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Neural Manifestations of Memory with and without Awareness

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Summary

Neurophysiological events responsible for different types of human memory tend to occur concurrently and are therefore difficult to measure independently. To surmount this problem, we produced perceptual priming (indicated by speeded responses) in the absence of conscious remembering. At encoding, faces appeared briefly while subjects' attention was diverted to other stimuli. Faces appeared again in either an implicit or explicit memory test. Neural correlates of priming were identified as brain potentials beginning 270 ms after face onset with more negative amplitudes for repeated than for new faces. Remembered faces, in contrast, activated a different configuration of intracranial sources producing positive potentials maximal at 600–700 ms. We thus disentangled and characterized distinct neural events associated with memory with and without awareness.

Introduction

Neuropsychological studies of memory have shown that *recollection*, the subjective experience of remembering, often accompanies the recall and recognition of facts and events (also known as *declarative memory*), whereas other forms of memory are commonly observed in the absence of conscious remembering (Gabrieli, 1998; Mayes and Downes, 1997; Schacter et al., 1993; Squire and Schacter, 2002). People typically exhibit *conscious memory* when they recognize that a specific stimulus had been presented earlier, and *perceptual priming* when processing of that stimulus is otherwise altered in certain ways due to its prior presentation, sometimes with no recollection of that prior episode. Patients with amnesia may be poor at recollecting faces, but like people without a memory disorder, they respond faster during an implicit memory test to recently viewed faces than to new faces (Paller et al., 1992). This pattern of performance is known as *preserved priming in amnesia* (Schacter and Buckner, 1998; Shimamura, 1986), and it implies that priming and conscious memory represent distinct forms of memory with neural substrates that are at least partially independent.

The further juxtaposition of memory with and without awareness and of the associated neural events can provide insights not only into the biological basis of both types of memory but also into the factors that can make the contents of memory accessible to awareness. A suitable way to contrast neural signatures of the two types of memory is to record responses to comparable stimuli within the same experiment so that any differences observed cannot be ascribed merely to stimulus, task, or other nonspecific factors. However, when both types of memory are operative, the associated processes may occur simultaneously, thus posing problems for segregating the critical neurophysiological events.

Here we present observations of distinct neural correlates of remembering with and without awareness, made using within-experiment contrasts under comparable stimulus and task conditions. Our results confirm that these processes overlap in time. Yet, they were disentangled by virtue of three experimental conditions: face repetition with priming but negligible conscious memory, face repetition with both priming and recollection, and face processing with neither priming nor recollection. These last two conditions were produced using remembered faces and new faces, respectively. The more difficult accomplishment was to include a large set of faces for the unusual condition of priming without recollection.

A divided-attention paradigm was used for this purpose in Experiment 1. Faces referred to as *studied-brief faces* were shown at fixation simultaneously with a cross at an unpredictable parafoveal location (Figure 1A). A masking stimulus shown 105 ms later disrupted processing of the face and the cross. Subjects responded according to whether the cross had a slightly longer vertical or horizontal element. With this combination of brief presentations, masking, and difficult parafoveal discriminations, processing of studied-brief faces was limited. *Studied-long faces* were shown for 300 ms, with no mask, no cross, and the task of committing those faces to memory. Approximately 2 min after faces appeared in either the studied-brief or studied-long condition, they were shown again while memory was explicitly tested (Figure 1B). Neural responses to faces were obtained by extracting time-locked average responses from the electroencephalogram. These event-related potentials (ERPs) are thought to reflect neuronal activity primarily produced by spatially aligned cortical neurons activated synchronously (Münte et al., 2000).

We used a similar strategy in Experiment 2, but without the cross-discrimination task; attention to faces in the study phase was limited by presenting face stimuli in a rapid stream of studied-brief and studied-long faces with no intervening gaps. Due to masking by the subsequent face stimulus, brief face presentations of 300 ms could not be processed as effectively as long face presentations of 3600 ms. This design allowed us to show that the additional task requirements of the cross task were not critical for an association between negative potentials and face priming found in both experiments. Furthermore, implicit memory testing in Experiment 2 enabled us to verify that the studied-brief condition yielded priming without recollection. Results from the two experiments taken together thus demonstrated that qualitatively different brain potentials are systematically

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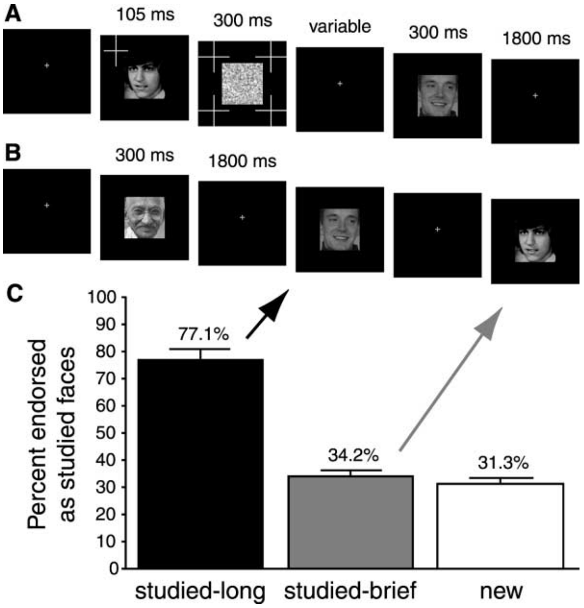

Figure 1. Excerpts of Stimulus Sequences Showing Timing Parameters and Recognition Results in Experiment 1

(A) Study phase. The primary task was a discrimination performed on a yellow cross (shown here in white) that appeared randomly in one of the four quadrants. No judgments were required on the simultaneous face stimuli (48 trials/run of 16 different studied-brief faces presented three times). So that subjects might not expect a face on every trial, the yellow cross was sometimes presented without a face (24 trials/run). Subjects were also instructed to remember faces presented without a simultaneous yellow cross (24 trials/run of eight different studied-long faces presented three times). Subjects were asked to maintain fixation on the central cross at eye level. Different trial types were presented in randomized sequences, with 8 study runs, each followed immediately by a test run. The faces of two coauthors are shown here for illustrative purposes and were not used in the experiment.

(B) Test phase. Each test run included 16 studied-brief and 8 studied-long faces from the prior study run, plus 16 new faces and 4 famous faces. Famous faces were included so that a control experiment (Experiment 1.3) could be conducted without changing stimulus sequences. Each studied face was shown four times in the experiment (three times in the study phase and once in the test phase). Each new face and each famous face was shown only once. Subjects indicated whether each face belonged to a famous person (famous), had been viewed in the prior study phase (studied), or had never been seen before (new).

(C) Recognition scores from the test phase in Experiment 1 for the three chief conditions (with error bars representing standard errors of the mean corrected for across-subject variance).

associated with memory with awareness (recollection) and memory without awareness (priming).

