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Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces

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Abstract

Recent studies from our laboratory have resulted in the identification of an event-related potential (ERP) correlate of a visual memory process. This memory process is reflected by a reduction in the voltage of the visual memory potential (VMP) to repeated pictures of unfamiliar faces compared to novel pictures of faces. In the current experiment we used unfamiliar and famous faces in an identical repetition priming paradigm, while the subject differentially recognized famous from non-famous faces. Significant differences in response times were obtained between primed and unprimed familiar faces, but not between primed and unprimed unfamiliar faces. The VMP was reduced to primed unfamiliar faces and significantly diminished to primed familiar faces compared to unprimed stimuli. Priming was typically reflected by a reduction of the VMP at the occipito-temporal region, whereas recognition resulted in a diminution of the VMP at both the occipito-temporal region and at the frontal region. These data support the involvement of differential neural systems for priming and recognition of visual stimuli.

Keywords: Recognition; Priming; Faces; Event-related brain potentials

1. Introduction

We have recently identified a component of the event-related potential (ERP) which appears to index visual short-term memory (visual memory potential, VMP) in humans (Begleiter et al., 1993). This component of the ERP was readily observed in a visual paradigm in which we used nonsense visual shapes in a modified delayed matching to sample task. We observed that an ERP component occurring between 170 and 240 msec was significantly smaller to a matching stimulus compared to a non-matching stimulus. As this ERP component indexes processes related to visual short-term memory we labeled this component the visual memory potential (VMP).

These ERP results in humans are quite consistent with single cell studies in temporal cortex in monkeys where decreases in neuronal activity were observed to matching visual stimuli (Mikami and Kubota, 1980; Miller et al., 1991; Riches et al., 1991). In our experiment using a delayed matching to sample paradigm, the task involved both priming and recognition and did not allow us to assess the specific antecedents to the VMP.

In order to assess the relationship between the VMP and priming and/or recognition we conducted another investigation using faces as stimuli (Hertz et al., 1994). Faces were used as ecologically relevant stimuli, because recognition of such stimuli is fundamental for the appropriate conduct of all social interactions in humans. Moreover, we selected to use unfamiliar faces because extensive behavioral (Bruce, 1991) and neurophysiological literature (Perrett et al., 1987) currently exists. In this study, we investigated the effects of repetition priming in one experiment, and of recognition in another experiment. Specifically, in the first study (priming condition) the subjects were presented with both unfamiliar faces and unrecognizable face scrambles which were matched to the faces in intensity and number of computer pixels. An equal number of face and scramble stimuli were randomly presented, and the subject was asked to press one button for faces and another button for scrambles. The subject was not told that half of the faces and half of the scrambles were repeated in order to study identical repetition priming. In a subsequent experiment conducted with the same group of subjects, the

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same sequence of stimuli was used. In this study, however, the subject was specifically told that the faces and scrambles would be repeated and was asked to press one button to repeated stimuli and another button to non-repeated stimuli. Our findings indicate that in the priming condition the amplitude of an ERP component occurring at approximately 240 msec was significantly reduced to primed faces with additional latency effects present as early as 180 msec. These ERP findings are more striking in the absence of significant response time differences between primed and unprimed stimuli. However, when the same stimulus sequence was used in an explicit recognition task, greater neuroelectric changes were evident in addition to significantly reduced response times to the recognized stimuli.

These findings suggested as one possible interpretation that stimuli which initially are particularly well encoded will subsequently be better recognized. Benton (1980) speculated that identification of familiar faces and discrimination of unfamiliar faces involve different brain mechanisms. Moreover, the differences between familiar and unfamiliar face processing may in large measure be due to the different sources of information that can mediate recognition of the different classes of faces. The knowledge that a face is familiar implies that this face activates a well encoded visual representation of the appearance of the familiar person (Bruce and Young, 1986). Indeed, it is hypothesized that for complex stimuli such as faces, significant ERP priming effects will result if such faces are familiar and well encoded by the subject.

