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Interactive report

Brain waves following remembered faces index conscious recollection [1]

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Abstract

At a glance, one can often determine whether a face belongs to a known individual. To investigate brain mechanisms underlying this memory feat, we recorded EEG signals time-locked to face presentations. In the study phase, 40 unknown faces were presented, 20 of which were accompanied by a voice simulating that person speaking. Instructions were to remember the faces with spoken biographical information (*R-faces*) and to forget the others (*F-faces*). In the test phase, famous and non-famous faces were presented in a visually degraded manner. Subjects made two-choice fame judgments and priming was observed in the form of faster and more accurate responses for old than for new non-famous faces. Priming did not differ between R-faces and F-faces. In a second experiment, faces were not degraded at test and behavioral responses were made only when faces were presented twice in immediate succession. Brain potentials elicited 300 to 900 ms after stimulus onset from frontal and parieto-occipital scalp regions were larger for R-faces than for F-faces. Recognition tested later was more accurate for R-faces than for F-faces. Because the study-phase manipulation influenced recognition but not priming, we conclude that this procedure succeeded in isolating neural correlates of recollective processing from more automatic uses of face memory as indexed by priming. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Memory provides us with the ability to re-experience the past. The subjective experience of remembering, or *conscious recollection*, is a complex cognitive process that generally entails the retrieval of a large assembly of information. If such processes could be monitored as they occur in the brain, investigations of recollection would greatly benefit. The present study is part of an ongoing search for neural correlates of recollection that can be used to support the study of its neural foundations.

Prior studies of amnesic patients have been particularly informative with respect to the neural substrates of human memory. Amnesic patients display characteristic deficits in the recall and recognition of facts and episodes, a type of memory called declarative memory [50,79,86]. Brain regions damaged in cases of amnesia presumably mediate a consolidation process that allows declarative memories to be preserved in the brain [52,54,55,58,89]. One respect in which declarative memory differs from other types of memory is in its strong association with recollection. Although studies of amnesia have significantly enhanced our understanding of consolidation, less is known about the brain mechanisms that support recollection.

Human faces are particularly potent stimuli for evoking recollective experience. Most people can remember a multitude of different faces remarkably well and without effort, although attaching a name to a face is more difficult. Furthermore, the face is of paramount importance for social interaction, emotional expression, and personal identity [23]. One particularly influential model of face processing postulated separate modules for determining the identity of familiar versus unfamiliar faces, for expression analysis, and for face–name associations [15]. Evidence supporting these dissociations has been derived from studies of brain-damaged patients with various face processing dysfunctions.

A selective deficit in identifying familiar faces—prosopagnosia—can occur in the presence of otherwise normal vision, normal knowledge about the unidentified people, and normal memory in all other respects [25]. Prosopagnosic patients often attempt to overcome their

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difficulties in identifying faces by relying on voice, gait, clothing, or single distinctive features. Facial expressions of emotions can often be perceived normally. Dissociations between prosopagnosia and other object recognition difficulties suggest that face recognition depends on distinct cortical mechanisms, perhaps a special holistic or global processing mode dependent on right-hemisphere regions, although this proposal remains controversial [32,73,88].

Perceptual processing of faces has also been investigated more directly through physiological methods. In monkeys, neurons in temporal cortex respond selectively to faces [27,66]. In humans, recordings from intracranial electrodes have shown face-specific responses from small regions of the left and right fusiform and inferior temporal gyri, and electrical stimulation from these same electrodes frequently disrupted naming of familiar faces [1]. The proposal that specific extrastriate regions are specialized for determining facial identity from visual input has also been supported by evidence from neuroimaging using positron emission tomography (PET) and functional magnetic resonance imaging (FMRI); face-related activations were found in or near the fusiform gyrus and were larger on the right than left side [22,37,46,69,80]. One speculation about face memory is that these same face-specific regions of temporal cortex that are necessary for face perception are also critical for face recollection. Indeed, the storage of declarative memory generally relies on cortical modules dedicated to processing particular sorts of to-be-remembered information [28,87]. Recollection cued by a face is likely to involve a rich set of connections between a facial representation and other stored knowledge, including knowledge about that individual, the spatio–temporal context of previous meetings, affective associations, and other associative information. However, in order to study the neural substrates of face recollection, we must distinguish it from other memory phenomena involving faces.

In particular, it can be useful to contrast face recollection with face *familiarity* in the absence of recollection. Consider the 'butcher-on-the-bus' phenomenon—in this case, the butcher seems highly familiar in the atypical context of a bus rather than a butcher shop, and a full recollective experience is not achieved (c.f., Mandler's dual-process theory of recognition [49]). One way to assess these two types of memorial experience is through a procedure in which subjects themselves attempt to discriminate between 'remember' and 'know' trials, corresponding to recollection and familiarity, respectively. In an experiment in which this procedure was used with faces, divided attention at study selectively reduced 'remember' responses [64], suggesting that the contrast between recollection and familiarity that has been extensively studied with verbal stimuli is also valid with facial stimuli.

Another memory phenomenon that occurs in the absence of face recollection is face *priming*, which is when a behavioral response to a face is specifically altered due to recent exposure to that face (for reviews, see [13,29,75]). For example, when subjects make speeded responses to faces, judging them as either familiar or unfamiliar, these responses are typically quicker for previously viewed faces. Furthermore, face priming appears to depend on encoding specific perceptual features [13,14,31]. Normal face priming in amnesic patients has been observed in an identity-matching task for both familiar and unfamiliar faces [63].

Face recollection and priming thus reflect two distinct uses of memory; the former allows one to remember an individual's identity whereas the latter may automatically give rise to altered behavioral responses to previously viewed faces. Processes underlying recollection and priming can be monitored through analyses of event-related brain potentials extracted from the electroencephalogram (for reviews, see [45,57,77]). In particular, Paller and Kutas [60] showed that responses to visual words presented during a priming test included potentials 500 to 800 ms after stimulus onset that reflected incidental recollection. In contrast, a different brain potential was found to reflect visual word-form priming [59,62]. Whereas these potentials were elicited by words, memory cued by faces may be associated with similar potentials. To investigate this possibility, we recorded event-related potentials (ERPs) to faces presented in a memory paradigm.

