Rapid Communication

The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered

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A common distinction in contemporary research on episodic memory is between *familiarity*, an unsubstantiated impression that an event was experienced previously, and *recollection*, remembering some information plus the spatiotemporal context of the episode in which it was acquired. The epitome of pure familiarity—the *butcher-on-the-bus phenomenon*—occurs when one believes that a person is familiar (often upon seeing their face in an atypical context) while failing to recall any information about that person whatsoever. Prior research on familiarity and recollection has relied on verbal material. Whereas word meanings and pronunciations are well learned in advance, here we produced pure familiarity and recollection using photographs of faces never seen before the experiment. When participants recognized a face, recollection was inferred if they also remembered either the occupation associated with that face earlier in the experiment or any other episodic detail. Pure familiarity was inferred when recognition occurred in the absence of any such contextual retrieval. Analyses of brain potentials recorded during initial encoding showed that right-sided neural activity predicted subsequent face familiarity, whereas bilateral potentials predicted subsequent face recollection. Results during memory testing were inconsistent with the popular idea that familiarity is generically indexed by reduced frontal N400-like potentials. Instead, both memory experiences were associated with bilateral, parietal-maximum brain potentials, although with smaller amplitudes and for a shorter duration for familiarity. These similarities between electrophysiological correlates of pure familiarity and recollection suggest that familiarity with faces may arise by virtue of a subset of the neural processing responsible for recollection.
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Introduction

Have you ever seen someone who looks familiar, while at the same time been unable to remember the circumstances of any previous meeting or anything else about the person? This common example of a memory failure is known as experiencing *familiarity in the absence of recollection*. It can occur when seeing someone in an atypical setting, as in George Mandler's (1980) classic example of seeing the butcher on the bus. The context of the bus provides none of the clues concerning the butcher's identity that are typically present when the butcher is encountered in the butcher's shop. The processing responsible for this *butcher-on-the-bus phenomenon* is the focus of the current investigation.

Memory theorists have described *recollection* and *familiarity* as two bases for recognition (Jacoby, 1991; Mandler, 1980; Tulving, 1985; Yonelinas, 2001). *Recollection* occurs when a person consciously remembers a given item or event and the context of its prior occurrence, whereas *familiarity* is an unsubstantiated sense of having previously encountered the item or event. Central to the distinction is the idea that familiarity includes an inability to recall the context of any prior episodes or any associative information that would explain the origin of the familiarity experience.

Three plausible relationships between recollection and familiarity have been proposed (Jones, 1987; Knowlton and Squire, 1995). (1) According to a *redundancy* model, familiarity and recollection both entail the same sense of having previously encountered a stimulus, whereas recollection entails retrieval of contextual information as well. (2) According to an *independence* model, recollection does not involve the sense of familiarity and the two processes are independent. (3) According to a *mutual exclusivity* model, familiarity and recollection are not only separate processes but also cannot occur simultaneously.

Studies of memory disorders have been used to shed light on the distinction between familiarity and recollection and to judge the suitability of these three different models. One widely accepted generalization about amnesia is that the memory impairment disrupts both recollection and familiarity (Knowlton and Squire, 1995; Yonelinas et al., 1998). Accordingly, a cortical storage process that relies on cortico-hippocampal interactions and is disrupted in amnesia (as assumed in many theories of amnesia, see Mayes and Downes, 1997; Paller, 2002; Squire and Schacter, 2002) may normally support both familiarity and recollection. Other evidence, however, implies that deficits in recollection can occur with spared familiarity following hippocampal damage early in life (Baddeley, 2002; Tulving, 2002; Vargha-Khadem et al., 1997), leading to the hypothesis that hippocampal processing contributes to recollection but is not

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required for familiarity. In line with this idea, memory results from patients with adult-onset amnesia have suggested that the hippocampus is centrally involved in recollection whereas surrounding cortical regions in the temporal lobe support familiarity (Holdstock et al., 2002; Mayes et al., 2002; Yonelinas et al., 2002). On the other hand, evidence from a study of patients with bilateral damage limited primarily to the hippocampal region suggests that the hippocampus supports recollection and familiarity to a similar extent (Manns et al., 2003). Although familiarity and recollection are undoubtedly distinct memory experiences, the extent to which familiarity is supported by a subset of the same neural mechanisms that support recollection, or by distinct mechanisms, remains highly controversial.

Investigations of the neural basis of recollection and familiarity in healthy individuals can also provide evidence useful for understanding these two experiences and the relationship between them. Towards this end, brain imaging has been applied using the *remember/know* paradigm. After reading a set of words, participants categorize words in another set as either *old* or *new* and, for each old word, use the label *remember* if aspects of the earlier episode with that word are retrieved, or the label *know* in the absence of contextual retrieval (i.e., recollection and familiarity, respectively; Gardiner and Java, 1991; Tulving, 1985). Some neuroimaging results suggest that familiarity and recollection are mediated by different brain areas. Eldridge et al. (2000) observed hippocampal activation for *remember* judgments (relative to correctly rejected new items), but not for *know* responses. However, Henson et al. (1999) did not report comparable effects in the medial temporal region, but did find prefrontal activation patterns that differed for *remember* and *know* responses.

This remember/know paradigm has also been used while event-related potentials (ERPs) were recorded from the brain, but with somewhat inconsistent findings. Positive ERPs have been reported for both *remember* and *know* conditions, with a posterior scalp topography, and larger amplitudes in the former case (Smith, 1993). This pattern of results could reflect activation of the same brain networks during recollective experiences and during familiarity experiences, only differing quantitatively. This conclusion is also consistent with findings from a subsequent study in which the *remember/know* paradigm was applied to words studied in a sentence context (Trott et al., 1999). In both young and older adults, posterior ERP amplitudes were larger for *remember* than for *know* judgments. A topographic analysis showed no differences between potentials associated with the two types of judgments.

In sharp contrast, other research beginning with the work of Düzel et al. (1997) suggested that electrophysiological data implicate separate neural mechanisms for *remember* and *know* items. In particular, words engendering familiarity were associated with reduced frontal negativity at 300–500 ms, corresponding to a potential known as N400, and ERP results from several experiments have been used to support the same conclusion (Curran, 2000; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999; Tsivilis et al., 2001). Interestingly, reduced frontal negativity to repeated words, the putative N400-like signature of familiarity, was observed in a patient with childhood hippocampal damage thought to have a memory disorder with intact familiarity (Düzel et al., 2001). In contrast, later positive potentials associated with recollection were absent in this patient, leading the authors to conclude that the N400 effects reflect the experience of familiarity without recollection. This conclusion, however, is debatable.