Results

Memory results from Experiment 1 showed that subjects were essentially unable to distinguish studied-brief faces from new faces (Figure 1C). Studied-brief faces tended to be endorsed only slightly more often than new faces [$t(15) = 2.03$, $p = 0.061$] and a bias-free measure of recognition sensitivity for studied-brief faces was at chance levels (d-prime = 0.08). Nearly all studied-brief faces endorsed as old were thus guesses. Any contribution to ERP averages from trials in which a studied-brief face was genuinely remembered was negligible because it was so heavily outweighed by the contribution from the overwhelming majority of trials wherein studied-brief faces were not remembered.

These interpretations were further substantiated by results from two companion experiments to Experiment 1 in which we collected more detailed memory performance measures without simultaneous ERP recordings but with otherwise nearly identical procedures. In Experiment 1.1 the experience of remembering for faces identified as studied faces was scored as either *remember*, which implies recall of aspects of the study episode, or *know*, which is based on familiarity alone (Knowlton, 1998; Tulving, 1985). The goal was to determine whether studied-brief faces would be recognizable if responses were based entirely on a sense of familiarity (i.e., a different criterion for registering recognition). However, *know* responses were not given any more often for studied-brief faces than for new faces [20.6% versus 19.2%, respectively, $t(11) = 0.47$], though *remember* responses were more common for studied-brief than for new faces [14.6% versus 9.3%, respectively, $t(11) = 3.76$, $p = 0.003$]. In contrast, recognition accuracy was higher for studied-long faces (24% *remember* responses and 26% *know* responses). In Experiment 1.2 we used two-alternative forced-choice recognition testing to obtain performance measures highly sensitive to low levels of memory and not subject to response bias. Recognition accuracy was 73.0% for studied-long faces, significantly better than the score of 56.3% correct for studied-brief faces [$t(11) = 5.93$, $p < 0.001$]. By this measure, recognition for studied-brief faces was significantly above chance [$t(11) = 3.67$, $p = 0.004$]. Even so, responses were likely to reflect purely guessing on 87.5% of the trials (see Experimental Procedures for formula to estimate guessing). We thus infer that explicit remembering was generally minimal for studied-brief faces, whereas studied-long faces were fairly well remembered.

Given that priming can occur in the absence of conscious remembering (e.g., Hamann and Squire, 1997), we sought to confirm that priming would be observed for studied-brief faces. Experiment 1, however, did not include valid implicit memory testing (reaction times were influenced by intentional retrieval attempts and did not differ significantly between conditions, averaging 921 ms). Accordingly, we measured priming in a behavioral companion experiment, Experiment 1.3. Contamination from recollection was limited by eliminating study-phase instructions to remember faces, providing no indications that memory was being tested, and requiring only famous/nonfamous discriminations in the test phase. Responses were 6 ms faster for studied nonfamous faces than for new nonfamous faces [$t(17) = 2.44$, $p = 0.026$], but not significantly different for studied-brief and studied-long faces [$t(17) = 0.84$]. Given this low magnitude of priming, a more robust measure of priming was sought in Experiment 2 to substantiate the claim that studied-brief faces were subject to priming, following a test procedure that we used previously to measure perceptual priming, with decision difficulty increased through the use of visually degraded faces (Paller et al., 1999).

Brain potentials elicited in the test phase of Experi-

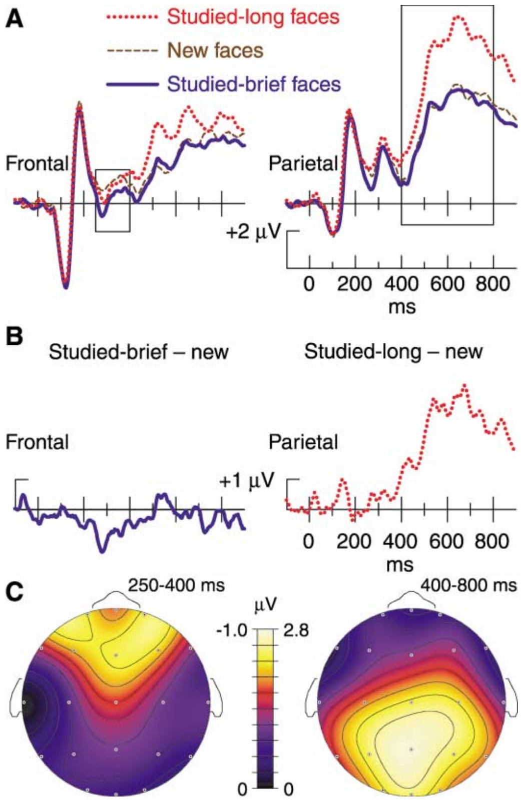

Figure 2. Brain Potentials from Test Phase of Experiment 1

(A) Potentials to the three types of nonfamous faces from midline frontal and parietal scalp locations show that a positive deflection was observed for studied-long faces, particularly from 400 to 800 ms after stimulus onset (large rectangle). In addition, a negative deflection was observed for studied-brief faces from 250 to 400 ms (small rectangle).

(B) Corresponding difference waves. Note that the two effects are of opposite polarity.

(C) Topographic representations of electrophysiological differences between pairs of conditions, studied-brief-minus-new (left) and studied-long-minus-new (right), over two latency ranges as labeled. Difference potentials between pairs of conditions were computed at each electrode location (small circles) and represented according to the color scale on a schematic view of the head from above, using a spline interpolation. The locations of maximal amplitude differences are shown in the lightest colors.

ment 1 (Figure 2A) were highly similar between conditions until about 250 ms after face onset (e.g., measurements of face-sensitive N170 potentials demonstrated no reliable difference across conditions). Subsequently, a differential response to studied-brief and new faces emerged at frontal locations. In an analysis of midline ERPs, mean amplitudes from 250 to 400 ms were significantly less positive for studied-brief faces than for new faces at frontal locations (Table 1). The frontal difference wave clearly shows the time course of this effect (Figure 2B). To determine approximate onset, measurements were made over consecutive 20 ms intervals from 200 to 300 ms. Consistent amplitude differences between conditions at the midline frontal location began at 260–280 ms [$t(15) = 2.93$, $p = 0.01$].

A very different electrophysiological response was elicited by studied-long faces (Figure 2A), which were remembered more accurately than studied-brief faces [$t(15) = 7.29$, $p < 0.001$; Figure 1C]. ERPs were more positive to studied-long than to new faces at all recording locations, and, in a midline analysis, differences from 400 to 800 ms were significant at frontal, central, parietal, and occipital locations (Table 1), with largest differences at parietal locations.

The contrasting topographies of these two ERP differences, the new-minus-studied-brief difference from 250 to 400 ms and the studied-long-minus-new difference from 400 to 800 ms, are shown in Figure 2C. The impression of a crossover difference between the anterior pattern and the posterior pattern was substantiated by submitting midline measurements to a standard topographic analysis [$F(4,60) = 3.48$, $p = 0.045$, with root-mean-square normalization and Geisser-Greenhouse correction]. Taking the time course of these two effects into account (Figure 3), different temporal and topographic patterns are both readily apparent. Studied-brief ERP differences were negative, reached largest amplitudes at 200–300 ms, and exhibited a frontal maximum. Studied-long ERP differences were positive, reached largest amplitudes at 600–700 ms, and exhibited a parietal maximum.