Although the natural process of becoming acquainted with a new person is typically a gradual, interactive, and multidimensional experience, it can be simulated in the laboratory. Accordingly, we sought to study the neural substrates of face recollection after subjects viewed 20 photographs of faces, each associated with a name and biography spoken in a unique voice (see Fig. 1A). Subjects were told to remember these faces, termed *Remember Faces* or *R-faces*. An additional set of 20 faces were intermixed with the R-faces and presented without any spoken information. Subjects were told to forget these other faces, termed *Forget Faces* or *F-faces*. Instructions to remember some stimuli and forget others (i.e., "directed forgetting", see [11,33,44]) tend to influence recognition but not priming, although some controversy surrounds this memory dissociation [5,47,56,78]. Here, directed forgetting instructions were combined with the inclusion of biographical information for R-faces only, in order to maximize differences between R- and F-faces in later recollection.

Experiment 1 was used to determine whether these procedures would influence recognition but not priming. In the test phase, faces were presented in a degraded fashion and non-famous faces were mixed with a set of famous faces. Stimulus degradation functioned to make judgments more difficult, and thus perhaps more sensitive to priming, and it also allowed us to examine priming as a function of different degradation levels. Subjects were asked to discriminate famous from non-famous faces under these perceptually demanding circumstances, and priming was measured in both accuracy and latency of fame-judgment responses. Our results showed that priming was produced

A   Study Phase

B   Test Phase in Experiment 1
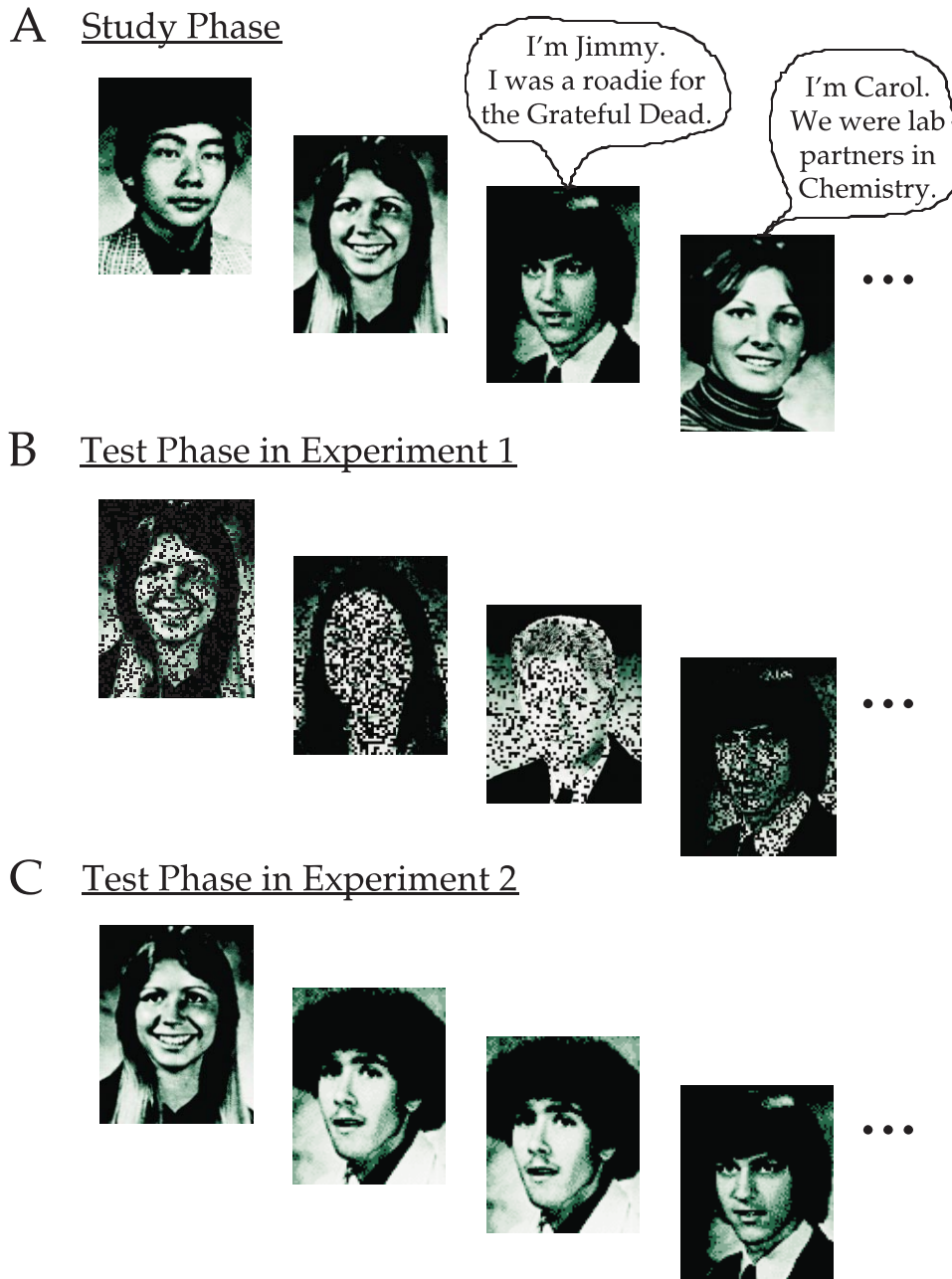

C   Test Phase in Experiment 2

Fig. 1. Schematic representation of stimuli shown in the study and test phases. In both experiments, the study phase included faces with voices (R-faces) and faces without voices (F-faces). In these examples, the study phase started with two F-faces and then two R-faces (A); the test phase in Experiment 1 started with an F-face, a new face, a famous face, and an R-face (B); and the test phase in Experiment 2 started with an F-face, a new face, a target, and an R-face (C).

by face presentations in the study phase and that the magnitude of priming did not differ between R- and F-faces.

The same study-phase procedure was used in Experiment 2, and brain potentials were analyzed to reveal differences in the neural responses to R-faces, F-faces, and new faces. Test-phase instructions were changed such that behavioral responses were made only to occasional target stimuli, famous faces were not included, and face stimuli were not degraded.

2. Methods

2.1. Subjects

Subjects were 22 men and women aged 18–24 years old. They were right-handed, native English speakers, and each gave informed consent. Those in Experiment 1 (7 women and 3 men) received course credit for their participation; those in Experiment 2 (7 women and 5 men) received monetary payment. Data from 3 additional per-

sons in Experiment 2 were excluded due to excessive electro–ocular artifacts.