Although these ERP findings may appear to be consistent with the hypothesis that distinct neural events are responsible for familiarity versus recollection, inferences concerning these two memory experiences depend on the validity of associations between (a) familiarity and reduced N400-like potentials and (b) recollection and enhanced positive potentials following N400. The second assumption has ample empirical support (for reviews, see Friedman and Johnson, 2000; Mecklinger, 2000; Paller, 2000; Rugg and Allan, 2000), but there are several reasons for calling the first assumption into question. In particular, the *remember/know* procedure with words may be problematic for elucidating the nature of pure familiarity. One concern is that subjects may not always be capable of accurately reporting on their introspective experiences of episodic retrieval. Also, when all items are known before the experiment, there is a high baseline familiarity against which *know* judgments are made. Putative neural correlates of *familiarity* in studies with words or namable pictures may actually be neural correlates of implicit memory (or more specifically, of verbally mediated conceptual priming, as proposed below). If N400 reductions with repetition reflect implicit memory, the electrophysiological data may not constitute valid evidence for separate neural mechanisms for recollection and familiarity after all.

For our investigation of recollection and familiarity, we developed a memory task using faces that participants had never previously viewed, thus minimizing subjects' pre-experimental knowledge of the to-be-remembered stimuli. Further, we obtained robust measures of the butcher-on-the-bus phenomenon by combining an objective measure of recollecting specific contextual details (face–occupation associations) with self-report concerning recollection, as shown in Fig. 1. It should be noted that the familiarity experiences produced in this paradigm reflect a single exposure to a face, and as such, these experiences may be different from familiarity experiences produced following a large number of exposures (e.g., when the butcher's face has been seen in the butcher's shop many times over months or years). However, one advantage of our use of single exposures in the study phase was that we were also able to include a powerful analysis of possible relationships between face encoding and subsequent memory. To determine whether encoding operations differed for recollection and familiarity, we incorporated the subsequent memory methodology (Paller and Wagner, 2002) by comparing responses recorded in the study phase as a function of later memory performance.

Several predictions can be made regarding neural activity that should accompany memory retrieval in the test phase of this paradigm. First, positive brain potentials maximal at posterior scalp locations can be anticipated to occur in association with face recollection, given that such potentials have repeatedly been observed in similar studies with facial stimuli (Paller et al., 1999, 2000, 2003b). In contrast, there are two opposing expectations with respect to familiarity. One prediction is that frontal N400 potentials should accompany face familiarity. Indeed, multiple groups of investigators have taken the position that amplitude reductions in frontal N400 potentials occur in conjunction with the memorial experience of familiarity (Curran, 2000; Düzel et al., 2001; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999; Tsivilis et al., 2001). In contrast, an alternative prediction
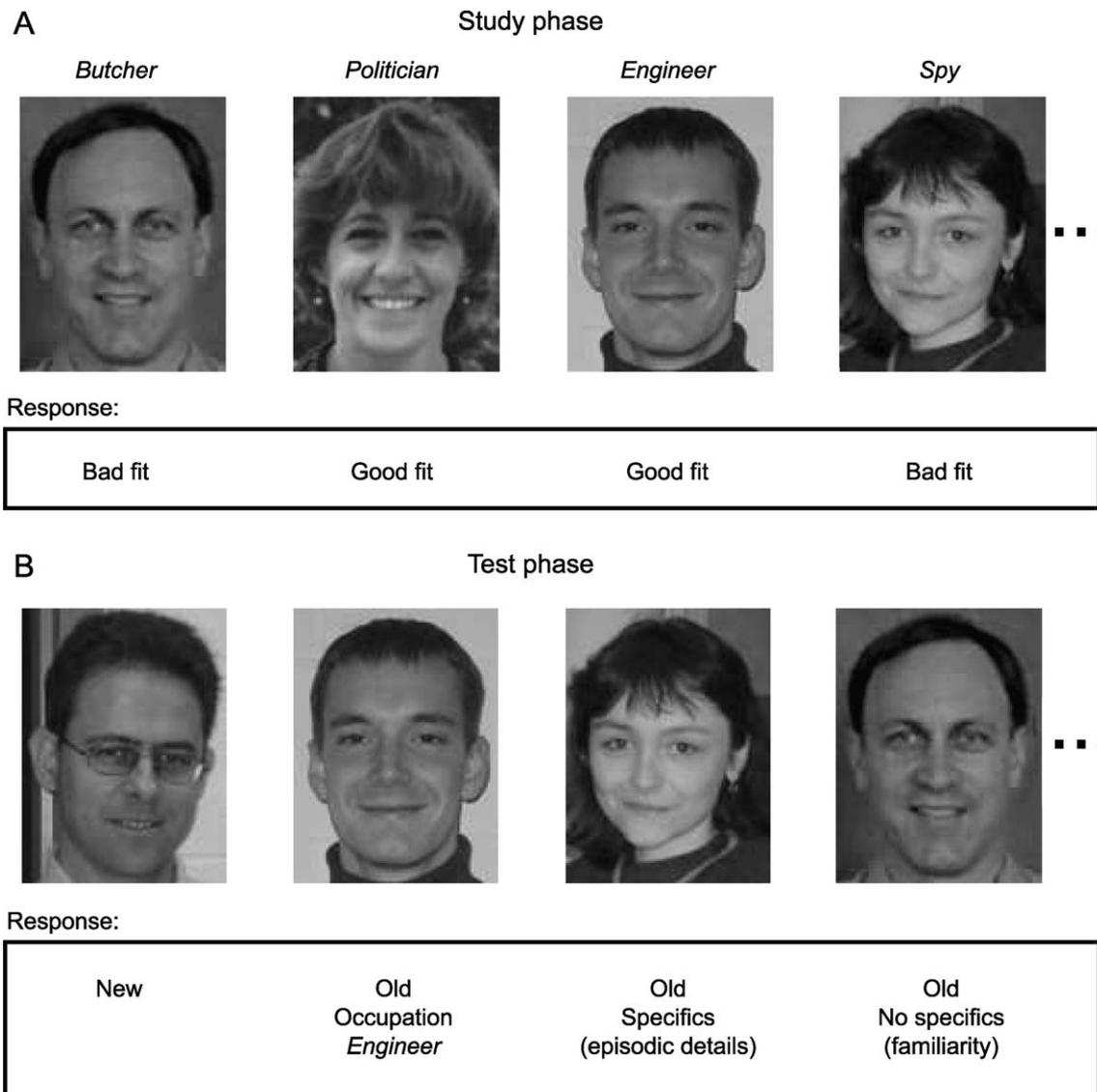
Fig. 1. Schematic representation of the memory paradigm. (A) In the study phase, participants viewed a series of faces, each paired with a unique spoken occupation. Participants were instructed to remember these face–occupation associations, and also to respond on each trial indicating whether the pairing was thought to be a good or bad fit. Pilot data showed that this procedure led to a high proportion of pure familiarity judgments. (B) In the test phase, faces were presented without occupations. The first response indicated whether the face was *old* or *new* (i.e., one from the study phase or not, respectively). A second response was made for faces endorsed as *old* to indicate whether (1) the occupation could be recalled, in which case the occupation was spoken as the third response; (2) only other specific details could be remembered from the study phase episode (such as an observation made about the expression or a noted resemblance to a friend); or (3) that no specific information from the study episode could be remembered (familiarity without recollection).

can be derived from the hypothesis that N400 reductions reflect conceptual priming elicited by verbalized material (Olichney et al., 2000)—by extension, N400 reductions would not be observed with novel faces, given the absence of systematic verbal processing and conceptual priming. To our knowledge, unequivocal neural correlates of familiarity with faces have not been reported previously.