An additional analysis was conducted by categorizing the recognition judgment on each trial as fast or slow based on a median split of reaction time for each subject and condition. Larger ERP differences between studied-brief and new faces were found when only fast trials were considered (Figure 4). For example, midline frontal measurements at 250–400 ms showed that ERP differences between studied-brief versus new faces were 1.73μV larger for fast trials than for slow trials [$t(15) = 4.01$, $p = 0.001$]. Interestingly, the enhanced amplitude for fast trials seemed to be centered on a peak at about 350 ms (Figure 4B), with a right frontocentral topographic focus (Figure 4C).

At the midline parietal location, ERP amplitude differences between studied-long and new faces were comparable between fast and slow trials (2.4μV versus 2.7μV, respectively, at the midline parietal location, 400–800 ms). However, the onset of these differences was later for fast trials (Figure 4B) than for all trials (Figure 2B). Amplitude measurements were made over consecutive 40 ms intervals from 300 to 580 ms in order to assess these latency effects. Results of this analysis showed that differences first became consistently reliable at 500–540 ms with fast trials only [$t(15) = 3.05$, $p = 0.008$] but at 420–460 ms for all trials [$t(15) = 2.4$, $p = 0.03$]. The most parsimonious explanation for this influence of reaction time on studied-long-minus-new ERP onset latency and on studied-brief-minus-new ERP amplitude is that both effects reflect differences in ERPs to new faces. Mean ERP amplitudes to new faces from 250 to 400 ms were 1.3μV larger for fast trials than for slow trials [$t(15) = 4.7$, $p < 0.001$]. On fast trials, higher ERP amplitudes to new faces thus produced an effectively delayed onset latency for studied-long-minus-new ERP differences as well as greater studied-brief-minus-new ERP amplitudes. The quickest button-presses to new faces may have occurred for new faces that did not appear to match or even somewhat resemble any faces processed recently. The slowest button-presses may reflect trials in which the recognition decision was

Table 1. Brain Potential Differences at Midline Locations in Experiment 1

Location	Amplitude (μV)	SE	t(15)	p
ERPs to Studied-Brief Faces Minus ERPs to New Faces, 250–400 ms				
Anterior frontal	−0.65	0.31	2.12	0.051
Frontal	−0.83	0.35	2.35	0.033
Central	−0.60	0.37	1.64	NS
Parietal	−0.39	0.33	1.16	NS
Occipital	−0.23	0.30	0.75	NS
ERPs to Studied-Long Faces Minus ERPs to New Faces, 400–800 ms				
Anterior frontal	0.46	0.65	0.70	NS
Frontal	1.23	0.54	2.26	0.039
Central	2.31	0.53	4.38	<0.001
Parietal	2.74	0.59	4.62	<0.001
Occipital	2.36	0.53	4.48	<0.001

NS, not significant.

made after some hesitancy and/or further memory searching, such that "new" responses were delayed. Although subjects had never viewed these new faces before, some of the new faces conceivably bore a resemblance to a face previously seen by the subject, either earlier in the experiment or, indeed, anywhere. We propose that the fastest "new" responses in the recognition test were for faces processed in the visual system without closely matching the attributes of any stored facial representation and that this matching function occurs as a normal facet of perceptual processing (e.g., see Valentine, 1991). On the other hand, known faces and faces that resemble known faces can lead to a match or resonance during early stages of perceptual processing. Our results suggest that this also happens for faces viewed recently, even when the viewing conditions are extremely restricted so as to lead to chance-level explicit recognition. Neural activity that produces ERP negativity in the 250–400 ms range as faces are perceptually processed may be precisely the neural activity that is responsible for perceptual priming.

This conceptualization of the neural correlates of perceptual priming would suggest that such effects should be produced for studied-long faces as well. This issue must be addressed with reference to a central premise of our experiment—that priming and recollection tend to occur concurrently and are therefore difficult to measure independently. Brain potentials associated with explicit recollection of face repetition have been observed to begin at a latency of 280 ms (Münte et al., 1997; Paller et al., 2000). Neural correlates of perceptual priming were evident here in the contrast between new faces and studied-brief faces, which were essentially forgotten by the subjects. In contrast, studied-long faces were well remembered, and this conscious face memory was associated with a prolonged ERP positivity. This positivity thus began prior to 400 ms, but during the interval from 250 to 400 ms negative potentials related to priming overlapped with positive potentials related to recollection. When only data from fast trials were considered, according to the reasoning above, the waveform for new faces at 250–400 ms was more positive because these new faces were less similar to known faces and so more quickly classified as new. Indeed, frontal midline negativity for studied-long faces compared to new faces was apparent (as shown in Figure 4); the difference measured 1.24μV and approached significance [$t(15) = 1.94$, $p = 0.071$]. A hint of this difference was apparent when all trials were included (Figure 2), but with a smaller magnitude.

A key strength of our approach is that the phenomenon of memory without awareness of remembering could be reliably produced for studied-brief faces. The finding of distinctive ERP differences between studied-brief and new faces argues against an alternative possibility, that the studied-brief condition simply generated weak conscious memory, because these ERP differences did not appear to be small-amplitude versions of ERP correlates of face recollection. Unfortunately, behavioral priming could not be measured directly in Experiment 1, because it was essential instead to determine whether any studied-brief faces could be recognized. Accordingly, we administered a suitable implicit memory test in a second ERP experiment. We simultaneously showed that a different procedure would also produce priming without recollection, thus ruling out the possibility that some specific feature of the cross task used in Experiment 1, such as the requirement to actively ignore studied-brief faces in the study phase, was responsible for the negative potential differences taken as electrophysiological correlates of priming.

Priming was observed in Experiment 2 as a facilitation in the time subjects took to decide whether a male or female individual was pictured, with black pixels superimposed on 30% of each face to increase decision difficulty (Figure 5). Reaction times were 17 ms faster for all studied faces combined compared to new faces [793 versus 810 ms, $t(11) = 2.43$, $p = 0.033$] but did not differ between studied-brief and studied-long faces [$t(11) = 1.20$]. This analysis was conducted with outlier trials excluded, as in the ERP analyses; the same pattern of results was observed when all trials were included, with an average priming effect of 22 ms [$t(11) = 2.87$, $p = 0.015$]. Priming of decision accuracy was also apparent, as accuracy was higher for studied-long compared to new faces [86.0% versus 81.9%, respectively, $t(11) = 3.04$, $p = 0.01$], although accuracy was not significantly enhanced for studied-brief compared to new faces [82.9% versus 81.9%, respectively, $t(11) = 0.58$].