In the present experiment we hypothesized that recognition of stimuli stored in long-term memory, such as highly familiar faces, would elicit differential VMPs compared to unrecognized stimuli such as unfamiliar faces. In addition we hypothesized that priming to familiar and unfamiliar faces would yield a significantly different VMP component. We recorded ERPs to familiar and unfamiliar faces in the course of an identical repetition priming paradigm, while the subject identified familiar and unfamiliar faces.

2. Methods

Twenty-two right-handed males (mean age = 20.7) volunteered for this experiment and were paid for their participation. All individuals were fitted with an electrode cap (ECI Electrocap International). For half of the subjects we recorded from 31 electrodes; for the other subjects we recorded from 62 electrodes. In all individuals we used the entire 10–20 montage and also recorded from an additional 12 sites as follows: AF3, AF4, FC5, FC6, FC1, FC2, CP1, CP2, CP5, CP6, PO1, and PO2. For the 62-channel montage we used all of the afore-mentioned electrodes plus the following sites: FPz, AF7, AF8, AFz, F1, F2, F5, F6, FC3, FC4, FCz, FT7, FT8, C1, C2, C5, C6, TP7, TP8, CPZ, CP3, CP4, P1, P2, P5, P6, PO7, PO8, POz, Oz. All scalp electrodes were referred to Cz according to methods described previously (Begleiter et al., 1993). Subjects were grounded with a forehead electrode, and all impedances were kept below 5 kΩ. Vertical eye movements were monitored with electrodes placed directly above and below the right eye, and horizontal eye movements were monitored with electrodes placed at the outer canthi of the eyes. Trials with excessive eye movements (> 73.3 μV) were eliminated from the final average. The electrical activity recorded at each electrode was fed to a set of amplifiers (Sensorium 2000) with a 10,000 gain and a bandpass of 0.02–100 Hz. The amplified activity was sampled at a rate of 256 Hz during an epoch of 100 msec preceding, and 1 sec following each stimulus presentation.

The subject was seated in a reclining chair located in a sound-attenuated RF shielded room (IAC) and fixated a point in the center of a computer display located 1 m away from his eyes. The famous face stimuli consisted of 120 male and female famous faces. These famous faces were selected from high quality photographs of well known personalities in the entertainment world, the world of politics, and the sports world. The non-famous 120 faces were carefully selected males and females from medical school yearbooks. Each face was presented in black and white on a high resolution computer screen for a duration of 300 msec subtending an angle of 8–10° as a frontal view without shoulders. The experimental paradigm was designed to examine the effects of repetition priming for both famous and unfamous faces. A continuous series of 240 faces were presented with an interstimulus interval (ISI) of 1.6 sec. For famous faces, 40 trials consisted of the immediate repetition of the same face (primed famous face), 40 trials were preceded by a different famous face (unprimed famous face), and 40 trials were preceded by a non-famous face. Similarly, for the non-famous faces, 40 trials consisted of the immediate repetition of the same face (primed non-famous face), 40 trials were preceded by different faces (unprimed non-famous faces), and 40 trials were preceded by famous faces. These conditions yielded a total of 240 trials which were equally likely to be presented with the restriction that no more than 5 famous or non-famous faces would be displayed in a row.

At the beginning of the experiment, the subject was only told that two types of stimulus would be presented: famous faces and non-famous faces; he was asked to press a button in one hand as quickly as possible if he recognized the person, and to press the button in the other hand if he did not recognize the individual. The order of the buttons was randomized across subjects.