Methods

Twelve right-handed individuals participated. They ranged in age from 18 to 27 years old, seven of them were men, and all were right-handed native English-speakers. Data were excluded from

four other individuals due to excessive eye-movement artifacts and from two others because of poor memory for occupations. All participants gave informed consent.

Participants viewed face stimuli on a monitor from a distance of 140 cm and listened to spoken occupations presented through speakers located above the monitor. Face stimuli were taken from monochromatic photographs and included minimal background information, with ordinary clothing somewhat visible near the neck, and generally neutral emotional expressions (Endl et al., 1998). Participants saw these faces for the first time during the experiment. Faces subtended 1.8° of visual angle horizontally. Occupations are listed in Appendix A and were spoken by a male voice. Behavioral and EEG data were acquired during 10 study-test blocks. In each block, participants studied 24 unique face–occu-
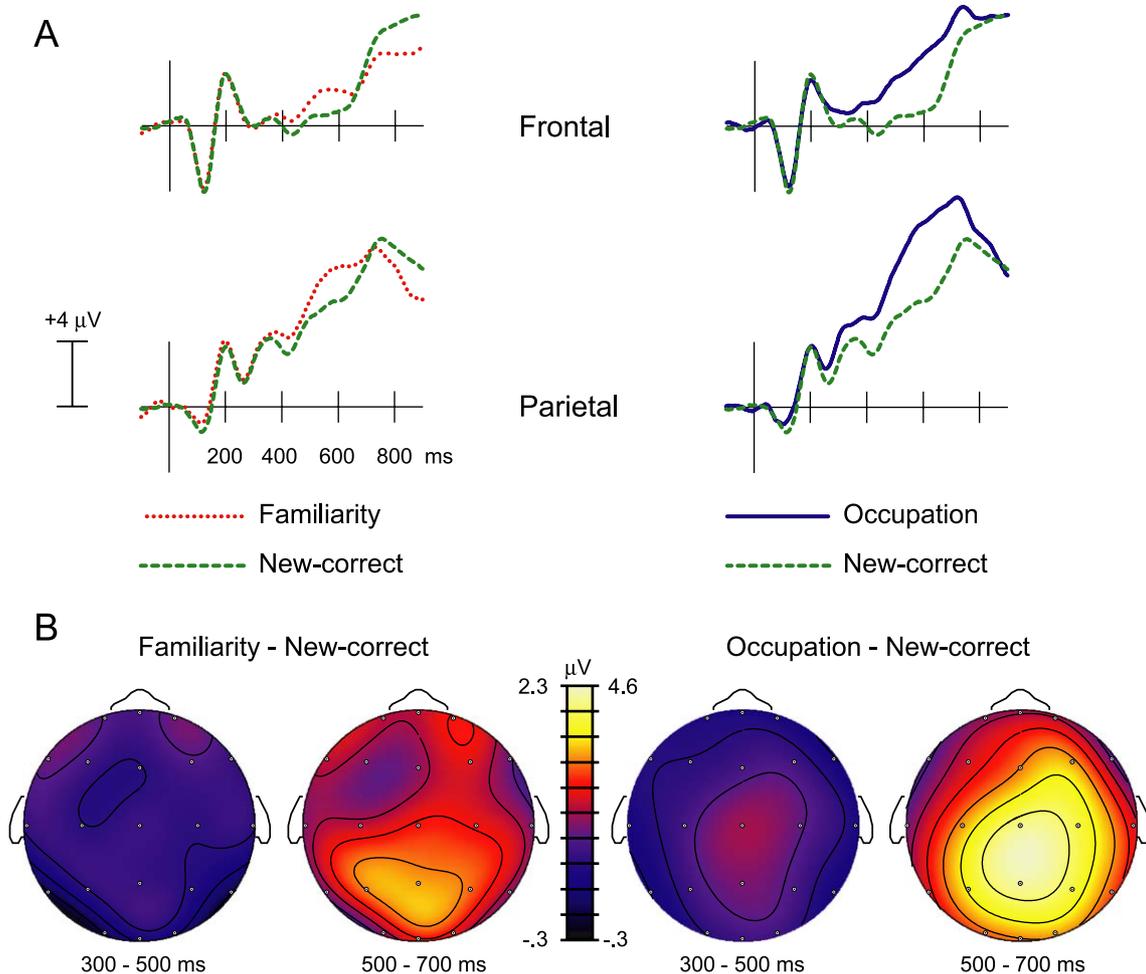
Fig. 2. Test-phase results. (A) ERPs from midline frontal and parietal locations for familiarity, occupation, and new-correct trials (based on an average number of trials per condition per participant of 66.6, 42.7, and 95.3, respectively). Familiarity trials included a positive shift from about 400 to 700 ms, followed by a negative shift, relative to new-correct trials. Occupation trials included a positive shift from about 250 to 850 ms, relative to new-correct trials. (B) Topographic maps (shown as if viewing the head from above) for the two experimental contrasts for two latency intervals. Different scales were used for the two different contrasts.

pation pairings and approximately 0.5 min later were tested with those 24 faces plus 12 new faces. Responses were registered using keys held in the right hand.

Fig. 1 shows the memory paradigm schematically. Each study trial included a 1-s gray fixation cross at eye level on a black background followed by a 2-s face presentation, with a spoken voice beginning simultaneously with face onset. Participants pressed one of two buttons on each trial according to whether they thought the face and occupation fit together or not. Participants were advised that there were no objectively correct or incorrect answers in this task. Participants were also told to try to remember the face–occupation associations for a subsequent memory test. Our pilot studies showed that requiring participants to judge face–occupation fit resulted in a larger proportion of familiarity responses compared to instructing participants only to remember the faces and occupations.

In the test phase, faces appeared without voices and participants pressed one of two buttons on each trial according to whether they thought the face had appeared in the study phase or not (i.e., *old* or *new*). Each test trial included 1.5-s fixation, 0.5-s face, fixation, and then response. If a *new* response was registered, the trial was terminated. If an *old* response was registered, the fixation cross was

replaced after a 600-ms delay with the three choices for the next response: *occupation*; *other specifics*; and *no specifics*. If an *occupation* response was registered, this signified that the associated occupation could be recalled, and it was then spoken aloud. Participants pressed a key to initiate the next trial after their final response was registered, unless that response was spoken, in which case the experimenter initiated the next trial after EEG artifacts had subsided. The average delay between presentation of a face in the study phase and its subsequent presentation in the test phase was 2.5 min.