Recognition was tested in Experiment 2 only in the

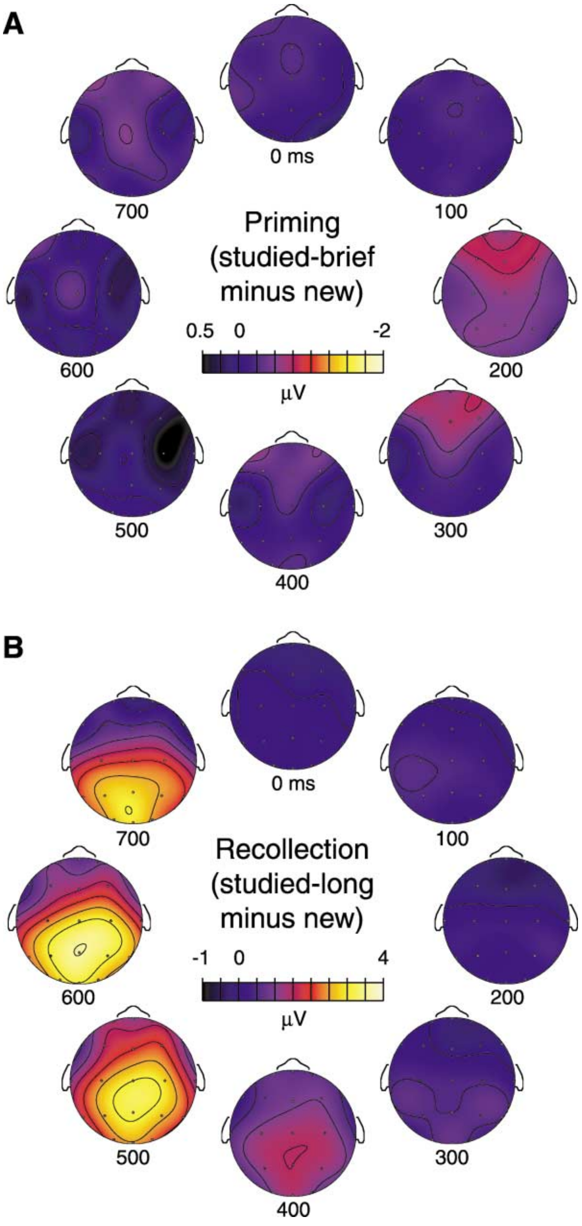

Figure 3. Changes in Topographic Patterns Over Time in Experiment 1

Amplitude differences were computed over 100 ms intervals beginning at the times indicated adjacent to each map (computations otherwise as in Figure 2C). The time course of topographic changes thus characterizes ERP correlates of face priming (A) and face recollection (B). Note that effects are of the opposite polarity.

final two runs (so that memory testing in the first six runs would be implicit). As in Experiment 1, recognition was at chance levels for studied-brief faces, but not for studied-long faces. When compared to the endorsement rate for new faces (49.9% false alarms), recognition was significantly better for studied-long faces [63.5%, $t(11) = 2.45$, $p = 0.03$], but at chance for studied-brief faces [46.0%, $t(11) = 0.80$, d-prime $= -0.10$].

ERPs recorded during implicit memory testing in Experiment 2 replicated the pattern of less positivity for studied-brief faces compared to new faces (Figure 6).

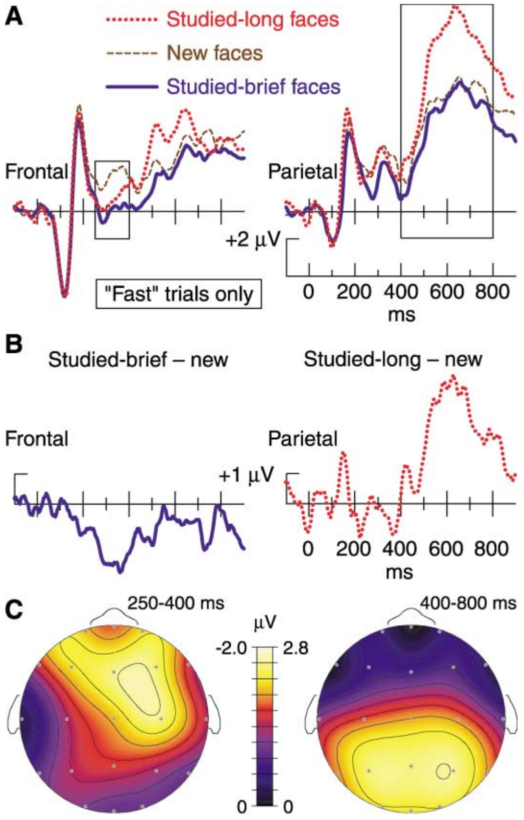

Figure 4. Brain Potentials from Test Phase of Experiment 1, Including Only Trials with a Reaction Time Faster Than the Median Reaction Time for that Condition and Subject

(A) Potentials to the three types of nonfamous faces from midline frontal and parietal scalp locations.

(B) Corresponding difference waves.

(C) Topographic representations of electrophysiological differences between pairs of conditions.

Studied-brief-minus-new ERP differences were found at 400–800 ms at the midline parietal location [$-1.19\mu V$, $t(11) = 2.58$, $p = 0.026$] but were not statistically significant at other midline locations. The topography of these ERP differences appeared more posterior than that in Experiment 1, and the latency prolonged. Given that different groups of subjects were tested in the two experiments, with stimuli that were degraded by darkened pixels in Experiment 2 but not in Experiment 1, interpretations of these apparent topographic differences are unclear. Both anterior and posterior ERP topographies have also been found with short-lag repetitions of faces (Begleiter et al., 1995; Pfutze et al., 2002; Schweinberger et al., 1995); however, the relevance of repetition within immediate memory for the present analysis of recognition and priming across longer delays has yet to be determined. In any event, a fruitful approach for making inferences concerning which specific brain regions are activated by faces that are primed but not recognized will be to apply other neuroimaging methods using these same memory-testing procedures. The prolonged latency of the studied-brief-minus-new ERP differences in Experiment 2 can be ascribed to the high difficulty of perceptually processing the degraded faces, which

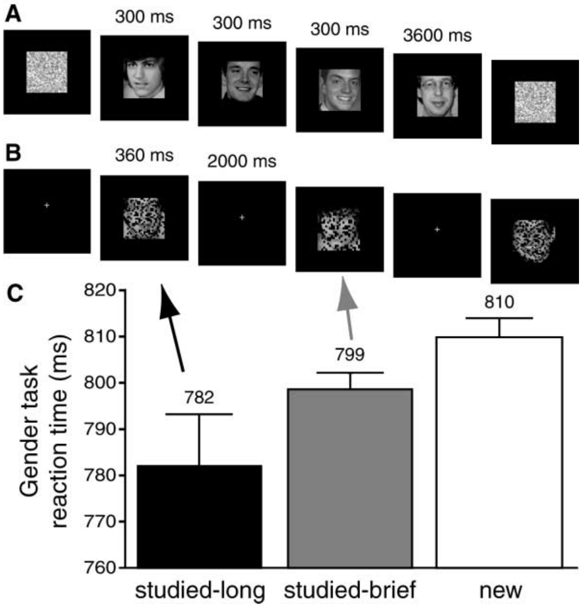

Figure 5. Excerpts of Stimulus Sequences Showing Timing Parameters and Priming Results in Experiment 2

(A) Study phase. Face stimuli were presented in quick succession such that the subsequent stimulus interfered with the processing of each face. Subjects were advised to attend to the faces but no task responses were required. The faces of the four coauthors are shown here for illustrative purposes and were not used in the experiment.