The ERPs were recorded to all stimuli and averaged for 6 cases: famous faces followed by repeated famous faces (repeat famous), famous faces followed by different famous faces (different famous), non-famous faces followed by repeated non-famous faces (repeat non-famous), non-famous faces followed by different non-famous faces (different non-famous), famous faces followed by non-famous faces (unprimed non-famous), and non-famous faces followed by famous faces (unprimed famous). This experiment yielded an ERP consisting of 4 different peaks most clearly discernible at the more posterior electrodes (Fig. 1): component 1 (C1, 30–65 msec), component 2 (C2, 90–105 msec), component 3 (C3, 150–175 msec), and component 4 (C4, 190–250 msec). In this experiment a downward deflection indicates greater negativity at the most posterior electrodes with respect to the vertex (Cz) electrode. Amplitudes and latencies were initially measured at electrode P8 where maximal amplitudes were obtained. Measurements at other electrodes were based on the latency of each component obtained at P8.

The topographic analyses of the ERP data were based on half of the ERP data set (62 electrodes only) using a spline-Laplacian transformation (Perrin et al., 1987; Gevins et al., 1991; Nunez and Pilgreen, 1991). The surface Laplacian is an estimate of the local current density through the skull into the scalp. In addition, the scalp current density (SCD) data were transformed to a measure of surface energy density (SED) which we have recently developed (Wang et al., 1994) in order to better visualize local scalp distributions.

3. Results

Subjects responded accurately on 99% of the trials in which a non-famous face was presented and not recognized. They were able to recognize the famous faces on 92% of the trials. The average response time between the repeated non-famous faces (543.44 msec) and the different non-famous faces (577.86 msec) was not significantly different. The response time to the repeated famous faces (503.40 msec) and the different famous faces (613.33 msec) was significantly different at $P < 0.001$.

Statistical analyses of ERP data were carried out on artifact-free trials with correct behavioral responses. We assessed regional potential differences by dividing the 31 electrode locations into 5 different regions as follows: frontal (FP1, FP2, AF1, AF2, F7, F3, Fz, F4, F8), central (FC5, FC1, FC2, FC6, C3, C4), parietal (CP1, CP2, P3, Pz, P4), temporal (T7, CP5, P7, T8, CP6, P8) and occipital (PO1, PO2, O1, O2). We conducted a number of MANOVAs separately for each ERP component using the amplitude or latency at each of the 5 regional electrode arrays as a dependent vector, namely comparing repeated