Recollection was inferred on trials classified as occupation or specifics trials as follows. An *occupation trial* occurred when an old face was correctly endorsed as such, followed by an *occupation* response and correct recall of the occupation. A *specifics trial* occurred when an old face was correctly endorsed as such, followed by an *other specifics* response, which signified that the participant could not recall the associated occupation but could remember other details of the study-phase episode (examples include remembering that the prior face presentation provoked the thought that the person resembled a friend, had a strange hairstyle, looked extremely young, or did not fit with the occupation). A *familiarity trial* occurred when
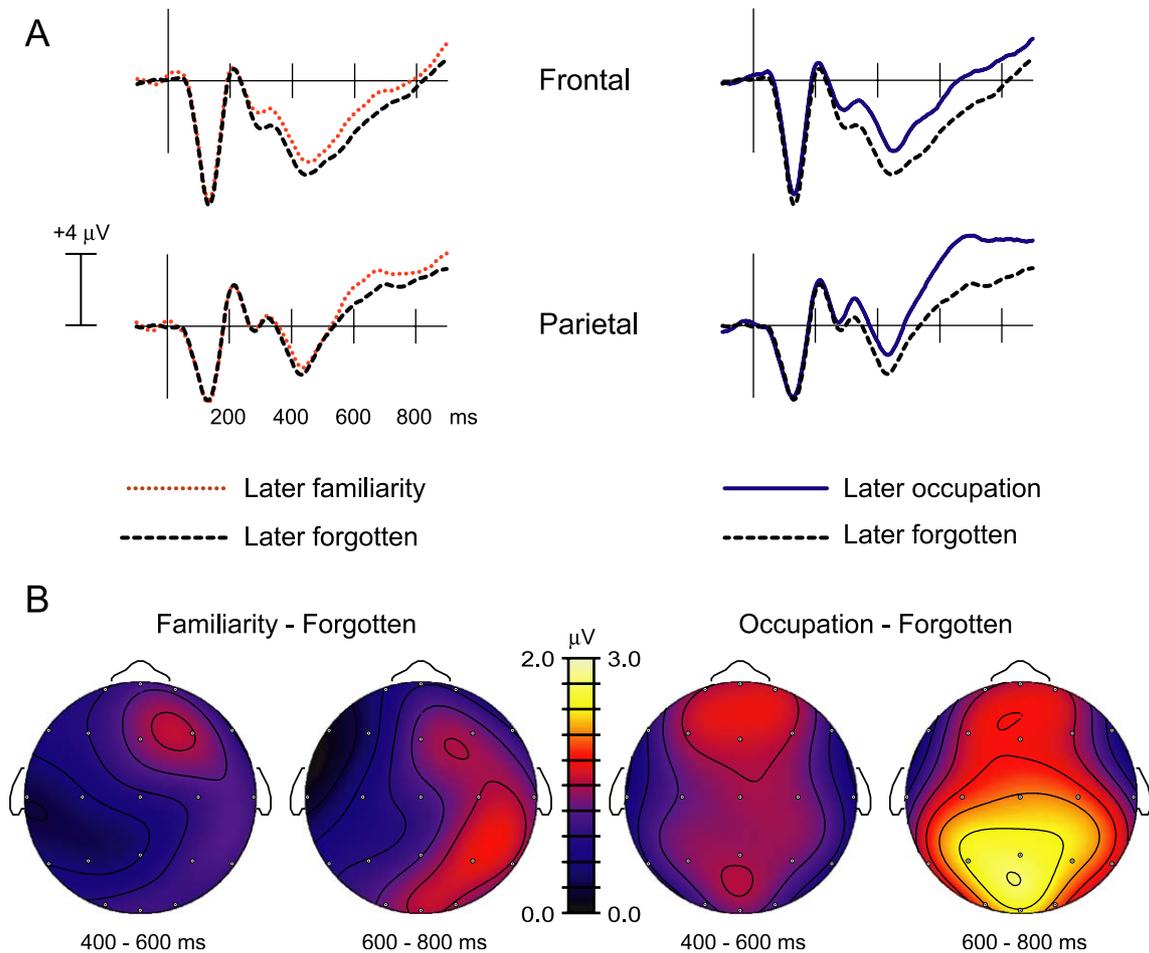
Fig. 3. Study-phase results. (A) ERPs from midline frontal and parietal locations for later-familiarity, later-occupation, and later-forgotten trials. Later-familiarity trials included a small positive shift, largest over the right parietal region from about 600 to 800 ms, relative to later-forgotten trials. Later-occupation trials included a positive shift beginning at about 300 ms and continuing to the end of the epoch, relative to later-forgotten trials. (B) Topographic maps for the two experimental contrasts for two latency intervals. Different scales were used for the two different contrasts.

an old face was correctly endorsed as such but with no recollection of the associated occupation or any other episodic details, indicated by a *no specifics* response. *Correct-new trials* occurred when a new face was correctly endorsed as such. *Miss trials* occurred when an old face was incorrectly endorsed as a new face.

ERPs were recorded from 21 scalp locations using methods described previously (Paller et al., 1999, 2000). The EEG band-pass was 0.1–100 Hz, sampling rate 250 Hz, trials with electro-oculographic artifacts were excluded, and an average-mastoid reference was used for analyses, with the Geisser–Greenhouse correction when necessary.

Results

Behavior

Recognition responses averaged 65.3% correct for old faces (range 46–84%), with 12.2% false alarms for new faces (2–46%). For recognized old faces, the associated occupation was recalled for 29.4% (17–39%), only other specifics were remembered for 24.0% (5–57%), and a pure familiarity trial was designated for 46.5% (17–76%). When an occupation was produced, it was

correct 88.2% of the time (62–100%). The mean reaction time for old faces in the test phase was 1277 ms and did not differ reliably as a function of whether the trial was sorted as occupation, specifics, familiarity, or miss. ERP responses described below were thus uncontaminated by potentials elicited after the behavioral response when choices for the second behavioral response were presented on the monitor.

Event-related potentials

Test phase

Midline. Fig. 2A shows that ERP responses were more positive for familiarity than for correct-new trials from about 400–700 ms, followed by a reversal,[2] and more positive for occupation than for

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[2] Why responses became more positive to new faces than to old faces provoking familiarity after 700 ms is unclear, but a reasonable explanation is that memory storage occurs for new faces in the recognition test (e.g., see Buckner et al., 2001). Both episodic retrieval and episodic encoding are associated with positive potentials. The amplitude of encoding-related potentials may be greater for new faces than for old faces and late in the epoch these potentials may begin to overwhelm retrieval-related potentials that are larger for old faces than for new faces.