2.2. Stimuli

Visual stimuli included photographs of 160 faces from a 1970's high school yearbook. Each face was presented in grayscale within a rectangular space measuring 12.5 cm by 16 cm in the center of a computer monitor. Faces were viewed from a distance of 135 cm (such that the rectangular stimuli subtended 5.9° by 7.5° visual angle). A set of 40 faces were used in the study phase. These were shown again in the test phase along with 60 new faces. Another 60 new faces were used in the recognition test. Each set of faces included an equal number of men and women. Visual stimuli were presented for brief durations in order to discourage eye movements and to maximize time-locking of relevant cognitive processes from trial to trial.

Auditory stimuli were paired with 20 of the faces in the study phase. These stimuli were spoken by 10 women and 10 men so as to simulate the experience of meeting the people depicted. Each voice included a name and some brief biographical information (see Table 1).

Faces of 24 well-known celebrities were also used in Experiment 1. These were scanned from photographs in magazines and altered so that the backgrounds were similar to those in the yearbook photos. All or nearly all of these faces were known to the subjects (Bill Clinton, Bill Cosby, Brad Pitt, Diana–Princess of Wales, Elvis Presley, Harrison Ford, Helen Hunt, Hillary Clinton, Jason Alexander, John F. Kennedy, Julia Roberts, Lucille Ball, Madonna, Marilyn Monroe, Martin Luther King, Jr., Michael Jordan, Michelle Pfeiffer, Mohandas Gandhi, Mother Theresa,

Nancy Reagan, Oprah Winfrey, Pamela Lee Anderson, Richard Dean Anderson, and Richard Nixon). In any event, responses to non-famous faces were of primary interest. All face stimuli in the test phase of Experiment 1 were modified by superimposing a variable number of black pixels at random locations.

2.3. Procedure

2.3.1. Experiment 1

The procedure included a study phase followed immediately by a test phase. Each subject was tested individually after providing informed consent. No electrophysiological recordings were made in Experiment 1.

During the study phase (Fig. 1A), subjects were instructed to observe a series of 40 faces, to try to remember the 20 faces paired with voices (*R-faces*), and to forget the other 20 faces (*F-faces*). Faces were shown for 300 ms at the rate of one every 5 s. The onset of the voice for each R-face coincided with the onset of the face presentation. The entire set of 40 faces was presented 3 times using different random orders. The sets of faces assigned to remember and forget conditions were counter-balanced across subjects. In other words, each face was an R-face for half of the subjects and an F-face for the others.

During the test phase (Fig. 1B), subjects were instructed to respond after each face according to whether the person shown was famous or not, moving a joystick down or up, respectively. Faces were shown for 300 ms at the rate of one every 3 s. Faces were presented in four runs in the absence of auditory stimuli. Each run included a randomly ordered set of 66 faces: the 40 faces from the study phase, 20 new faces, and 6 famous faces (9% of the trials). R-

Table 1
Spoken information associated with remember faces

I'm Tracy.	I'm homeless — got any spare change?
I'm Alison.	I won the Boston Marathon twice.
I'm Carol.	We were lab partners in Chemistry.
I'm Cindy.	I got pregnant with twins when I was fifteen.
I'm Emily.	I'm an art dealer — want to buy some sculpture?
I'm Helga.	I inspect underwear for Hanes.
I'm Jane.	I write comics for the New York Times.
I'm Julie.	I lived next door freshman year and always came home drunk.
I'm Megan.	I'm a news anchor on ABC and I stutter.
I'm Susie.	I've starred in 48 adult movies.
I'm Kyle.	I fought in the Gulf War and was paralyzed from the waist down.
I'm Benny.	We met at the keg — I puked on your shoes.
I'm Bruce.	I publish a gay men's magazine.
I'm Cliff.	I play quarterback for the Nebraska Cornhuskers.
I'm Norman.	I pulled you over for speeding last week.
I'm Otto.	We went to high school together — I killed six people last week.
I'm Roger.	I was your freshman-year roommate.
I'm Stan.	I've seen Star Wars 100 times.
I'm Tony.	I've been off crack for five weeks.
I'm Jimmy.	I was a roadie for the Grateful Dead.

and F-faces were repeated across runs, whereas new and famous faces each appeared on only one occasion. All faces in the test phase were presented in a degraded format formed by superimposing black pixels in random locations on the picture. The percentage of black pixels was set to either 50% (level 1), 40% (level 2), or 26% (level 3) for each face on a random basis.

2.3.2. Experiment 2

In Experiment 2, electrophysiological recordings were made during the study and test phases as described below. To reduce artifactual contamination of EEG recordings, subjects were instructed to minimize muscle tension, eye movements, and blinks during experimental runs.

The study phase (Fig. 1A) was identical to that in Experiment 1, except that subjects were told that their monetary payment would be increased by 50 cents for each name and biography that they could recall at the end of the experiment. The test phase (Fig. 1C) was similar except that faces were not degraded and target faces were presented in place of famous faces. Target faces were faces identical to the immediately preceding face and were randomly selected such that targets in each run included two remember, two forget, and two new faces (9% of the trials). Subjects were instructed to press a button whenever any face appeared twice in immediate succession. This task was assigned so that subjects would be required to attend to perceptual aspects of each face. Stimulus degradation was not used in this experiment in order to minimize any doubt about the identity of each face. Subjects were also instructed that when an R-face appeared they should retrieve the associated biographical information and rehearse it in preparation for the subsequent recognition test.

For the recognition test given at the conclusion of the experiment, the subject was given 5 pages showing 20 faces per page, including the 40 faces from the study phase randomly mixed with 60 new faces not previously seen by the subject. Instructions were to attempt to label each of the 20 R-faces and each of the 20 F-faces, and to write down the name and biographical information corresponding to each R-face (although exact wording was not required for retrieved biographical information to be scored as correct). Due to an error in instructions for 1 subject, recognition performance for F-faces and new faces was analyzed only for the remaining 11 subjects.