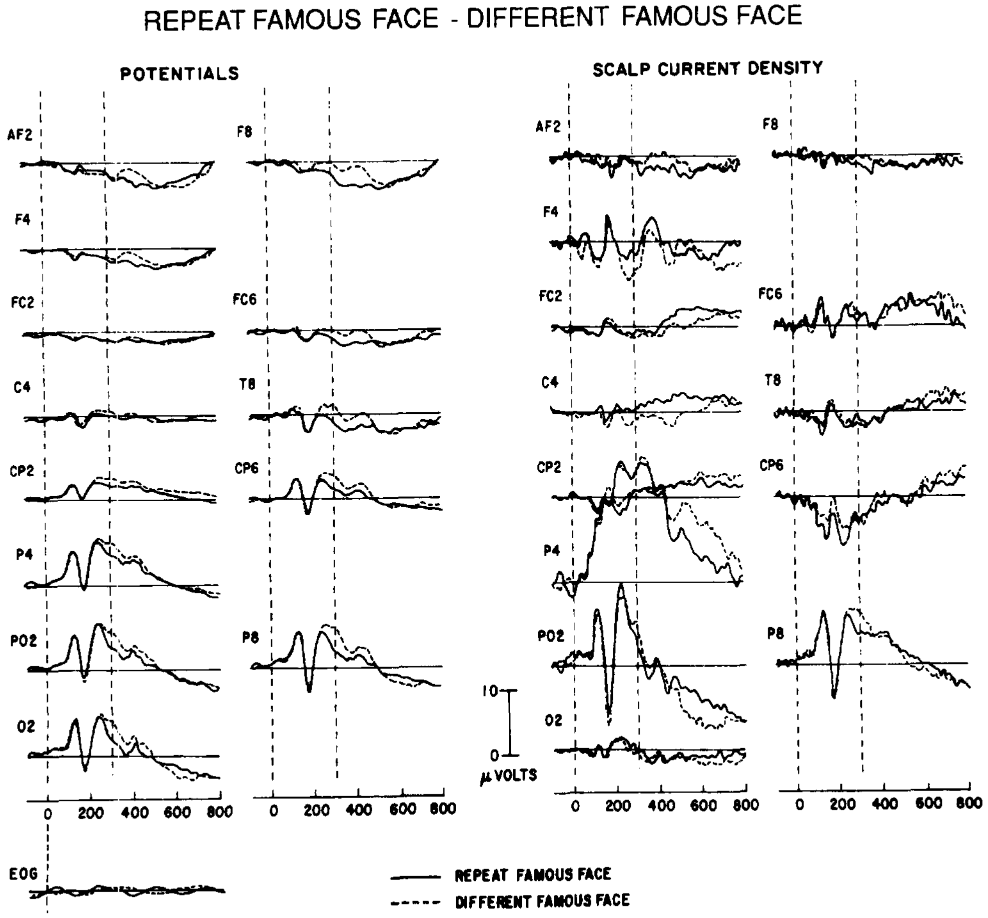


Fig. 1. Grand mean ERP wave form: repeat famous face and different famous face. Left two columns illustrate potential recordings; right two columns reflect the same data transformed as scalp current density. In this experiment a downward deflection indicates greater negativity at the most posterior electrodes with respect to the vertex (Cz) electrode.

Table 1
MANOVA results for C4 amplitude comparisons (P values)

Conditions	Electrode group				
	F	C	P	T	O
Primed vs. unprimed non-famous faces				< 0.04	
Primed vs. unprimed famous faces	< 0.005	< 0.01		< 0.01	
Famous faces vs. non-famous faces	< 0.03			< 0.004	
Primed famous faces vs. primed non-famous faces				< 0.01	

(primed) and different (unprimed) stimuli for both famous faces and non-famous faces.

The C4 component (VMP) yielded significant differences ($P < 0.04$) between the primed and unprimed non-famous faces at the temporal region only (Fig. 1). The comparison between primed and unprimed famous faces yielded a number of significant differences for the C4 component as follows: frontal region, ($P < 0.005$); central region ($P < 0.01$); temporal region ($P < 0.01$) (Table 1 and Fig. 1). Moreover, primed famous faces yielded a significantly lower amplitude of the C4 component compared to the primed non-famous faces at the temporal region only ($P < 0.01$). The C4 component was significantly smaller for the recognized famous faces compared to the non-recognized recognized non-famous faces at the frontal region ($P < 0.03$), and at the temporal region ($P < 0.004$; see Fig. 2).

In addition to the amplitude differences mentioned above, there were several latency differences as follows: the C3 component occurred significantly earlier for the primed famous faces compared to the unprimed famous faces at the frontal region ($P < 0.02$), central region ($P < 0.02$), temporal region ($P < 0.01$), and occipital region ($P < 0.02$). Finally, the C2 component occurred significantly earlier for non-famous faces compared to famous faces at the parietal region ($P < 0.006$), temporal region ($P < 0.005$), and occipital region ($P < 0.03$).

In order to differentiate priming effects yielded by famous faces from those evoked by non-famous faces, we obtained difference wave forms between primed and unprimed famous faces as well as primed and unprimed non-famous faces. As illustrated in Fig. 3 the difference wave forms for the non-famous faces indicate substantial amplitude differences at the posterior electrodes with a