Table 1
Mean ERP amplitudes from midline electrode locations (in microvolts with standard errors of the mean in parentheses) for test-phase conditions (A and B) and study-phase conditions (C and D), including data from the subset of participants with a sufficient number of trials in the Specifics condition (B and D)

Latency range (ms)	Condition			
	New-correct	Familiarity	Specifics	Occupation
A	N = 12			
300–500	2.1 (1.0)	2.6 (0.9)		3.7 (1.0)
500–700	3.9 (0.9)	5.1 (0.9)		7.3 (1.2)
B	N = 8			
300–500	1.6 (1.3)	2.1 (1.0)	3.2 (1.1)	3.1 (1.3)
500–700	3.3 (1.2)	4.6 (1.2)	6.0 (1.2)	6.5 (1.7)
	Later forgotten	Later familiarity	Later specifics	Later occupation
C	N = 12			
400–600	− 2.1 (0.9)	− 1.4 (0.9)		− 0.6 (0.9)
600–800	0.5 (0.8)	1.3 (0.8)		2.6 (0.9)
D	N = 8			
400–600	− 2.2 (1.0)	− 1.6 (1.1)	− 1.0 (1.0)	− 0.3 (1.1)
600–800	0.6 (0.9)	1.4 (1.1)	2.2 (1.3)	3.1 (1.1)

correct-new trials from about 250 to 850 ms. Our analyses emphasized the positive ERP differences before 700 ms. The enhanced positivity for remembered faces in both comparisons was formally analyzed over two intervals, 300–500 and 500–700 ms, and corresponding measurements are shown in Table 1A. In the interval from 300–500 ms, occupation responses diverged from new responses but familiarity responses did not [repeated-measures ANOVA with factors Condition (new/familiarity/occupation) and Location (Fpz/Fz/Cz/Pz/Oz), Condition main effect $F(2,22) = 11.81$, $P < 0.0001$, with occupation/new t tests at each midline electrode $P < 0.01$]. In the latter interval (500–700 ms), in contrast, three-way differences were apparent, with ERPs most positive for occupation, intermediate for familiarity, and least positive for new [$F(2,22) = 30.86$, $P < 0.0001$; Condition × Location interaction $F(2.88,88) = 4.80$, $P < 0.01$, with significant pairwise differences at all locations for occupation/new, P's < 0.005; at all locations except Fpz and Fz for familiarity/new, P's < 0.01; and at all locations except Fpz for occupation/familiarity, P's < 0.005; for distributional comparisons, see results with normalized data below]. To further substantiate the finding that familiarity/new differences were apparent only in the later interval, we conducted a three-way ANOVA with factors Interval (300–500/500–700 ms), Condition (familiarity/new-correct), and Location (Fpz/Fz/Cz/Pz/Oz). There was a significant Interval × Condition interaction [$F(1,11) = 8.18$, $P = 0.016$], due to significant differences between the familiarity and new-correct conditions for the late interval [$F(1,11) = 14.79$, $P = 0.003$] but not the early interval [$F(1,11) = 3.46$, $P = 0.36$].[3]

Lateral. The same patterns observed at midline locations were also observed over the left and right hemisphere, as shown in Fig.

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[3] Although not central to the present analysis, inspection of ERPs to recognition misses showed that they closely resembled ERPs to correctly rejected new faces.

2B. Measurements from the eight lateral electrode pairs were submitted to ANOVAs with Hemisphere as a factor, and no reliable hemispheric effects were observed, suggesting a similar pattern of response in the two hemispheres.

Specifics. Eight participants reported remembering specific episodic information other than the occupation on at least 20 trials. Their ERPs for specifics trials were compared to their ERPs for occupation and familiarity trials (Table 1B). At midline locations from 300 to 500 ms, specifics and occupation ERPs did not differ except at Fpz ($P < 0.05$), where mean amplitudes were larger for specifics [Condition × Location interaction $F(8,56) = 3.92$, $P < 0.001$]. Specifics ERPs were larger than familiarity ERPs at Fpz, Fz, and Cz ($P < 0.05$). At midline locations from 500 to 700 ms, specifics ERPs did not differ from occupation ERPs and were marginally larger than familiarity ERPs at Fpz, Fz, and Cz [$P < 0.1$, Condition × Location interaction $F(8,56) = 2.49$, $P < 0.05$].

Topography. The above results show that recollection, as indexed by successful recall of the appropriate occupation, or of specific episodic details, was associated with a different neural response than that elicited on familiarity trials. The most obvious way responses differed was in the much larger positive amplitudes for recollection than for familiarity. Given that both recollection and familiarity engendered potentials significantly more positive at 500–700 ms relative to correct-new trials, it is important to determine if the distribution of effects across the scalp was similar or dissimilar. Indeed, the maximum of the familiarity effect appears more posterior than that of the recollection effect (Fig. 2B), but when amplitude differences were taken into account, this trend was found to be unreliable. Mean amplitude measurements at each location at 500–700 ms were normalized using a standard procedure (McCarthy and Wood, 1985), yielding a nonsignificant interaction between Location and Condition [$F(2.82,220) = 1.19$, $P = 0.33$]. Similarly, there were no significant topographic differences for the 300–500 ms interval [$F(1.89,220) = 1.26$, $P = 0.30$].

Study Phase

Fig. 3A shows that ERPs to face/occupation pairings during the study phase differed as a function of later memory performance during the test phase. Starting at about 400 ms after stimulus onset, later-forgotten faces elicited the lowest amplitudes, faces that later cued occupation recall elicited the highest amplitudes, and faces that were purely familiar during the test phase elicited intermediate amplitudes. Corresponding measurements are shown in Table 1C.

Midline. At 400–600 ms, ERP amplitudes were significantly higher for later-occupation trials than for later-forgotten trials [$F(1,11) = 9.90$, $P < 0.01$]. This ERP difference can be termed a *recollection Dm* (ERP *D*ifference based on later *m*emory performance; Paller et al., 1987). At 600–800 ms, ERPs to faces for which the occupation was later recalled were significantly higher in amplitude compared to those that were later-familiar [$F(1,11) = 9.04$, $P < 0.05$] or later-forgotten [$F(1,11) = 17.03$, $P < 0.005$]. The ERP difference between later-familiar and later-forgotten trials (or *familiarity Dm*) was not significant at 400–600 ms [$F(1,11) = 2.03$, $P = 0.18$] but was marginal at 600–800 ms [$F(1,11) = 3.34$, $P = 0.1$].

Lateral. As shown in Fig. 3B, Dm for familiarity was not bilaterally symmetric, as indicated by a marginal Condition (occupation/familiarity/forgotten) by Hemisphere interaction at 600–800 ms [$F(2,22) = 3.31$, $P = 0.055$]. An ANOVA for left-hemisphere data showed that ERPs did not differ for later-familiar versus later-forgotten trials [$F(1,11) = 1.66$, $P = 0.22$]. In contrast, this difference approached significance over right-hemisphere locations [$F(1,11) = 4.09$, $P = 0.07$], and measured 1.2 μV at P4 and 1.0 μV at C4 and at T6. Later-occupation ERPs from 600 to 800 ms were significantly more positive than later-forgotten ERPs, and than later-familiar ERPs, over both hemispheres, with no laterality effects. The laterality of Dm for familiarity but not Dm for recollection was further substantiated by a two-way interaction of Condition × Hemisphere [normalized mean difference amplitudes at lateral locations from 600 to 800 ms, $F(1,11) = 5.29$, $P < 0.05$].