2.4. Electrophysiology

Electroencephalographic recordings were made from 21 scalp electrodes embedded in an elastic cap at standard locations (Fpz, Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, P3, P4, O1, O2, T3, T4, T5, T6). A left mastoid reference electrode was used on-line and the reference was

changed off-line to the average of left and right mastoid recordings. In addition, two channels were used for monitoring horizontal and vertical eye movements and trials contaminated by electroocular artifacts were excluded from the analyses (16.1% on average). The band pass was 0.1–100 Hz. Recordings were sampled at a rate of 250 Hz and ERPs were computed for 1024-ms epochs beginning 100 ms prior to stimulus onset. ERP measurements were evaluated using analysis of variance (ANOVA), and in analyses involving electrode as a factor, critical F ratios were based on degrees of freedom adjusted according to the Huynh–Feldt procedure to control for Type I errors in repeated-measures designs. To compare scalp distributions of ERPs, amplitude measurements were normalized by scaling by the square root of the sum of squared voltages over all electrode locations, because in the absence of scaling, amplitude differences between conditions can masquerade as topographic differences [51].

3. Results

3.1. Experiment 1

Fig. 2 shows behavioral results from the fame judgment task given during the test phase. The most important comparisons based on our hypotheses were between the three types of non-famous faces. Correct responses were produced less often for new faces than for R-faces [$t(9) = 4.4$, $p = .002$] or for F-faces [$t(9) = 6.9$, $p < .001$]. The
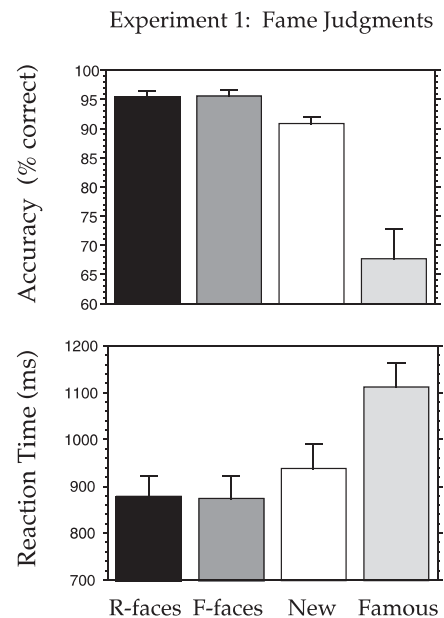

Experiment 1: Fame Judgments

Fig. 2. Results from the fame-judgment test in Experiment 1, showing priming in the form of higher accuracy and faster responses for studied faces than for new faces.

average difference in accuracy was 4.6%. Judgment accuracy did not differ between R- and F-faces [$t(9) = 0.1$]. Likewise, reaction times were slower for new faces than for R-faces [$t(9) = 4.1$, $p = .003$] or F faces [$t(9) = 3.5$, $p = .006$], differing by 62 ms on average. Reaction times did not differ between R- and F-faces [$t(9) = 0.6$]. In short, responses in the fame-judgment task were faster and more accurate for studied faces than for non-studied faces, but did not differ between the two types of studied faces.

Judgment accuracy and latency were also analyzed separately for each stimulus-degradation level (Table 2). First, two-way ANOVAs were computed with factors degradation level (1, 2, or 3) and fame (famous or non-famous, collapsing across the three categories of non-famous faces). Judgments were less accurate for famous than for non-famous faces [$F(1,9) = 25.7$, $p = .001$] and responses were also slower [$F(1,9) = 48.9$, $p < .001$]. The extent of degradation did not reliably influence reaction time [$F(2,18) = 0.6$], nor was the interaction of degradation level by fame significant [$F(2,18) = 2.9$, $p = .078$]. On the other hand, accuracy was influenced by degradation level, as evidenced by a main effect of degradation level [$F(2,18) = 27.9$, $p < .001$] and a degradation level by fame interaction [$F(2,18) = 38.4$, $p < .001$]. For famous faces, degradation level had a clear and systematic effect on accuracy [$F(2,18) = 33.5$, $p < .001$]. The most degraded famous faces (level 1) were the ones most likely to be misidentified as non-famous, and accuracy improved as degradation decreased such that each of these pairwise differences was significant by Tukey Test. For non-famous faces, there was also a significant effect of degradation level [$F(2,18) = 5.7$, $p < .012$], and a Tukey Test showed that accuracy was higher for level 3 than for level 2, whereas none of the other pairwise comparisons were significant.

Table 2
Fame judgments in Experiment 1 for each stimulus degradation level

Measure	Condition			
	Non-famous faces			Famous faces
	R-faces	F-faces	New faces	
Level 1:				
Accuracy (% correct)	95.2	95.0	92.4	52.7
SE	1.2	1.2	1.6	5.9
Reaction Time (ms)	908	904	911	1135
SE	51	46	52	70
Level 2:				
Accuracy (% correct)	93.9	95.7	87.6	68.0
SE	1.2	1.0	2.2	6.2
Reaction Time (ms)	884	871	1017	1068
SE	42	56	65	52
Level 3:				
Accuracy (% correct)	96.8	96.0	92.2	81.0
SE	1.5	1.3	1.6	4.4
Reaction Time (ms)	839	840	899	1127
SE	46	43	49	53

In analyses restricted to results with non-famous faces, priming effects were analyzed for each degradation level by collapsing across the two types of old faces, R- and F-faces (R + F). Two-way ANOVAs were computed with factors degradation level (1, 2, or 3) and condition (R + F or new faces). As in the analyses collapsed across degradation level, accuracy was better overall for R + F faces than for new faces [$F(1,9) = 33.7$, $p < .001$], and this effect did not vary as a function of degradation level [$F(2,18) = 1.3$]. In a parallel analysis of reaction time results, responses were significantly faster overall for R + F faces than for new faces [$F(1,9) = 15.9$, $p < .003$], but this effect did vary with degradation level [$F(2,18) = 5.8$, $p = .02$]. The reaction time difference between R + F and new faces was nonsignificant at degradation level 1 [$t(9) = 0.2$], but was significant at level 2 [$t(9) = 3.4$, $p = .008$] and at level 3 [$t(9) = 3.6$, $p = .006$]. Numerically, priming effects were largest at degradation level 2 for both reaction time (140 ms) and accuracy (7.2%), suggesting that an intermediate level of stimulus degradation may be optimal.

Because our chief conclusions turn on the finding that priming did not differ between R- and F-faces, we conducted an additional analysis to verify this finding. Accuracy and reaction time did not differ between R- and F-faces when results were collapsed across degradation level (Fig. 2). Results in Table 2 show that differences between these two conditions were also extremely small within each degradation level. The largest trends for any difference between R- and F-faces were at degradation level 2; t-tests on these values showed that the trends were nonsignificant for both accuracy [$t(9) = 1.6$] and reaction time [$t(9) = 0.4$]. Furthermore, the nonsignificant differences at degradation level 2 were in the opposite direction to that which would be expected if face recollection had contaminated fame-judgment priming results, as were the slight differences between means collapsed across degradation level (Fig. 2).