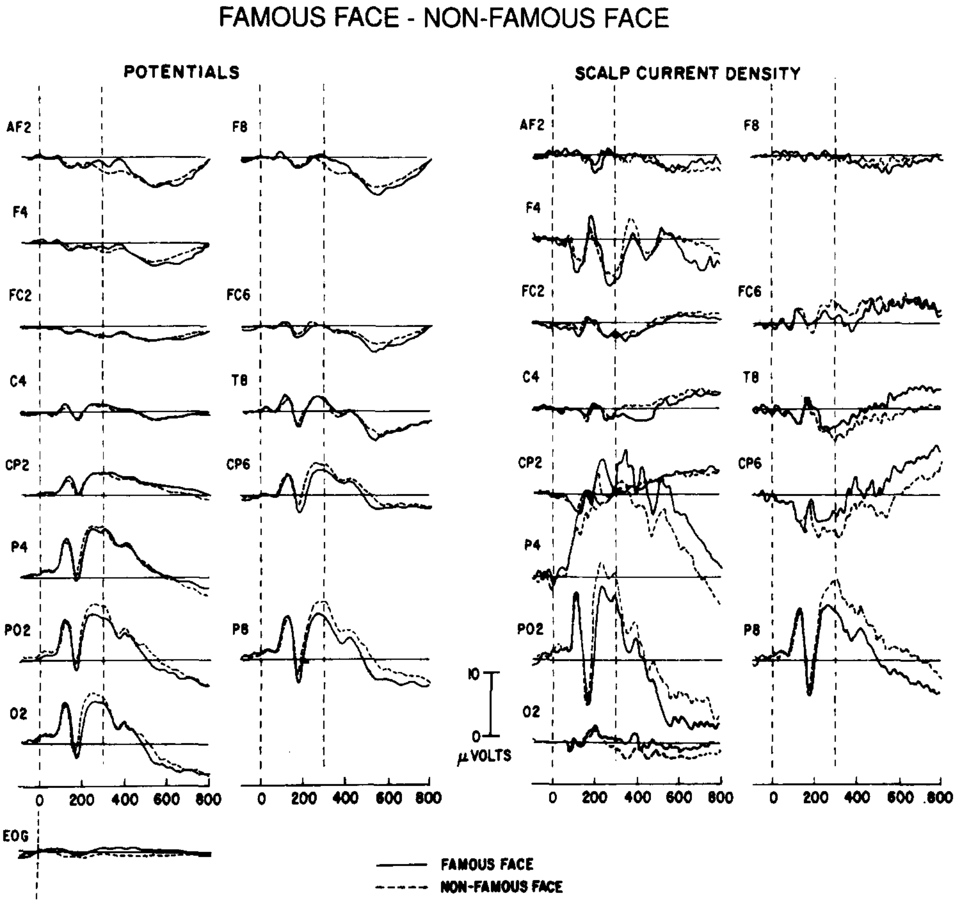


Fig. 2. Grand mean ERP wave form: famous face and non-famous face. Left two columns and right two columns same as in Fig. 1. Polarity same as in Fig. 1.