Specifics. A further analysis was performed for the eight participants who remembered episodic specifics on more than 20 trials. At 400–600 ms for midline locations, later-specifics ERPs were larger than later-forgotten ERPs [$F(1,7) = 15.24$, $P < 0.01$], except at Fpz [interaction $F(4,28) = 16.22$, $P < 0.0001$]. Differences between later-specifics and later-familiar or later-occupation trials were nonsignificant. A similar pattern was found at 600–800 ms; later-specifics ERPs differed significantly from later-forgotten ERPs [$F(1,7) = 11.33$, $P < 0.05$] at Cz, Pz, and Oz ($P < 0.05$) but not frontally [interaction $F(2.04,28) = 4.76$, $P < 0.05$], and did not differ from later-familiar or later-occupation ERPs.

Discussion

Distinct recollection and familiarity experiences were reliably produced in our experiment and were systematically associated with enhanced positive brain potentials. This positivity was apparent with larger amplitudes and for a longer time interval with recollection, though topographic patterns of scalp electrical activity were otherwise similar in the two conditions. These results are inconsistent with prior speculations that familiarity per se has a unique signature of brain electrical activity in the form of reduced frontal N400 potentials. Furthermore, as discussed in the next section, our results suggest that familiarity[4] may be a consequence of neural activity in some of the same networks activated during recollection, but with a greatly reduced magnitude.

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[4] It would be problematic if a majority of the familiarity trials resulted from pure guessing rather than familiarity in the absence of recollection. Indeed, some correct responses in each of the experimental conditions may have been due to guessing. The low false alarm rate for new faces (12.2%), however, suggests that only a small percentage of old faces elicited *old* responses due solely to guessing in the absence of veridical memory. With the conservative assumption that these correct guesses were all classified as familiarity trials, 43% of the familiarity trials would have been due to correct guesses. In addition, brain potentials were clearly not the same for familiarity trials versus new-correct trials (nor for later-familiar versus later-forgotten trials in the study phase), as would be expected if familiarity trials resulted from pure guessing. Thus, familiarity trials were not merely an artifact of guessing. Possibly, the influence of guessing on ERP for familiarity trials was negligible. Even some contamination from guessing does not restrict our interpretations of ERP observations from the test phase. We therefore attribute familiarity/new ERP differences in the test phase to memory for facial information that supported correct recognition decisions in the absence of recollection.

The neural basis of recollection and familiarity

Recollection experiences generally include a sense of familiarity plus additional episodic retrieval. This view of a redundant relationship between recollection and familiarity is consistent with neuropsychological evidence (Knowlton, 1998), and it is also supported by our electrophysiological results. Familiarity experiences provoked by faces were associated with positive potentials from 400 to 700 ms. Conceivably, the same positivity was also elicited by recollected faces, superimposed upon additional positivity associated with a high level of familiarity and extensive contextual retrieval that supported recollection. Further research using neuroimaging techniques that provide higher spatial resolution, such as ERP recordings from intracranial electrodes and functional magnetic resonance imaging (fMRI) of blood-oxygenation-level-dependent signals, may bear out this hypothesis. Although we have emphasized the possibility that the same neural processes were engaged during face familiarity and face recollection, it is also possible that familiarity and recollection were mediated by adjacent medial temporal regions with different functional roles (Brown and Aggleton, 2001). Relevant medial temporal activity may not have produced different scalp ERPs in our study due to the orientation and location of current generators (see McCarthy et al., 1987; Paller and McCarthy, 2002), but evaluating this possibility requires further experimentation.

A reasonable interpretation of the additional positivity elicited by recollected faces, which emerged about 300 ms after face onset, is that it reflects the retrieval of information associated with those faces and the consequent experience of recollection. Recalling the corresponding occupation or other specific contextual details, our two ways of operationalizing recollective experience, produced largely identical brain potentials at all scalp locations except the most anterior ones. Prefrontal activity engaged in association with recollection may have been partially responsible for the substantial positive potentials elicited during both occupation and other specifics trials. Our ERP results did not strongly implicate prefrontal activity in this regard, but the idea that prefrontal activity reflects processing pivotal for the experience of recollection is supported by neuroimaging data (Eldridge et al., 2000; Henson et al., 1999) as well as by findings from patients with memory disorders (Wheeler et al., 1997).

Whereas our findings are in agreement with the idea that recollective experience is associated with widespread, parietal-maximum positivity, they cast serious doubt on the position that familiarity can be indexed generically by frontal N400-like potentials, a hypothesis endorsed by many investigators (Curran, 2000; Düzel et al., 1997, 2001; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999; Tsivilis et al., 2001). This hypothesis predicts that familiarity experiences would be accompanied by reductions in N400-like potentials, whether produced by verbal or nonverbal stimuli. As pointed out above, there are some drawbacks in relying on the *remember/know* paradigm with common words, as widely used in investigations of recollection and familiarity (Düzel et al., 1997; Eldridge et al., 2000; Friedman and Trott, 2000; Henson et al., 1999; Smith, 1993). Words are associated with an abundance of information from pre-experimental episodes, thus clouding the experience of pure familiarity. There are at least two ways in which a high baseline for *know* judgments could produce misleading data. First, weak episodic memories from pre-experimental experiences with study words could erroneously be attributed to study-phase familiarity. Second, some words could be

appropriately classified in the familiarity category, but, in addition, elicit valid recollection of a pre-experimental episode with that word, thus contaminating the brain signals in the familiarity condition. Another worry about the *remember/know* procedure is that it depends critically on participants' understanding of the two types of memory and their ability to access and report on these experiences. Here we avoided these limitations through a novel paradigm for eliciting recollective and familiarity experiences, using to-be-remembered faces never viewed before the experiment, and including an objective categorization of memory experiences corresponding to recollection and pure familiarity.