3.2. Experiment 2

3.2.1. Behavioral data

In the test phase, subjects were fairly accurate at detecting target events (immediate repeats) and averaged 94% correct ($SE = 7.0$). The mean reaction time was 766 ms ($SE = 116$). Recognition results are shown in Fig. 3. The study phase clearly had the desired effect of producing better recognition for R-faces than for F-faces [$t(10) = 5.7$, $p < .001$]. This recognition difference persisted even though each R-face and each F-face had been viewed seven times previously (three times in the study phase and four times in the test phase). Recognition performance for F-faces can be considered to be significantly better than chance as estimated by the false alarm rate, 12.3% [$t(10) = 7.0$, $p < .001$]. Names for R-faces were recalled correctly on 46.7% of the trials ($SE = 6.0$) and the gist of
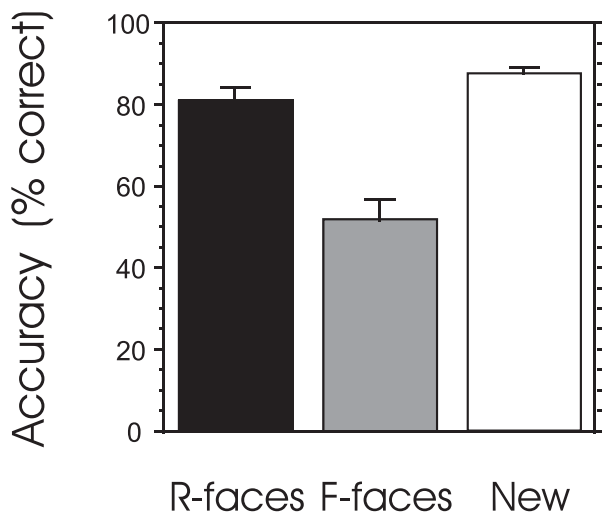
Experiment 2: Recognition

Fig. 3. Results from the recognition test in Experiment 2, showing more accurate recognition for R-faces than for F-faces.

the biographical information was recalled correctly on 73.3% of the trials ($SE = 4.0$).

3.2.2. Electrophysiological data

In the study phase, there was a large effect of stimulus repetition on ERPs for both R-faces (Fig. 4a) and F-faces (Fig. 4b). For example, at the Oz electrode (located over the occipital region at the midline), mean ERP amplitudes from 200–800 ms measured -1.7 μV, 0.5 μV, and 2.6 μV, for first, second, and third presentations of R-faces, and -0.9 μV, 1.0 μV, and 0.6 μV, for first, second, and third presentations of F-faces, respectively. A two-way ANOVA verified this pattern of results via a significant main effect of repetition [$F(2,22) = 7.1$, $p.004$], a non-significant effect of stimulus type [R- vs. F-face, $F(1,11) = 0.1$], and a nonsignificant stimulus type by repetition interaction [$F(2,22) = 2.0$]. These effects were apparent at almost all scalp locations but were largest at posterior locations. However, interpretations of these results are complicated by the fact that ERPs to R-faces reflect the presentation of both face and voice information, whereas F-faces were presented without accompanying voice information. Thus, our analyses are focused on test-phase ERPs.

In the test phase, ERPs to targets included a positive deflection that reached a peak at about 500 ms, whereas lower-amplitude ERPs were elicited by non-targets at this latency (Fig. 4c). At the Oz electrode, the mean ERP amplitude measured from 200 to 800 ms was significantly larger for targets than for non-targets [$t(11) = 2.8$, $p = .018$], averaging 4.4 μV ($SE = 1.4$) versus 2.4 μV ($SE = 1.0$), respectively. This positive deflection to targets (i.e., P300 potential) was apparent at all locations and was maximal at the parietal midline region.

The most important comparisons in this experiment were within the non-target category in the test phase: R-faces versus F-faces versus new faces (Fig. 4d). The
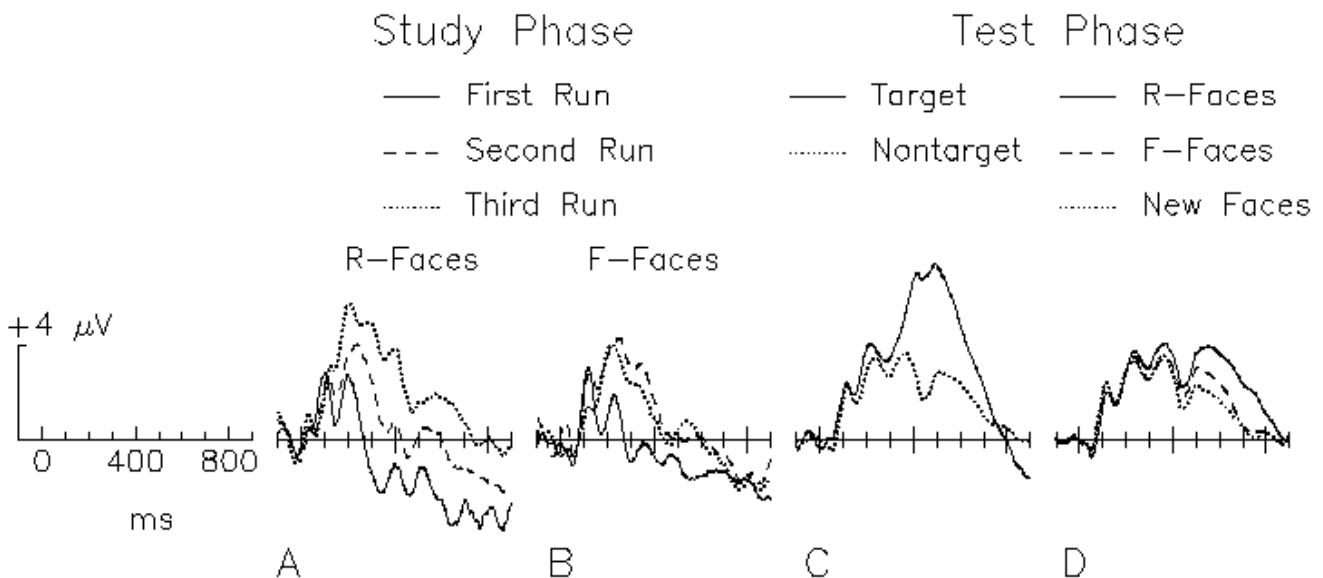