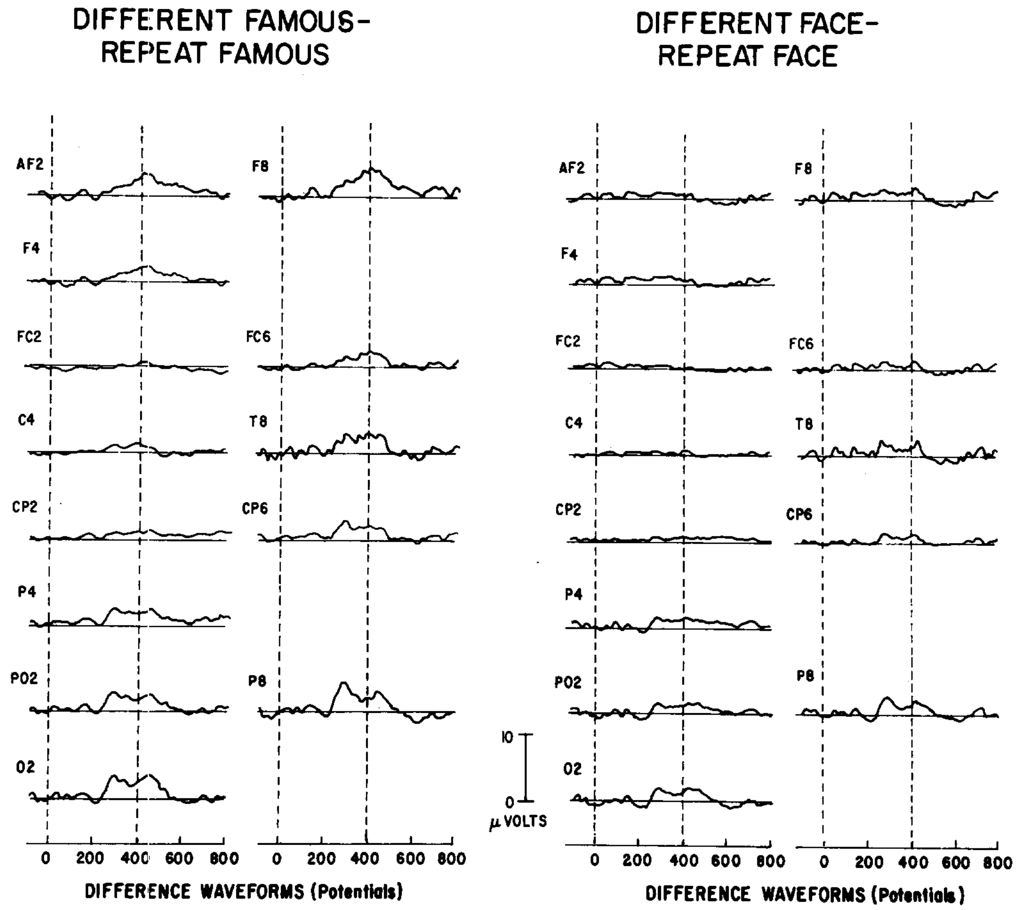


Fig. 3. Difference wave forms obtained by subtracting scalp potentials between different famous faces minus repeat famous faces (left columns), and different non-famous faces minus repeat non-famous faces (right columns).

maximum difference at the P8 electrode. The difference wave forms for the priming effect with famous faces have a very similar topography with an increased amplitude effect. In addition, the difference wave forms for the famous faces also show a frontal difference in the scalp potentials. This is best illustrated in the surface energy density plots (Wang et al., 1994) (Fig. 4).

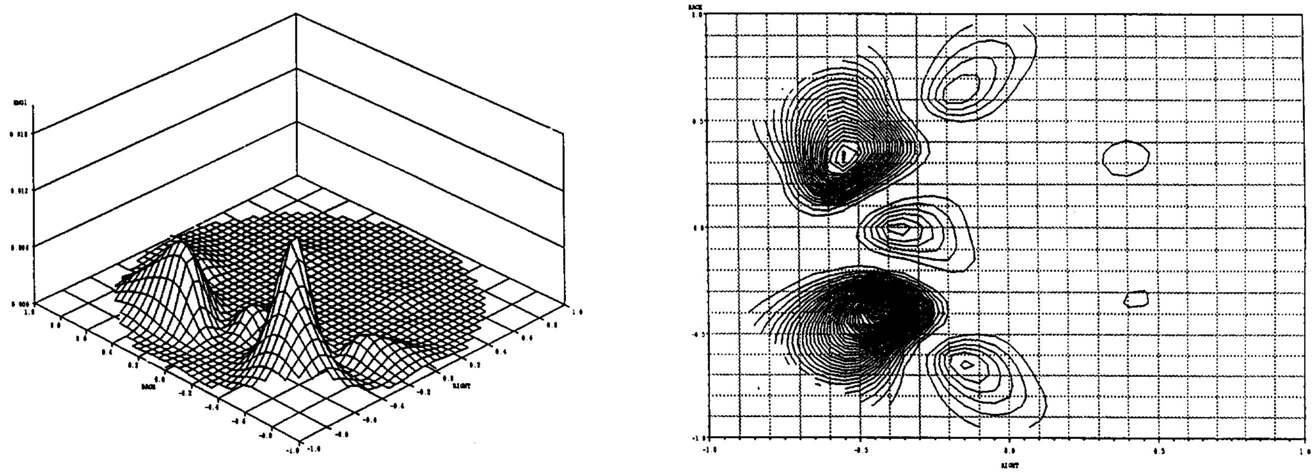
The current source density map for famous faces is illustrated for the VMP component (Fig. 5) and indicates a strong source at the occipito-temporal border. The surface energy density (SED) maps (Fig. 4) illustrate (top row) that priming of non-famous faces produces specific energy (VMP) at the occipito-temporal regions. The bottom row illustrates that the recogniton of famous faces is associated with specific energy at the occipito-temporal regions in addition to the frontal region.