Moreover, we propose that N400 effects in prior memory studies with words or other stimuli that can consistently provoke subjects to produce a verbal label do not reflect pure familiarity (Curran, 2000; Düzel et al., 1997, 2001; Mecklinger, 2000; Rugg et al., 1998; Tendolkar et al., 1999; Tsivilis et al., 2001), but rather reflect processes specific to verbal information processing. This proposal must be considered tentative, of course, as it may be the case that familiarity with words and familiarity with faces simply rely on different cortical regions but reflect analogous processes. Further investigation is required to test our proposal that N400 effects in memory studies do not implicate familiarity. Yet, important additional support for our proposal comes from the observation of intact N400 reductions with word repetition in patients with amnesia (Olichney et al., 2000). On the basis of the premise that familiarity is generally impaired in amnesia, Olichney et al. attributed these preserved N400 effects to intact conceptual priming. Although identical words were repeated, perceptual priming was not invoked because N400 can generally be influenced by semantic priming, and because posterior potentials at the same latency have been associated specifically with perceptual priming of visual word form (Paller and Gross, 1998; Paller et al., 1998). Conceptual priming can be preserved in amnesia (e.g., Keane et al., 1997; Levy et al., in press) and we postulate that it can help support the high competence amnesic patients display in language comprehension. N400 reductions may reflect a contribution of implicit memory to language comprehension in general.[5]

By this scenario, N400-like reductions might not be predicted when familiarity is studied with nonverbal stimuli. We are aware of only three relevant ERP studies with nonverbal stimuli. In one study, repeated pictorial stimuli presented in the absence of their old context—somewhat analogous to the butcher-on-the-bus experience—did not elicit reduced negativity during the N400 interval (Tsivilis et al., 2001). Reduced N400s were in fact elicited by recollected pictures presented in their old context, but it is difficult to rule out the possibility that N400s reflected subvocal naming of picture–context combinations. In another study, pictures of namable objects appeared at test either in an identical format or left–right reversed (Curran and Cleary, 2003). In addition to the problem that subjects probably named stimuli subvocally, the finding that N400 amplitudes were only increased for new items is entirely consistent with our interpretation that there is less conceptual priming for new items than for all other conditions. This alternative interpretation also applies to parallel findings with verbal stimuli (Curran, 2000). Third, Penney et al. (2001) reported that repeated possible and impossible objects elicited less negative frontal potentials. This

effect is not subject to the criticism that objects were named subvocally, although it is curious that it did not differ between possible and impossible objects, given probable differences in familiarity. The authors invoked the idea of facilitated access to conceptual, semantic, and visuo-spatial representations, but the fact that repetition occurred without any significant retention delay leaves open the possibility that the ERP effects reflect operations specific to working memory rather than episodic recognition.

Even though face stimuli can elicit N400s (e.g., Münte et al., 1998), we found no association between familiarity and N400s in the present study. Likewise, in an experiment in which correct recognition in the absence of accurate source retrieval was taken to signal pure familiarity, an independent ERP correlate of familiarity was also not observed (Wilding and Rugg, 1996). We suggest that prior claims that N400 reductions constituted electrophysiological correlates of the general experience of familiarity should be called into question, and that such findings may reflect verbally mediated conceptual priming effects, *not* familiarity.

An intuitively appealing conception of familiarity experiences is that they are supported by the same sort of nonconscious processes that support priming in implicit memory tests (e.g., fluent perception). However, evidence from patients with amnesia due to medial temporal damage suggests that this is not the case (Knowlton and Squire, 1995), given that these patients exhibit normal priming but are impaired both in recollection and in familiarity. Particularly striking findings were obtained from severely amnesic patients who exhibited preserved priming while recognition and measures of familiarity were at chance levels (Levy et al., in press; Stark and Squire, 2000). On the other hand, there are circumstances when familiarity in amnesia appears to be based partly on fluency (Verfaellie and Cermak, 1999; Verfaellie et al., 2001), and so the possibility that familiarity in healthy individuals might be based on fluency in some circumstances remains viable. Interestingly, ERPs associated with perceptual priming for faces in recent experiments from our lab (Paller et al., 2003a) bore no resemblance to those associated with face familiarity in the present study, contrary to what one might predict if familiarity were derived from perceptual priming. A reasonable conclusion is thus that perceptual priming and familiarity constitute distinct types of memory. Possible connections between conceptual priming and familiarity remain a prime topic for further investigation.

Finally, we note that familiarity has sometimes been associated with the concept of *semantic memory*, given that general knowledge is commonly expressed without any reference to learning episodes. However, our consideration of familiarity clearly pertains to episodic memory, given that explicit reference is made to prior autobiographical episodes when faces were viewed, as in the prototypical butcher-on-the-bus experience.

Differential neural correlates of encoding for familiarity and recollection

Brain activity associated with the formation of episodic memories has been observed repeatedly using both ERP and fMRI methods (Paller and Wagner, 2002). In particular, several sorts of neural responses during encoding are stronger for later-remembered than later-forgotten items. Here we found that ERP responses to face/occupation pairs were reliably larger in amplitude at 400–800 ms for later-recollection trials, such as when the face successfully cued the retrieval of the correct occupation. Responses were

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[5] Notably, N400 reductions in the verbal paradigm used by Trott et al. (1999) were not interpreted as correlates of explicit familiarity, consistent with our hypothesized association between these potentials and conceptual priming.

also larger for later-recollection than for later-familiarity trials. Significant hemispheric differences between later-familiarity and later-forgotten trials, with amplitude differences present only over the right hemisphere, most likely reflect encoding of the facial information per se without effective encoding of the whole multidimensional episode.

With verbal materials, subsequent memory (Dm) effects associated with recollection and familiarity have been somewhat inconsistent. ERP results from Smith (1993) reported comparable Dm effects for later-*remember* responses and later-*know* responses, whereas Friedman and Trott (2000) found significant Dm effects only for later-*remember* responses. Data acquired from elderly individuals showed a similar Dm for *remember* and *know* responses, and Dm amplitudes were larger over the left hemisphere in the young group but not in the elderly group (Friedman and Trott, 2000). In an experiment with pictures of objects, left-lateralized positivity was associated with later familiarity, whereas right-lateralized positivity was associated with later recollection (Duarte et al., in press). Lateralized Dm effects have also been observed with fMRI. Henson et al. (1999) found that activity in left inferior and middle frontal gyrus and left precuneus was greater for words later provoking a *remember* response than for words later provoking a *know* response (although activity could not be measured for words later forgotten due to an insufficient number of trials). Ranganath et al. (in press) found that activity in rhinal cortex selectively predicted familiarity-based recognition, whereas activity in the hippocampus and posterior parahippocampal cortex selectively predicted recollection. In an experiment with pictorial material, fMRI responses in right prefrontal cortex and in bilateral parahippocampal cortex predicted subsequent memory for indoor and outdoor scenes, with stronger effects associated with later recollection than with later familiarity (Brewer et al., 1998). With regard to the laterality of these findings, Golby et al. (2001) suggested that lateralized medial temporal and prefrontal activations at encoding vary systematically with stimulus verbalizability. These investigators found that encoding activations were approximately symmetrical for faces and scenes, but they argued that verbal mediation for such stimuli depends on subjects' processing strategies, task requirements, and time pressure.

Our findings suggest that the neural events that support facial encoding not only presage the probability of later retrieval success, but also influence the nature of the remembering experience with respect to whether recollection or pure familiarity occurs. Successful encoding of a face–occupation association, or of the episode in general, may rely on multidimensional associations formed across multiple cortical regions. This sort of encoding was conceivably reflected by the broad topography of the face recollection Dm (Fig. 3B). Encoding that subsequently gave rise to pure familiarity, on the other hand, may have engaged processing in restricted cortical regions, corresponding to the focal right posterior topography of the face familiarity Dm.