Fig. 4. ERPs from the midline occipital electrode. ERPs elicited by R-faces (A) and F-faces (B) presented during the study phase are shown separately for each of the three experimental runs. Voices were presented simultaneously with R-faces but not F-faces. ERPs elicited by faces in the test phase are shown separately for targets (immediate repetitions of the same face) and non-targets (C). ERPs to non-targets are also shown separately for R-faces, F-faces, and new faces (D).

experiment was designed such that the comparison between R- and F-faces isolated processing related to recollection while balancing other factors: (a) the number of previous presentations was equal; (b) priming was matched; (c) the specific faces were counterbalanced across subjects; and (d) behavioral responses were the same, in that these faces were all non-targets in the target–detection task and so required no overt response.

ERPs were more positive for R-faces than for F-faces at nearly every scalp location, though amplitudes varied across time and location. These effects can be observed in difference waves computed by subtracting ERPs to F-faces from ERPs to R-faces. Difference waves arranged topographically are shown in Fig. 5 (solid line). Quantification of these effects focused on differences from 300 to 600 ms and from 600 to 900 ms, henceforth called the *early* and *late* time intervals. These values are listed in Table 3. For the early time interval, differences between ERPs to R-faces and ERPs to F-faces were largest over frontal and parieto-occipital regions. Differences were statistically significant by *t*-test at Fpz and F7 electrodes and marginally significant at 4 nearby electrodes. This pattern differed from that for the late time interval, in that the late difference was prominent only over parieto-occipital regions. The late difference was statistically significant at Pz and P3 electrodes and marginally significant at 5 nearby electrodes.

In addition, another analysis was conducted using peak amplitude measurements instead of mean amplitude measurements. A late positive peak was maximal at the mid-line parietal location. The maximal ERP deflection between 400 and 700 ms was measured for each subject from this location. Peak amplitudes were significantly greater for R-faces than for F-faces [$t(11) = 2.4$, $p = .0325$], averaging 9.4 μV ($SE = 1.2$) and 7.6 μV ($SE = 0.9$), respectively. Corresponding peak latencies were 599 ms ($SE = 17$) for R-faces and 573 ms ($SE = 18$) for F-faces and did not differ significantly between these two conditions [$t(11) = 1.6$]. These results thus confirm the results obtained with mean amplitude measurements over the early and late time intervals.

The topographic distributions of the early and late difference ERPs are shown in Fig. 6. These two topographies were compared by first scaling the difference measurements using the vector-length method [51] and then conducting a two-way ANOVA with location (21 sites) and temporal interval (early or late) as factors. Results confirmed that the topography of R-face minus F-face ERPs changed from the early to the late interval [$F(20,220) = 3.6$, $p = .032$]. In particular, posterior activity was greatest in the late time interval, whereas frontal activity appeared sooner and did not persist into the late time interval.

In another analysis, ERPs to F-faces were compared to ERPs to new faces. Corresponding difference waves are shown in Fig. 4 (dotted line). The largest difference between these two conditions occurred over anterior locations late in the epoch. Mean amplitude measurements from 600 to 800 ms revealed significant differences at five
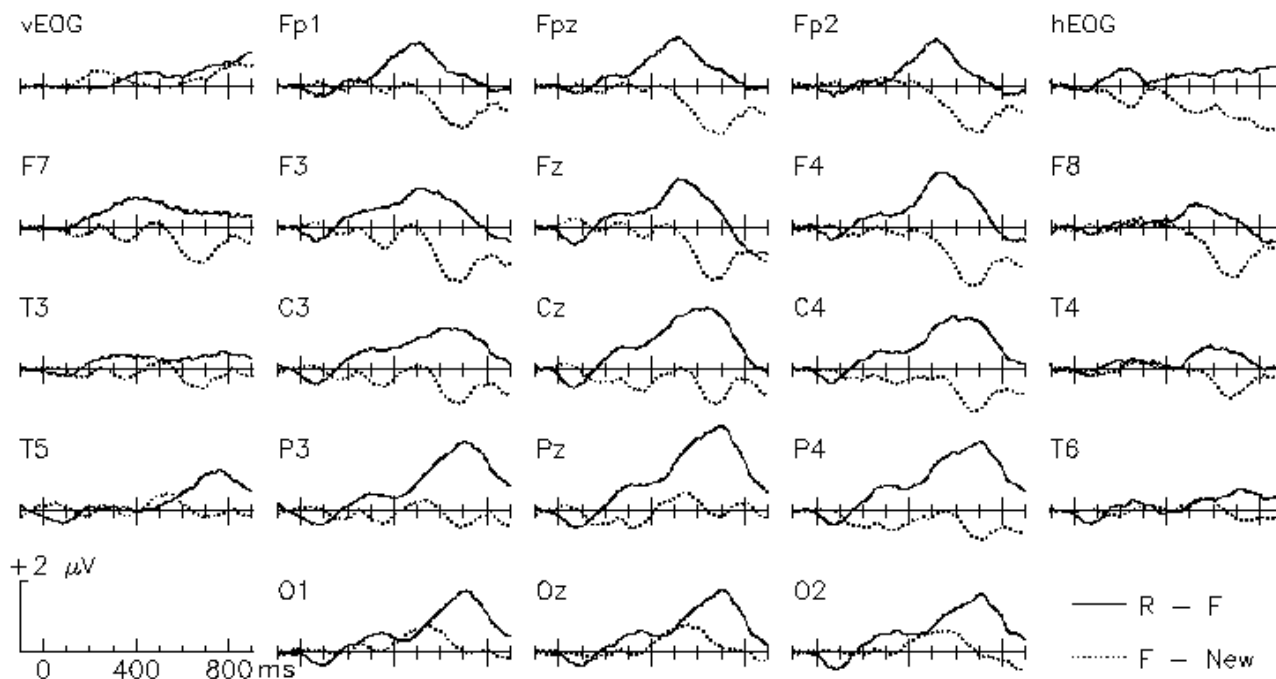

Fig. 5. ERP difference waves from all electrode locations, computed by subtracting ERPs to F-faces from ERPs to R-faces (solid line) and ERPs to new faces from ERPs to F-faces (dotted line). Electrode abbreviations denote scalp locations as follows: frontopolar (Fp), frontal (F), central (C), parietal (P), occipital (O), the midline (z), the left side (odd numbers), and the right side (even numbers).