4. Discussion

Our findings replicate our recent results (Hertz et al., 1994) where repetition priming to unfamiliar faces did not yield significant response time differences, but resulted in significant ERP differences of the VMP (C4 component). Specifically, the VMP component was significantly smaller to the primed compared to the unprimed unfamiliar faces in a task requiring subjects to determine whether a face or a scramble had occurred. The lack of a significant difference in response time between primed and unprimed unfamiliar faces is consistent with past behavioral studies (Bentin and Moscovitch, 1988; Young and De Haan, 1988; Ellis et al., 1990; Paller et al., 1992). It is becoming increasingly evident that a significant priming effect with unfamiliar faces cannot be demonstrated at the behavioral level. However, our present findings indicate that a significant response time effect is present with a repetition priming paradigm using well encoded famous faces. While differential response time effects were obtained only for priming of famous faces, it should be noted that the ERP component occurring at approximately 240 msec (VMP-C4) was significantly smaller for the primed stimuli compared to the unprimed stimuli, regardless of whether the faces were famous or non-famous. Moreover, the VMP component was significantly smaller for the primed famous faces compared to the primed non-famous faces at the temporal region only.

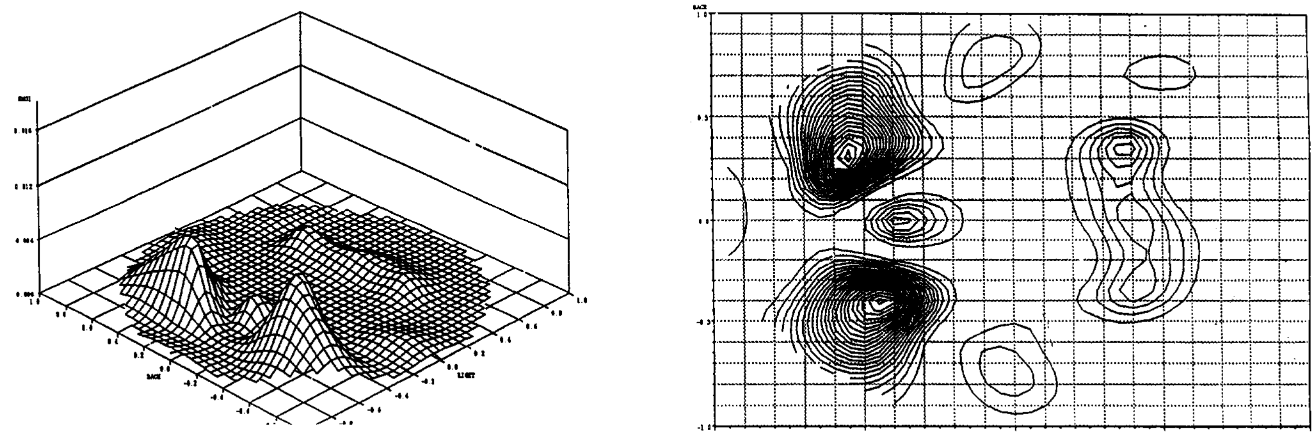
Our present study using repetition identity priming with famous and non-famous faces replicates the response time findings typically reported in the behavioral literature (see review by Ellis, 1992). Repetition priming has been most commonly demonstrated in studies using the familiarity decision task, where individuals are presented with familiar and unfamiliar faces and are required to make a speeded response to indicate whether the face stimulus was familiar or unfamiliar. In this paradigm, repetition priming is observed to familiar stimuli using familiarity decisions. Our ERP findings obtained in the present experiment indicate that for the famous faces, the VMP component is quite consistent with the response times. However, while we did not obtain significant differences in response time between primed and unprimed non-famous faces, we did observe a significant, although weak ($P < 0.04$), difference in VMP. This suggests that the VMP component of the ERP may be more sensitive to repetition priming of non-famous faces than response time.