Implications

To summarize, with a novel memory task we obtained a valid classification of familiarity and recollection experiences provoked by pre-experimentally unfamiliar faces. Neural responses associated with familiarity were of reduced magnitude and shorter duration than those associated with recollection, probably reflecting the absence of contextual retrieval during familiarity. Despite these quantitative differences, electrophysiological correlates of recollection and familiarity appeared qualitatively similar. These findings suggest that familiarity with faces may arise by virtue of a subset of the neural processing responsible for recollection.

Our ERP findings reflect the activity of a subset of neurons with spatial orientation and temporal synchrony suitable for generating potentials observable at the scalp (Münte et al., 2000), and not necessarily all neural activity responsible for memory functions. In particular, relevant neural activity from medial temporal regions might not have been evident in scalp-recorded ERPs. It is likely that recollection and familiarity both depend on medial temporal processing. Moreover, some medial temporal regions such as the hippocampus may make a disproportionate contribution to recollection (Brown and Aggleton, 2001). Although details of functional parcellation within this region have yet to be determined decisively, it is reasonable to suppose that multiple medial temporal subregions are instrumental for retrieving stored information. Given likely stages of processing from neocortex, to perirhinal cortex and parahippocampal cortex, to subiculum, and to hippocampal subfields, the latter pathways may be most critical for the higher degrees of associative retrieval that are needed for contextual retrieval and recollection.

Are other parts of this circuitry especially critical for familiarity? Brown and Aggleton (2001) hypothesized that the novelty of a single item can provoke familiarity due to perirhinal activity. Another possibility is that perirhinal activity contributes to both familiarity and recollection. In fact, the fMRI findings of Eldridge et al. (2000), which showed hippocampal activation for *remember* but not *know* responses, also showed parahippocampal gyrus activation to both *remember* and *know* responses relative to correct rejections. Another possible familiarity signal has been noted across several fMRI studies in an anterior medial temporal region, where activation decreases were observed for repeated items (Henson et al., 2003). Determining whether some neural mechanisms selectively contribute to familiarity will require further empirical attempts to dissociate the relevant neurocognitive processes.

Intriguingly, right-sided neural activity at encoding was predictive of subsequent experiences of pure familiarity. Indeed, recollection and familiarity must have been driven in part by differential encoding. Some time later, at retrieval, neural activity associated with face familiarity was bilateral, possibly reflecting memory storage dependent on some representational collaboration between the two hemispheres. Further work is needed to build a better understanding of how faces are remembered and associated with biographical information to support person recognition. Neuro-imaging holds promise for contributing new insights into these phenomena, particularly if recollection and familiarity are taken into account.[6]

Our results further suggest that a heavy reliance on verbal paradigms in this research should be avoided. Verbal paradigms have led to apparent associations between N400-like ERP measures and familiarity that can be disputed, as discussed above. A better understanding of *pure familiarity* may be more readily

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[6] A large number of neuroimaging studies have fruitfully investigated memory for faces to date (e.g., Bernstein et al., 2002; Campanella et al., 2001; Dubois et al., 1999; George et al., 1999; Gorno Tempini et al., 1998; Haxby et al., 1996; Herholz et al., 2001; Kapur et al., 1995; Leveroni et al., 2000; Paller et al., 2003b; Phillips et al., 1998; Rossion et al., 2001; Shah et al., 2001; Sperling et al., 2001; Wiser et al., 2000). However, this research has not included separate assessments for face recollection versus face familiarity.

obtained using paradigms that do not rely on memory for over-learned material such as lists of words or for readily namable pictures. Important advances in understanding pure familiarity—including how it differs from the full-blown recollection that can make us feel as if we are reliving the past, and the extent to which familiarity and recollection share neural substrates—may result from simulating everyday memorial experiences like the butcher-on-the-bus phenomenon.

Appendix A. Spoken occupations from the study phase

accountant	composer	internist	pirate	taxidermist
acrobat	computer programmer	janitor	playwright	teacher
actor	cook	jazz musician	plumber	telemarketer
actuary	cosmetologist	judge	podiatrist	telephone repair technician
administrator	counselor	kindergarten teacher	pole-vaulter	thief
advertising agent	curator	lab technician	police officer	tobboganist
aerobics instructor	custodian	lawyer	politician	tombstone maker
airline pilot	dancer	lecturer	pool cleaner	tour operator
alchemist	dentist	legal assistant	preacher	train conductor
ambulance driver	detective	librarian	prison guard	translator
anesthetist	diamond cutter	life guard	private investigator	trash collector
animal trainer	dietician	linguist	prosecutor	travel agent
archaeologist	diplomat	locksmith	rabbi	tree surgeon
architect	dish-washer	long-distance runner	race car driver	trombonist
astronomer	district attorney	lumberjack	radio newscaster	truck driver
athlete	doctor	magazine publisher	radiologist	TV camera operator
auctioneer	draftsman	magician	rancher	TV show producer
audiologist	drug dealer	mail carrier	rental car agent	typist
author	drummer	mathematician	repair person	union leader
baby-sitter	economist	meat packer	reporter	upholsterer
bail bondsman	electrical engineer	mechanic	research assistant	urban planner
baker	embalmer	meditation instructor	restaurant owner	used car salesperson
bailiff	engraver	messenger	roadie	veterinarian
ballet dancer	exporter	meteorologist	rock star	violinist
bank teller	factory worker	milkman	roofer	waiter
barber	farmer	model	sailor	wall street investor
bartender	fashion designer	movie director	saxophonist	web designer
baseball player	film editor	nephrologist	sculptor	white collar criminal
bellhop	fire chief	news anchor	secretary	wine maker
bingo worker	fisher	newspaper editor	security officer	wrestler
blacksmith	flight attendant	nurse	set designer	writer
bodyguard	flutist	obstetrician	sewer	zoo keeper
building inspector	football referee	occupational therapist	ship builder	
bus driver	gardener	oceanographer	shoe seller	
butcher	gas-station attendant	office receptionist	shoe maker	
cabinet maker	geographer	opera singer	shopkeeper	
cardiologist	geologist	operator	short-order cook	
carpenter	ghostbuster	optometrist	soccer player	
cartographer	goldsmith	orchestra conductor	social worker	
chemist	golfer	orderly	soldier	
chief-of-state	groundskeeper	organist	speech pathologist	
chimney sweep	harpist	painter	speed skater	
chiropractor	helicopter pilot	paralegal	sports announcer	
circus performer	high school principal	parole officer	spy	
civil engineer	historian	patent clerk	stock broker	
clothing designer	hotel manager	personal trainer	store cashier	
coal miner	housekeeper	pharmacist	surgeon	
clown	hunter	philanthropist	swimmer	
club owner	ice cream vendor	philosopher	systems analyst	
coach	ice hockey player	photographer	tailor	
coal miner	importer	physicist	tax collector	
company executive	interior designer	pianist	taxi driver	

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