(B) Test phase. Stimuli were perceptually degraded and subjects attempted to make a gender judgment for each face (male/female).

(C) Reaction times from the gender task in the test phase in Experiment 2 for the three chief conditions (with error bars representing standard errors of the mean corrected for across-subject variance).

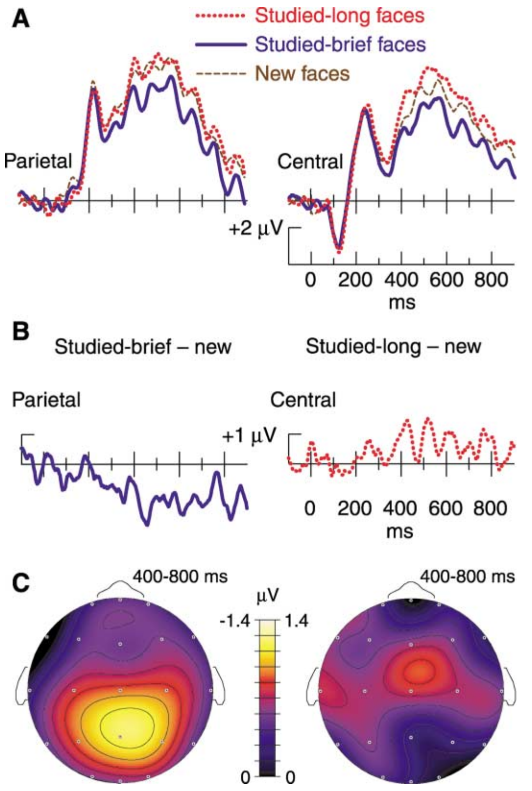

Figure 6. Brain Potentials from Test Phase of Experiment 2

(A) Potentials to the three types of nonfamous faces from midline parietal and central scalp locations.

(B) Corresponding difference waves.

(C) Topographic representations of electrophysiological differences between pairs of conditions.

would also lead to greater variability across trials in the timing of perceptual processing.

The amplitude of studied-long-minus-new ERP differences at 400–800 ms were much reduced from those in Experiment 1, but positive differences were still apparent (e.g., 0.22μV at the midline parietal location, 0.77μV at the midline central location). Measurements of these differences were largely nonsignificant, though with a trend toward positive amplitude differences at all but one location. The small amplitudes of studied-long-minus-new ERP differences could reflect (1) poor time-locking of perceptual processing for degraded faces; (2) overlapping with prolonged negative potentials associated with perceptual priming; (3) the difficulty of remembering studied-long faces exacerbated by stimulus degradation at test; and (4) the minimal attention paid to face repetition while ERPs were recorded, due to the implicit memory testing procedures. Repetition was not task-relevant and incidental recollection was probably minimal due to stimulus degradation and difficulty of the primary task. Furthermore, recognition sensitivity for studied-long faces based on explicit memory testing in the last two runs was relatively low (d-prime = 0.36).

As in Experiment 1, the studied-brief-minus-new ERP difference increased when the analysis included only data from fast trials from a median split on reaction time (-1.74μV at the midline parietal location at 400–800 ms), whereas the studied-long-minus-new ERP difference was relatively unchanged. This could reflect better time-locking of perceptual processing for new faces with the least resemblance to known faces, and consequently greater positivity at 250–400 ms for new faces yielding a larger studied-brief-minus-new ERP difference.

Discussion

Although conscious memory and priming coincide in many circumstances, our experimental procedures made it possible to disentangle their electrophysiological manifestations. Neural events presumably responsible for priming for studied-brief faces in Experiment 1 produced a distinctive brain potential, a frontal negativity beginning approximately 270 ms after face onset. Behavioral measures of priming were obtained in Experiment 2 while the ERP negativity was replicated, albeit with a more posterior topography and prolonged latency. Speculatively, these changes may reflect an influence of visual degradation such that face processing was prolonged and the timing of face processing more variable across trials. Nonetheless, in both experiments neural responses associated with memory for studied-brief and studied-long faces were qualitatively different, thus providing strong support for two central interpretations—that the positive ERPs constitute neural correlates of recollection, and that the earlier negative ERPs constitute separate neural correlates of priming, derived from different brain sources.

Importantly, electrophysiological differences between studied-brief and new faces cannot be ascribed to differences in stimulus factors because the specific faces used in these two conditions were counterbalanced across subjects. Also, the tendency for subjects in Experiment 1 to indicate that a face had been seen earlier was virtually the same for studied-brief and new faces. Whereas these two conditions were so closely matched, our behavioral findings support the generalization that studied-brief faces were primed but not recollected. Robust priming of gender decisions was found in Experiment 2—and this finding adds a new example of a priming measure to the literature, which includes very few other examples of perceptual priming with unfamiliar faces (e.g., see Goshen-Gottstein and Ganel, 2000).

Accordingly, we propose that the negative deflection at 250–400 ms in ERPs to studied-brief faces relative to ERPs to new faces reflects altered neural processing due to perceptual learning of the specific studied-brief face stimuli, learning that occurred despite minimal conscious memory for those stimuli. Our findings from analyzing trials with the fastest responses suggest that the speed of the decision that a face has not been seen before varies systematically, with intriguing implications. For repeated faces, and perhaps also for new faces that in some way resemble known faces, perceptual processing involves relatively more contact with preexisting facial representations, even when there is minimal awareness of any match between perceived faces and stored facial representations (as in studied-brief faces). Therefore, it appears that face priming, even in the absence of explicit recognition, is associated with negative brain potentials in the interval from 250 to 400 ms.

Neural measures of priming have been reported previously, often with verbal rather than facial stimuli. Neuroimaging findings using fMRI and PET methods have suggested that reduced activity in certain brain regions can reflect facilitated perceptual processing associated with priming (Donaldson et al., 2001; Henson et al., 2000; James et al., 1999; Schacter and Buckner, 1998), possibly related to cholinergic and GABA-related plasticity (Thiel et al., 2001). Fusiform, prefrontal, and parietal cortical regions have thus been implicated, although contamination from conscious memory remains a concern. Action potentials from single neurons in monkey visual cortex likewise tend to show reduced activity in response to a repeated visual stimulus (Desimone, 1996). Both this phenomenon, known as *repetition suppression*, and the reduced activation in human neuroimaging studies, have been ascribed to a perceptual learning process that occurs when the same stimulus is repeatedly processed (Buchel et al., 1999; Rolls et al., 1989; Wiggs and Martin, 1998).

