 old/new differences were

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[2] As for the FN400 results, parietal results were qualitatively similar with analysis of mastoid-referenced mid-line channels.

[3] Recent debates about the use of rescaled amplitudes concern the vector length method rather than the range normalization method used here (Dien and Santuzzi, 2005; Urbach and Kutas, 2002, 2006; Wilding, 2006).

A Familiarity Hit - Correct Rejection (CR)

300 - 500 ms   500 - 700 ms

B Occupation Hit - Correct Rejection (CR)
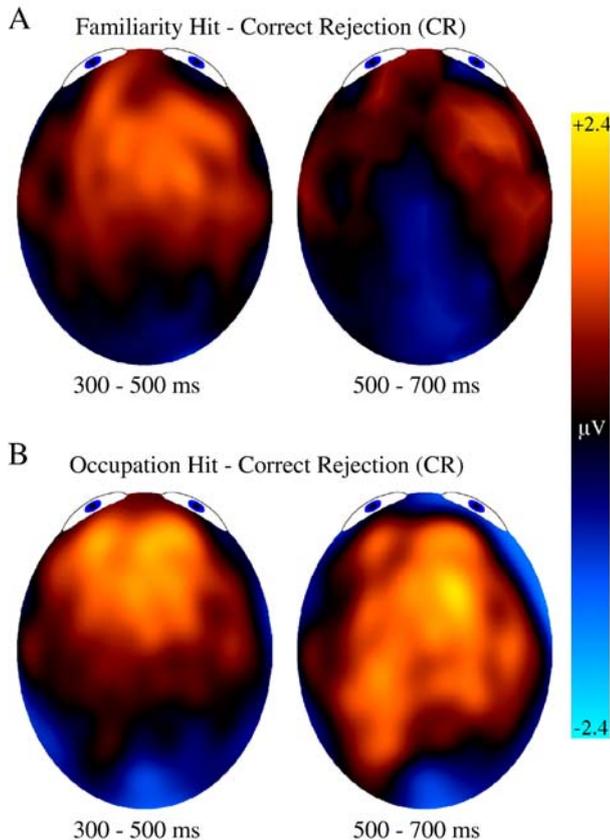

300 - 500 ms   500 - 700 ms

Fig. 4. Topographic maps comparing familiarity and recollection. (A) Familiarity-related differences at the time of the FN400 (300–500 ms) and parietal effects (500–700 ms). (B) Recollection-related differences at the time of the FN400 (300–500 ms) and parietal effects (500–700 ms).

significant even when responses were presumably familiarity-based (i.e., "no details"), despite a previous report that familiar faces are not differentiated from new faces until a later 500- to 700-ms time frame associated with the parietal old/new effect (Yovel and Paller, 2004). Overall, the pattern of mean amplitudes observed for the FN400 was consistent with a familiarity-based process such that amplitudes corresponding to hits, with or without recollection, were more positive than both correct rejections and misses. Conversely, the 500- to 700-ms parietal old/new differences were only observed when occupations were correctly remembered, supporting the association between recollection and the parietal effect (see Supplementary Materials for analyses contrasting recollection and confidence).

Why do the present results differ from those of Yovel and Paller (2004)? We predicted that using a more heterogeneous set of stimuli should have enhanced familiarity-based discrimination between old and new faces, as would be expected if familiarity reflects an assessment of the global similarity between a test item and all previously studied information (Dennis and Humphreys, 2001; Gillund and Shiffrin, 1984; Hintzman, 1988; Norman and O'Reilly, 2003; Shiffrin and Steyvers, 1997). Other research has previously shown that the FN400 discriminates old from dissimilar lures, but not from similar lures (Curran, 2000; Curran and Cleary, 2003; Nessler and Mecklinger, 2003; Nessler et al., 2001). In essence, highly similar materials potentially cause more inter-ference than dissimilar materials, leading to an inability to

effectively use familiarity to discriminate between old and new items. Other recent research has shown that the FN400 old/new effect observed with faces is susceptible to interference caused by manipulations of list length (Norman et al., submitted for publication).

As detailed in Table 2, overall face recognition accuracy was higher in the present experiment ($d'=2.16$) than Yovel and Paller's experiment ($d'=1.56$). To compare discrimination accuracy within the various response categories while minimizing the influence of response bias, d' was computed within each category. To compute d' (Table 2D), results originally reported as the proportion of hits within each response category (Table 2B) were transformed to the proportion of overall old trials in each response category (Table 2C) to compare with the overall false alarm rates. In each and every category d' was higher in the present experiment, including familiarity-based responses. As previously argued, we believe familiarity-based discrimination was enhanced by the use of a more heterogeneous face set.