Table 3
ERP differences between R- and F-faces in Experiment 2

Location	Measure							
	Early interval (300–600 ms)				Late interval (600–900 ms)			
	μV	SE	F(1,11)	p	μV	SE	F(1,11)	p
Midline								
Fpz	0.95	0.39	5.9	.034	0.26	0.38	0.5	> .1
Fz	0.82	0.57	2.1	> .1	−0.03	0.41	0.0	> .1
Cz	1.03	0.57	3.3	.099	0.91	0.42	4.8	.051
Pz	1.10	0.64	3.0	> .1	1.65	0.59	7.9	.017
Oz	0.66	0.55	1.5	> .1	1.11	0.52	4.5	.058
Left side								
Fp1	0.85	0.40	4.5	.057	0.15	0.44	0.1	> .1
F3	0.78	0.46	2.9	> .1	0.2	0.41	0.2	> .1
F7	0.74	0.31	5.7	.036	0.47	0.37	1.6	> .1
C3	0.68	0.53	1.6	> .1	0.76	0.43	3.2	> .1
P3	0.66	0.61	1.2	> .1	1.47	0.55	7.1	.022
T3	0.34	0.32	0.1	> .1	0.39	0.37	1.1	> .1
T5	0.15	0.54	0.1	> .1	0.88	0.57	2.4	> .1
O1	0.60	0.54	1.2	> .1	1.25	0.60	4.3	.061
Right side								
Fp2	0.86	0.50	3.7	.08	0.12	0.42	0.1	> .1
F4	0.92	0.49	3.5	.087	0.33	0.33	1.0	> .1
F8	0.37	0.40	0.8	> .1	−0.01	0.36	0.0	> .1
C4	0.80	0.52	2.3	> .1	0.86	0.45	3.7	.081
P4	0.97	0.59	2.7	> .1	1.37	0.63	4.7	.053
T4	0.28	0.28	1.0	> .1	0.33	0.39	0.7	> .1
T6	0.12	0.59	0.0	> .1	0.43	0.55	0.6	> .1
O2	0.70	0.62	1.3	> .1	1.07	0.63	2.9	> .1

frontal locations: Fpz, Fz, F3, F4, and F8 [$t(11)$'s > 2.4, p's < .034]. At all of these locations, ERPs to F-faces were less positive than ERPs to new faces. The maximum voltage difference was 1.35 μV at the F4 location.
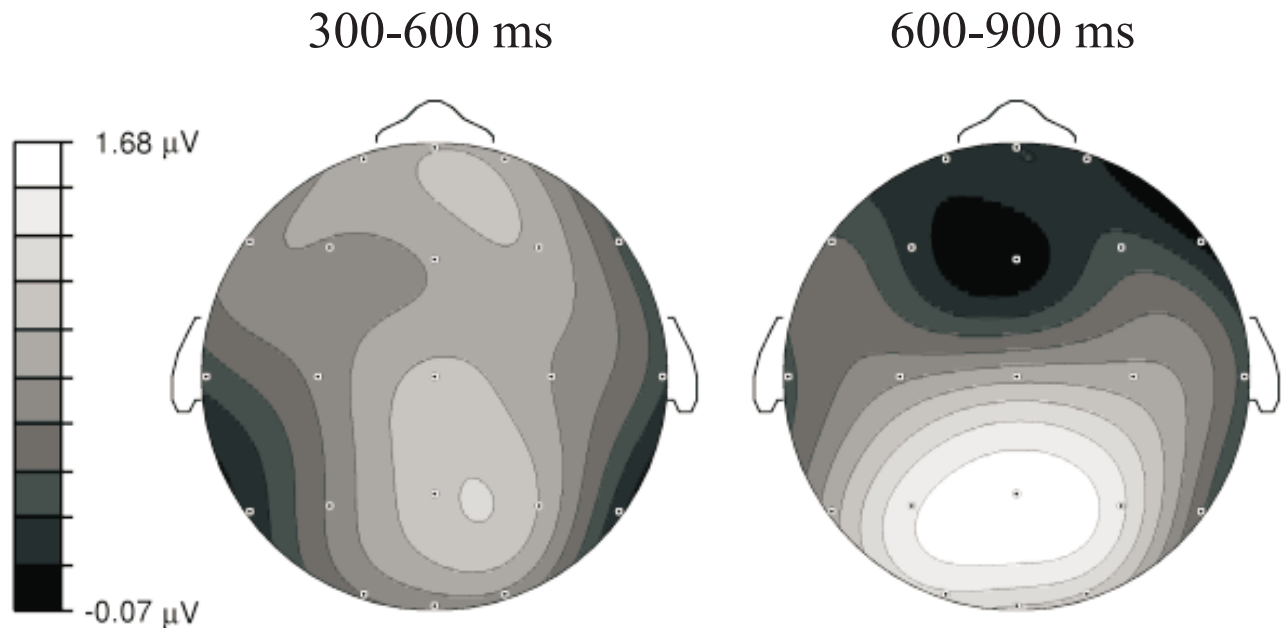
300-600 ms   600-900 ms

Fig. 6. Topographic maps of ERP differences across the scalp, as viewed from above. ERPs to F-faces were subtracted from ERPs to R-faces and mean amplitudes measured from 300 to 600 ms (left) and 600 to 900 ms (right) and displayed using a surface spline interpolation. Small circles represent electrode locations.

4. Discussion

The behavioral results from these two experiments demonstrated a dissociation between two types of memory. The study-phase manipulation — which combined directed forgetting instructions with richer encoding for R-faces versus F-faces — influenced recognition but did not influence priming. Priming was measured in Experiment 1 using a fame-judgment task with degraded stimuli. Recognition was measured in Experiment 2 using a paper-and-pencil test following ERP recordings.