In ERP studies of stimulus repetition, it has been difficult to rule out contamination from conscious memory, even when implicit memory tests have been used (e.g., Badgaiyan and Posner, 1997); the majority of findings have been linked with recognition and evaluation processes rather than priming (for reviews, see Friedman and Johnson, 2000; Mecklinger, 2000; Paller, 2000; Rugg and Allan, 2000; Rugg and Wilding, 2000). For example, ERP responses to visual words that were more positive from 500 to 900 ms for well-remembered words compared to poorly remembered words were associated with recollective processing (Paller and Kutas, 1992; Paller et al., 1995). On the other hand, ERPs in related experiments were associated with priming of visual word-form, based on manipulations of presentation format during the study phase that influenced priming more than recognition (Paller and Gross, 1998; Paller et al., 1998). These putative ERP correlates of visual word-form priming took the form of an enhanced positivity at 300–500 ms over posterior scalp locations. Similarly, positive ERP correlates of priming were also identified based on insensitivity to the recognition decision and to elaborative processing at study (Rugg et al., 1998) and using cross-modality manipulations (Joyce et al., 1999; Rugg and Nieto-Vegas, 1999). In contrast, ERP correlates of face priming in the present experiment were negative in polarity; this divergence may reflect cortical processing of words versus faces in different regions such that the spatial orientation of activated neurons generates different extracellular fields (Münte et al., 2000). In several experiments, negative ERP repetition effects have been observed with visual shapes and drawings, but generally using immediate repetitions, which can engage additional operations specific to working memory (Penney et al., 2001; Rugg et al., 1995; Van Petten and Senkfor, 1996; Viggiano and Kutas, 2000). Additional data are needed to determine how neural events associated with implicit memory may differ as a function of the type of stimulus used.

Negative potentials to repeated faces have also been observed in several other experiments. For example, Eimer (1999) noted that a negativity at 300–500 ms (labeled N400f) was enhanced for faces of well-known celebrities compared to faces of unknown individuals. Topographic analyses of such effects have shown a parietocentral focus in some circumstances (Eimer, 1999) and a frontocentral focus in others (Bentin and Deouell, 2000). Contrasts between known and unknown faces pose noteworthy problems because a serious effort is required to hold constant the large number of factors that tend to differ across these two categories (Debruille et al., 1998), which underscores the advantages of the use of preexperimentally unknown faces, as in the present experiment. Nonetheless, the negative potentials associated with face priming in the present experiment may be related to N400f potentials in other experiments, and perhaps also to N320 potentials observed when a face mismatched the immediately preceding face (Mills et al., 2000). Potentials thought to be related to access to stored facial representations have also been characterized in this same latency interval, but with opposite polarity and using memory tests with short lags between first and second presentation (Pfutze et al., 2002; Schweinberger et al., 1995). Using realistic drawings of faces following extensive familiarization, N400-like potentials termed "mismatch negativities" were observed when eyes and eyebrows did not match those of learned faces compared to when they did (Olivares et al., 1999, 2003). It remains an open question whether these effects, or the negativities observed in the present experiment, correspond to the mismatch negativity most commonly observed with auditory stimuli (Picton et al., 2000).

Our inference that ERP differences between studied-long faces and new faces primarily reflect recollection provoked by studied-long faces receives ample support from prior results from our lab (Paller et al., 1999, 2000, 2003). Specifically, we associated characteristic posterior potentials with face recollection by virtue of a contrast between study conditions yielding different levels of recognition but matched on other factors (Paller et al., 1999). Importantly, elaborative study enhanced recognition but did not influence the magnitude of priming observed in fame judgments made on visually degraded faces. Analogous brain potentials were observed using memory tests similar to the test used here in Experiment 1, wherein subjects discriminated studied faces from new faces (Paller et al., 2003). We can confidently assert that positive ERP differences between studied-long faces and new faces in Experiments 1 and 2 be taken to index conscious memory, because they so closely resemble ERPs associated with face recollection in these prior experiments. Furthermore, similar ERPs were also recorded in association with recollective experiences in a recent experiment wherein faces that provoked recollection were distinguished from those that provoked only familiarity (G. Yovel and K.A.P., submitted).

We conclude that two distinct memory phenomena were engaged in response to unfamiliar faces repeated after a short delay, as summarized in Figure 3. Perceptual priming was associated with a brain potential that was maximal 200–300 ms after face onset and that may reflect a facilitated analysis of repeated faces. Such facilitation constitutes a specific instance of altered neural processing in cortical networks that generally may support performance changes in implicit memory tests. Recollection, in contrast, was associated with a brain potential arising from a different configuration of intracranial sources and reaching maximal amplitudes 600–700 ms after face onset. Indeed, remembering faces may require more extensive and time-consuming associative retrieval in order for study episodes to be recalled. The divergence between neural correlates of face priming and face recollection is consistent with the contention that the perceptual learning underlying priming does not contribute to recalling and recognizing autobiographical events (Donaldson et al., 2001; Stark and Squire, 2000; Wagner et al., 1997). Our data likewise argue against the position that priming and recognition are derived from access to the same episodic information (Ostergaard, 1999), given that this position does not predict that neural correlates of the two processes would be qualitatively different.

A great impediment toward understanding the neural basis of implicit memory has been the inability to obtain measures of the relevant neural events without contamination from other sorts of memory phenomena. The two electrophysiological responses to faces described here may not have been observed together previously because brief neural correlates of priming tend to be obliterated by prolonged neural correlates of conscious memory. We suggest that the brain events responsible for both types of memory first surface at nearly the same latency, but that they initially cancel each other out such that electrophysiological correlates of face recollection appear to emerge later. Our use of faces that were primed but not recollected, however, made it possible to clearly observe an uncontaminated electrophysiological indication of implicit memory for faces for the first time. Monitoring neural activity associated with both priming and recollection in this manner is a critical step toward elucidating the biological substrates of memory with and without awareness, as well as the enigmatic border between the two.

Experimental Procedures

Subjects in Experiment 1 (n = 16) were an equal number of right-handed men and women, aged 18–31 years. Subjects in Experiment 2 (n = 12) were two men and ten women, aged 18–28 years, and all but one were right handed. EEG was recorded as described below, and subjects were paid for participating. Subjects in Experiments 1.1, 1.2, and 1.3, which did not entail EEG recordings, were given course credit for participating. Each subject participated in only one of these five experiments and gave informed consent in advance.

The design of Experiment 1 is shown schematically in Figure 1. Grayscale face stimuli were presented centrally and subtended a horizontal and vertical visual angle of 1.8°. Subjects were familiar with most of the famous faces but prior to the experiment had never viewed the nonfamous faces, which were selected from a high-school yearbook. Yellow crosses in the cross-discrimination task were presented 1.8° from the center of the face. Responses in all tasks were indicated with fingers of the right hand using a response pad with multiple keys. For the cross task, advance practice was given prior to the first study-test block, with a gradually decreasing stimulus duration so that subjects could learn to make accurate discriminations. Although this discrimination was subjectively difficult, responses were correct on 84% of the study-phase trials. To help subjects maintain their focus on the cross task, error feedback was provided in the form of a beep following each incorrect response. The next trial began approximately 1 s after the response. There were eight study-test blocks, such that the total number of trials in the test phase included 64 studied-long faces, 128 studied-brief faces, and 128 new faces. Both types of studied faces were presented three times in the study phase. To eliminate stimulus-specific effects from the key contrast in the test phase between studied-brief and new faces, stimuli in these two conditions were counterbalanced across subjects.