Other minor differences between the present experiment and that of Yovel and Paller (2004) are less likely to have influenced the FN400 results. First, an increase in test stimulus duration from 500 to 1000 ms cannot influence 300–500 ms ERPs. Second, changes made to the occupations (visual rather than auditory study, less confusable, more typical) may influence occupation recollection but should have no bearing on the familiarity of the faces themselves.

The present results add to a growing body of evidence questioning the sufficiency of the hypothesis that FN400 old/new effects are related to conceptual priming. Like the present results, other research has shown FN400 old/new differences using previously unfamiliar faces that are unlikely to have conceptual representations (Johansson et al., 2004; Nessler et al., 2005; Norman et al., submitted for publication). Other stimuli possibly lacking conceptual representation for which FN400 old/new differences have been observed include novel dimensional shapes (Curran et al., 2002; Groh-Bordin et al., 2006). Furthermore, if conceptual priming is thought to be implicit (e.g., Voss and Paller, 2006; Yovel and Paller, 2004), one might expect to observe FN400 old/new differences regardless of recognition memory accuracy (e.g., hits=misses>correct rejection; Rugg et al., 1998), but no such implicit influences were observed in the present experiment.

Table 2
Accuracy in comparison with Yovel and Paller (2004)

	Curran and Hancock	Yovel and Paller
A. Overall recognition performance		
Hits	0.81	0.65
False alarms	0.10	0.12
d'	2.16	1.56
B. Proportion of hits in each response category		
Occupation	0.30	0.29
Other details	0.34	0.24
No details	0.36	0.47
C. Proportion of old trials in each response category		
Occupation	0.24	0.19
Other details	0.28	0.16
No details	0.29	0.30
D. d' in Each Response Category		
Occupation	0.58	0.29
Other details	0.68	0.16
No details	0.73	0.65

Although conceptual representations alone seem insufficient to explain all reported FN400 old/new differences, this does not necessarily rule out a relationship between the FN400 and conceptual priming in some circumstances. Conceptual features are likely to contribute to familiarity under some circumstances, such as when perceptual features vary between study and test (Curran and Dien, 2003), and these same features may contribute to conceptual priming.

It is important to note the relationship between the present results and those that we have previously related to face familiarity. Tanaka, Curran, Porterfield, and Collins (2006) described an N250 potential, occurring earlier than the FN400, that seems to be amplified by face familiarity both in the generic pre-experimental sense of familiarity (e.g., own face vs. unfamiliar face) as well as in the experimental sense (e.g., repeated targets vs. non-targets that were previously unfamiliar). Unlike the present FN400 results, in which a single face presentation was sufficient to subsequently discriminate old and new faces, Tanaka et al. found that the N250 modulation required up to 35 repetitions before targets and non-targets were differentiated. Thus, one possible difference between the FN400 and N250 concerns the number of learning trials necessary to differentiate familiar from unfamiliar faces. Perhaps the N250 reflects the activity of a process with a slower learning rate than the FN400 (e.g., McClelland, McNaughton, & O'Reilly, 1995), with the FN400 being better suited to the type of one-trial learning that typically characterizes familiarity-based recognition memory. Previous indications have suggested that the N250 is face selective (Schweinberger, Huddy, & Burton, 2004), but we have more recently observed learning-related increases in N250 amplitude following extensive training with birds (Scott, Tanaka, Sheinberg, & Curran, 2006). Although the N250 does not seem to be face specific, it is likely to reflect a visually specific form of memory, unlike the FN400 that can generalize across learning modalities (Curran & Dien, 2003).

Conclusions

Faces associated with correct rejection or misses showed a significantly more negative FN400 (300–500 ms) than faces that were correctly recognized as old, regardless of whether or not subjects could also recollect the associated occupation from the study episode. This result is consistent with the hypothesis that the FN400 is related to familiarity, and that the underlying mechanism applies to novel faces as well as to other previously examined stimuli such as words, identifiable pictures and novel shapes. Later, 500–700 ms, parietal old/new effects were only observed when subjects could recall the associated occupation, as would be expected from the hypothesis that parietal old/new effects are associated with recollection. These results support the dual-process perspective that separate familiarity and recollection processes contribute to recognition memory, and these processes are indexed by separate ERP components.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2006.12.016.

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