Face priming has been studied most often using famous faces [30]. Priming with non-famous faces has usually been found to be negligible, unreliable, or apparent only with immediate repetition at extremely short retention intervals [6,8,9,74]. In fact, priming of familiarity judgments was not observed with famous faces that could not be spontaneously recognized as famous [16]. These results dovetail with evidence that there are fundamental differences between how the brain processes familiar and unfamiliar faces [3,10,21,48,65,93]. Priming effects have thus been interpreted within the context of a modular account of face processing [15] as effects restricted to representations of facial identity ('face recognition units'). However, priming with non-famous faces has been observed in a few circumstances, including in gender judgments with face stimuli modified to show only internal face features [35], in identity matching with pairs of faces [63,92], and in expression matching [92]. Here we showed that fame-judgment responses to degraded non-famous faces were modified as a function of prior exposure to those faces. On average, subjects were 4.6% more accurate and 62 ms faster for studied than non-studied faces. Furthermore, the study-phase manipulation between R- and F-faces did not alter the magnitude of face priming in either accuracy or response latency.

The priming of fame-judgments that we observed in Experiment 1 appears on the surface to resemble ''becoming-famous-overnight'' effects studied by Jacoby and colleagues [40,41], but the resemblance is actually minor due to several critical differences. Becoming famous overnight refers to a tendency for non-famous names to be judged famous. A feeling of familiarity elicited by non-famous names that were also presented earlier may have been misattributed as a feeling elicited by a mildly famous name. Importantly, all of the famous names in these experiments were only mildly famous. In contrast, stimuli in our experiment differed in three ways: (1) faces were used rather than names, (2) famous faces were highly famous rather than mildly famous, and (3) test stimuli were perceptually degraded. The priming effect reflected a tendency for non-famous faces to be judged non-famous (i.e., higher accuracy for studied faces). We suggest that the priming we observed is more closely related to priming in perceptual identification paradigms in which degraded stimuli must be identified. In this case, degraded faces

were identified more quickly and accurately if they were presented earlier in the experiment. Such effects have been modeled using an interactive activation model [19,20], but they can also be conceptualized as a bias [72].

A critical issue for evaluating priming results is the difficulty of obtaining performance measures that are not contaminated by explicit memory retrieval. Jacoby's process-dissociation procedure [39], in particular, has been used recently to attempt to disentangle the influence of multiple processes on such performance measures, although some controversy surrounds the use of this procedure [17,24,36,76,91]. Results from Experiment 1 suggest that the performance measures from the fame-judgment task were not contaminated by explicit memory retrieval. Based on later recognition results, we presume that subjects were able to recognize R-faces better than F-faces during the test phase. If fame judgments had been influenced by recognition, results might be expected to differ between R- and F-faces, although it is possible that this influence was precisely counteracted by more priming for F-faces than for R-faces. Such influences on fame judgments might also be expected to differ as a function of degradation level. Yet there were no differences at any degradation level. Thus, the priming measures appear to have been largely uncontaminated. In short, even though R-faces tended to be recognized better than F-faces, the same magnitude of priming was observed for both types of faces.

This dissociation between recognition and priming not only adds to the literature on memory dissociations but also provides a basis for interpretations of the ERP results. The specificity of the study-phase manipulation between R- and F-faces implies that the ERP difference in the test phase between R- and F-faces can be taken as an ERP correlate of face recollection, divorced from priming and other factors that are normally confounded in ordinary comparisons between old and new items. This logic of interpretation was used previously in studies of ERPs elicited by words [34,60,61]. The present results attest to the generality of this phenomenon, although it is highly likely that important differences exist between the cognitive processing associated with recollection in these different circumstances (e.g., see [84]). Nonetheless, the present results show that the experience of seeing a face and recollecting information about that person (i.e., 'person recognition') is associated with a characteristic pattern of brain electrical activity at the scalp. We further argue that this ERP correlate of face recollection is distinct from any ERP correlates of priming that may be produced simultaneously, by virtue of our finding that priming did not differ between R- and F-faces.

Although these experiments were not designed to reveal ERP correlates of priming, some differences between responses to F-faces and new faces were found. At frontal scalp locations, ERPs to F-faces were less positive than ERPs to new faces. The latency of this effect (600–800

ms) suggests that it probably does not index processing that determined priming of behavioral responses to faces. Experimental manipulations that specifically influence priming may be required to isolate ERP correlates of face priming, as has been done in studies with word stimuli [59,62], and we are currently exploring this possibility.

Several previous studies have examined ERPs elicited by faces. For example, some early ERPs in the range of 150 to 200 ms have been related to face-specific and eye-gaze-specific perceptual processing [7,12,42,43]. FMRI and intracranial ERP results suggest that these early potentials reflect cortical activity in occipitotemporal and posterior fusiform regions [2,68,70]. Subsequent ERPs appear to reflect encoding of important facial features, given that such potentials have been found to be predictive of later face recognition [84,85]. ERPs have also been identified with facial working memory in identity and expression-matching tasks [4,53,67] and in other paradigms in which comparisons were made between familiar and unfamiliar faces [26,90]. ERP repetition effects have been reported for familiar and unfamiliar faces [8,9,83]. Begleiter and colleagues recorded ERPs to familiar and unfamiliar faces and attempted to relate their results to priming and recognition [6,38]. However, these results are different from the present results in several respects. First, face repetition was immediate (1.6 s interstimulus interval), so that corresponding ERP effects may be attributable to basic perceptual processing in working memory. Second, ERP repetition effects that were found at approximately 240 ms after face onset may not be specific to priming but may instead have reflected recognition of the repetition, even though it was irrelevant to the task of discriminating famous from non-famous faces. A clear distinction thus cannot be made between priming and recognition with respect to these results [6,38].

Results from the topographic analyses of the ERP correlate of face recollection in the present study suggest that multiple brain regions were involved, although inferences about intracranial generators await additional evidence from other methods. Nevertheless, it is likely that activity from prefrontal cortex produced some of the scalp-recorded activity, particularly from 400 to 600 ms. In contrast, posterior activity was present both in the early and later intervals, suggesting that the frontal contribution may have been particularly relevant for controlling the retrieval of information stored in posterior neocortical regions. This pattern of topographic results is similar to that found previously for visual word recollection [60]. The ERP correlate of recollection in that study was evident first at frontal regions and later over most regions of the scalp. Based on these patterns of ERP scalp topographies, and on other ERP and neuropsychological evidence [18,71,81,82], we speculate that prefrontal regions are important both for strategic search processes that precede successful retrieval and for maintaining the retrieved information in working memory. Person recognition in the present study probably depends on interactions between prefrontal regions and posterior neocortical regions, which mediate the retrieval and continued processing of facial information, biographical information, and contextual information pertaining to the study episodes.

Acknowledgements

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