The study task was adapted from one used previously (S.D. Smith and P.M. Merikle, Assessing the duration of memory for information without awareness, Fourth international conference of the Association for the Scientific Study of Consciousness, Brussels, Belgium [2000]). Subjects in these experiments viewed words while performing the cross-discrimination task, followed by a modified stem-completion test (Jacoby et al., 1992). Subjects were asked to complete each stem to form a word other than one presented in the study task. Those words could generally be recollected if there was no delay between study and test, and thus they were excluded for stem completion. When a delay was interposed before the test, however, subjects often produced studied words instead of excluding them. This pattern of exclusion performance after a short delay and exclusion failure (i.e., memory without awareness) after a long delay suggested that this sort of experimental design was suitable for our goal of producing priming without recollection.

Variations on the design of Experiment 1 were used in three companion experiments. Subjects in Experiment 1.1 (n = 12) gave *remember/know* responses in addition to *old/new* responses to provide experiential measures of memory for faces from the study phase, with five study-test runs. Studied-long faces were presented for 195 ms and followed by a mask, so that they were more similar to studied-brief presentations. In Experiment 1.2, subjects (n = 12) were instructed to try to remember all faces in the study phase, presented as in Experiment 1, and the test phase was altered such that two faces were presented simultaneously on each trial. Subjects indicated which face they thought had been presented in the study phase. Each studied-long and studied-brief face was paired with a different new face, such that guessing would produce 50% correct responding. An estimate of the percentage of trials for which the response was based purely on guessing was computed [guessing = (100 − percent correct) × 2], based on the assumption that guessing in two-choice forced-alternative recognition varies linearly with accuracy from 0% guessing with 100% accuracy to 100% guessing with 50% accuracy. Subjects in Experiment 1.3 (n = 18) made *famous/nonfamous* judgments in the test phase, which thus constituted an implicit memory test. Only the test-phase instructions were altered from the design of Experiment 1 to make this change.

The design of Experiment 2, shown schematically in Figure 5, paralleled that of Experiment 1 but with a different procedure for producing priming without recollection and with alterations to produce an implicit memory test. In the study phase, faces were presented in randomly ordered sequences with no delay between stimuli ("rapid serial visual presentation"), with 8 studied-long faces for 3600 ms and 16 studied-brief faces for 300 ms. Processing of each studied-brief face was interfered with by the subsequent face. The final face in each sequence was always a studied-long face, and a scrambled face image was presented prior to and at the end of each sequence. After a 2 s delay, the sequence was shown a second time in a different order, and following another 2 s delay a third time. Each face was thus presented three times, as in Experiment 1. In contrast to Experiment 1, however, subjects were not told to remember a subset of the faces but were instead instructed to attend to and process all faces.

In the test phase of Experiment 2, subjects viewed studied and new faces and made a speeded gender judgment for each face. No reference was made to the fact that some faces had appeared in the study phase. Furthermore, each face stimulus was visually degraded by darkening a randomly selected set of pixels to black (as in Experiment 2 of Paller et al., 1999). Approximately 30% of each face was thus obscured, increasing the difficulty of gender judgments. Faces were displayed for 360 ms, followed by a fixation cross for 2000 ms. Priming was measured as faster reaction times for studied faces than for new faces. In the final two runs of the test phase, instructions were changed in order to provide some indication of recognition memory for faces from the study phase. Viewing the same sort of degraded faces, subjects indicated which they remembered from the immediately preceding study phase. ERPs were analyzed only for the first six runs.

In both Experiment 1 and Experiment 2, EEG was recorded from 21 scalp locations using an amplification band-pass of 0.1–100 Hz and a sampling rate of 250 Hz. Time-locked responses were calculated excluding trials with an electroocular artifact, a missing behavioral response, or with an outlier response either too fast or too slow (±2 × SD for that individual and condition). N170 potentials were measured using right-temporal mean amplitudes from 140 to 200 ms for ERPs referenced to the average of recordings from all locations. All other ERP analyses were conducted using an average-mastoid reference. Other methodological details have been described previously (Paller et al., 1999, 2000).

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References

Badgaiyan, R.D., and Posner, M.I. (1997). Time course of cortical activations in implicit and explicit recall. J. Neurosci. *17*, 4904–4913.

Begleiter, H., Porjesz, B., and Wang, W. (1995). Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. Electroencephalogr. Clin. Neurophysiol. *94*, 41–49.

Bentin, S., and Deouell, L.Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. Cogn. Neuropsychol. *17*, 35–54.

Buchel, C., Coull, J.T., and Friston, K.J. (1999). The predictive value of changes in effective connectivity for human learning. Science *283*, 1538–1541.

Debruille, J.B., Guillem, F., and Renault, B. (1998). ERPs and chronometry of face recognition: following-up Seeck et al., and George et al. Neuroreport *9*, 3349–3353.

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. Proc. Natl. Acad. Sci. USA *93*, 13494–13499.

Donaldson, D.I., Petersen, S.E., and Buckner, R. (2001). Dissociating memory retrieval processes using fMRI: evidence that priming does not support recognition memory. Neuron *31*, 1047–1059.

Eimer, M. (1999). Event-related brain potentials distinguish processing stages involved in face perception and recognition. Clin. Neurophysiol. *110*, 1–12.

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

Gabrieli, J.D.E. (1998). Cognitive neuroscience of human memory. Annu. Rev. Psychol. *49*, 87–115.

Goshen-Gottstein, Y., and Ganel, T. (2000). Repetition priming for familiar and unfamiliar faces in a sex-judgment task: evidence for a common route for the processing of sex and identity. J. Exp. Psychol. Learn. Mem. Cogn. *26*, 1198–1214.

Hamann, S.B., and Squire, L.R. (1997). Intact perceptual memory in the absence of conscious memory. Behav. Neurosci. *111*, 850–854.

Henson, R., Shallice, T., and Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. Science *287*, 1269–1272.

Jacoby, L.L., Lindsay, D.S., and Toth, J.P. (1992). Unconscious influences revealed. Attention, awareness, and control. Am. Psychol. *47*, 802–809.

James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., and Goodale, M.A. (1999). Repetition priming and the time course of object recognition: an fMRI study. Neuroreport *10*, 1019–1023.

Joyce, C.A., Paller, K.A., Schwartz, T.J., and Kutas, M. (1999). An electrophysiological analysis of modality-specific aspects of word repetition. Psychophysiology *36*, 655–665.

Knowlton, B.J. (1998). The relationship between remembering and knowing: a cognitive neuroscience perspective. Acta Psychol. *98*, 253–265.

Mayes, A.R., and Downes, J.J. (1997). Theories of Organic Amnesia (Hove, UK: Psychology Press).

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

Mills, D.L., Alvarez, T.D., St George, M., Appelbaum, L.G., Bellugi, U., and Neville, H. (2000). Electrophysiological studies of face processing in Williams syndrome. J. Cogn. Neurosci. Suppl. *12*, 47–64.

Münte, T.F., Brack, M., Grootheer, O., Wieringa, B.M., Matzke, M., and Johannes, S. (1997). Event-related brain potentials to unfamiliar faces in explicit and implicit memory tasks. Neurosci. Res. *28*, 223–233.

Münte, T.F., Urbach, T.P., Düzel, E., and Kutas, M. (2000). Event-related brain potentials in the study of human cognition and neuropsychology. In Handbook of Neuropsychology, F. Boller, J. Grafman, and G. Rizzolatti, eds. (Amsterdam: Elsevier Science), pp. 139–234.

Olivares, E.I., Iglesias, J., and Bobes, M.A. (1999). Searching for face-specific long latency ERPs: a topographic study of effects associated with mismatching features. Brain Res. Cogn. Brain Res. *7*, 343–356.

Olivares, E.I., Iglesias, J., and Rodriguez-Holguin, S. (2003). Long-latency ERPs and recognition of facial identity. J. Cogn. Neurosci. *15*, 136–151.

Ostergaard, A.L. (1999). Priming deficits in amnesia: now you see them, now you don't. J. Int. Neuropsychol. Soc. *5*, 175–190.

Paller, K.A. (2000). Neural measures of conscious and unconscious memory. Behav. Neurol. *12*, 127–141.

Paller, K.A., and Gross, M. (1998). Brain potentials associated with perceptual priming vs explicit remembering during the repetition of visual word-form. Neuropsychologia *36*, 559–571.

Paller, K.A., and Kutas, M. (1992). Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming. J. Cogn. Neurosci. *4*, 375–391.

Paller, K.A., Mayes, A.R., Thompson, K.M., Young, A.W., Roberts, J., and Meudell, P.R. (1992). Priming of face matching in amnesia. Brain Cogn. *18*, 46–59.

Paller, K.A., Kutas, M., and McIsaac, H.K. (1995). Monitoring conscious recollection via the electrical activity of the brain. Psychol. Sci. *6*, 107–111.

Paller, K.A., Kutas, M., and McIsaac, H.K. (1998). An electrophysiological measure of priming of visual word-form. Conscious. Cogn. *7*, 54–66.

Paller, K.A., Bozic, V.S., Ranganath, C., Grabowecky, M., and Yamada, S. (1999). Brain waves following remembered faces index conscious recollection. Brain Res. Cogn. Brain Res. *7*, 519–531.

Paller, K.A., Gonsalves, B., Grabowecky, M., Bozic, V.S., and Yamada, S. (2000). Electrophysiological correlates of recollecting faces of known and unknown individuals. Neuroimage *11*, 98–110.

Paller, K.A., Ranganath, C., Gonsalves, B., LaBar, K.S., Parrish, T.B., Gitelman, D.R., Mesulam, M.-M., and Reber, P.J. (2003) Neural correlates of person recognition. Learn. Mem., in press.

Penney, T.B., Mecklinger, A., and Nessler, D. (2001). Repetition related ERP effects in a visual object target detection task. Brain Res. Cogn. Brain Res. *10*, 239–250.

Pfutze, E.M., Sommer, W., and Schweinberger, S.R. (2002). Age-related slowing in face and name recognition: evidence from event-related brain potentials. Psychol. Aging *17*, 140–160.

Picton, T.W., Alain, C., Otten, L., Ritter, W., and Achim, A. (2000). Mismatch negativity: different water in the same river. Audiol. Neurootol. *5*, 111–139.

Rolls, E.T., Baylis, G.C., Hasselmo, M.E., and Nalwa, V. (1989). The effect of learning on the face selective responses of neurons in the cortex in the superior temporal sulcus of the monkey. Exp. Brain Res. *76*, 153–164.

Rugg, M.D., and Allan, K. (2000). Event-related potential studies of memory. In The Oxford Handbook of Memory, E. Tulving and F.I.M. Craik, eds. (Oxford, UK: Oxford University Press), pp. 521–537.

Rugg, M.D., and Nieto-Vegas, M. (1999). Modality-specific effects of immediate word repetition: electrophysiological evidence. Neuroreport *10*, 2661–2664.

Rugg, M.D., and Wilding, E.L. (2000). Retrieval processing and episodic memory. Trends Cogn. Sci. *4*, 108–115.

Rugg, M.D., Soardi, M., and Doyle, M.C. (1995). Modulation of event-related potentials by the repetition of drawings of novel objects. Brain Res. Cog Brain Res *3*, 17–24.

Rugg, M.D., Mark, R.E., Walla, P., Schloerscheidt, A.M., Birch, C.S., and Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. Nature *392*, 595–598.

Schacter, D.L., and Buckner, R.L. (1998). Priming and the brain. Neuron *20*, 185–195.

Schacter, D.L., Chiu, C.Y., and Ochsner, K.N. (1993). Implicit memory: a selective review. Annu. Rev. Neurosci. *16*, 159–182.

Schweinberger, S.R., Pfuetze, E.-M., and Sommer, W. (1995). Repetition priming and associative priming of face recognition: evidence from event-related potentials. J. Exp. Psychol. Learn. Mem. Cogn. *21*, 722–736.

Shimamura, A.P. (1986). Priming effects in amnesia: evidence for a dissociable memory function. Q. J. Exp. Psychol. A *38*, 619–644.

Squire, L.R., and Schacter, D.L. (2002). Neuropsychology of Memory, Third Edition (New York: Guilford Press).

Stark, C.E., and Squire, L.R. (2000). Recognition memory and familiarity judgments in severe amnesia: no evidence for a contribution of repetition priming. Behav. Neurosci. *114*, 459–467.

Thiel, C.M., Henson, R.N., Morris, J.S., Friston, K.J., and Dolan, R.J. (2001). Pharmacological modulation of behavioral and neuronal correlates of repetition priming. J. Neurosci. *21*, 6846–6852.

Tulving, E. (1985). Memory and consciousness. Can. Psychol. *26*, 1–12.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q. J. Exp. Psychol. A *43*, 161–204.

Van Petten, C., and Senkfor, A.J. (1996). Memory for words and novel visual patterns: repetition, recognition, and encoding effects in the event-related brain potential. Psychophysiology *33*, 491–506.

Viggiano, M.P., and Kutas, M. (2000). Overt and covert identification of fragmented objects inferred from performance and electrophysiological measures. J. Exp. Psychol. Gen. *129*, 107–125.

Wagner, A.D., Gabrieli, J.D., and Verfaellie, M. (1997). Dissociations between familiarity processes in explicit recognition and implicit perceptual memory. J. Exp. Psychol. Learn. Mem. Cogn. *23*, 305–323.

Wiggs, C.L., and Martin, A. (1998). Properties and mechanisms of perceptual priming. Curr. Opin. Neurobiol. *8*, 227–233.