Our ERP results indicate that the VMP component is significantly different between recognized (famous) faces and non-recognized (non-famous) faces. This recognition effect is obtained at both the temporal and frontal regions. A similar recognition effect is obtained at the temporal and frontal regions when primed and unprimed famous faces are compared. In this task the presentation of repeated (primed) and non-repeated (unprimed) famous faces leads inevitably to recognition of all stimuli. This process of recognition involves both temporal and frontal processing. The involvement of frontal cortex in the recognition of visual stimuli has been demonstrated with single cell recordings in primates (Goldman-Rakic, 1988). The priming effects obtained in our study appear to be restricted to the temporal region only. These ERP findings suggest that priming of face stimuli may involve processing in the temporal region, whereas recognition of familiar face stimuli may involve both the temporal and frontal regions. These data do support the notion that priming and recognition of stimuli may involve different neural systems (Schacter, 1992; Squire, 1992; Paller and Kutas, 1992). It is, however, quite possible that the spatial resolution yielded by our technique is not sufficient to unequivocally resolve the issue of differential system involvement, particularly of structures such as the hippocampus known to be



SED (primed non-famous face)

SED Contour (primed non-famous face)



SED (famous face)

SED Contour (famous face)

Fig. 4. Surface energy density (SED). Leftmost axis represents back of the head, right axis represents front of the head. Top row is the SED on the left and its contour map for the primed non-famous face. The greatest energy is located at the temporal sites with emphasis on the right temporal region. Bottom row illustrates the SED and its contour for the energy involved in processing the recognition of famous faces. Note the energy at the temporal region with additional involvement of the frontal region.

involved in long-term recognition (Mishkin, 1982; Squire and Zola-Morgan, 1991). Nevertheless, our results do address the issue of differential neural system involvement in the process of recognition and priming.

The findings in the current experiment indicate that the ERP component we (Begleiter et al., 1993) labeled the VMP (visual memory potential) is a neuroelectric event, which appears to be quite sensitive to priming and recognition of faces, and is primarily manifested by a strong current source at the occipito-temporal border. It should be noted that other investigators have studied face recogniton with the use of positron emission tomography. In face matching tasks, Sergent et al. (1992) and Grady et al. (1994) demonstrated that the fusiform gyrus was significantly activated.

The present ERP data suggest that the VMP is sensitive to both, priming and recognition. Our results suggest that the VMP recorded from humans is influenced by the traces of stimuli stored in memory (Begleiter et al., 1993; Hertz et al., 1994). When the present stimulus matches a stored trace, the VMP to that stimulus is significantly diminished. In our present study the manifestations of priming and recognition are not simply demonstrated by the amplitude or latency of the VMP but, in addition, by the topographical distribution of the VMP under different behavioral conditions. Our findings indicate that priming is manifested by neurophysiological changes at the temporal region, whereas for recognition of familiar faces, both the temporal and frontal regions are involved. The surface energy density (SED) plots displayed in Fig. 4 indicate that priming of faces is manifested by significant occipito-temporal activity, whereas recognition of familiar faces involves both the occipito-temporal region and the frontal region.

These data in humans are in agreement with single cell recordings in monkeys which have demonstrated that inferotemporal (IT) neurons show a significant reduction in activity to the presentation of stimuli held in memory (Baylis and Rolls, 1987; Mikami and Kubota, 1980; Rolls et al., 1989; Riches et al., 1991). Furthermore it has also

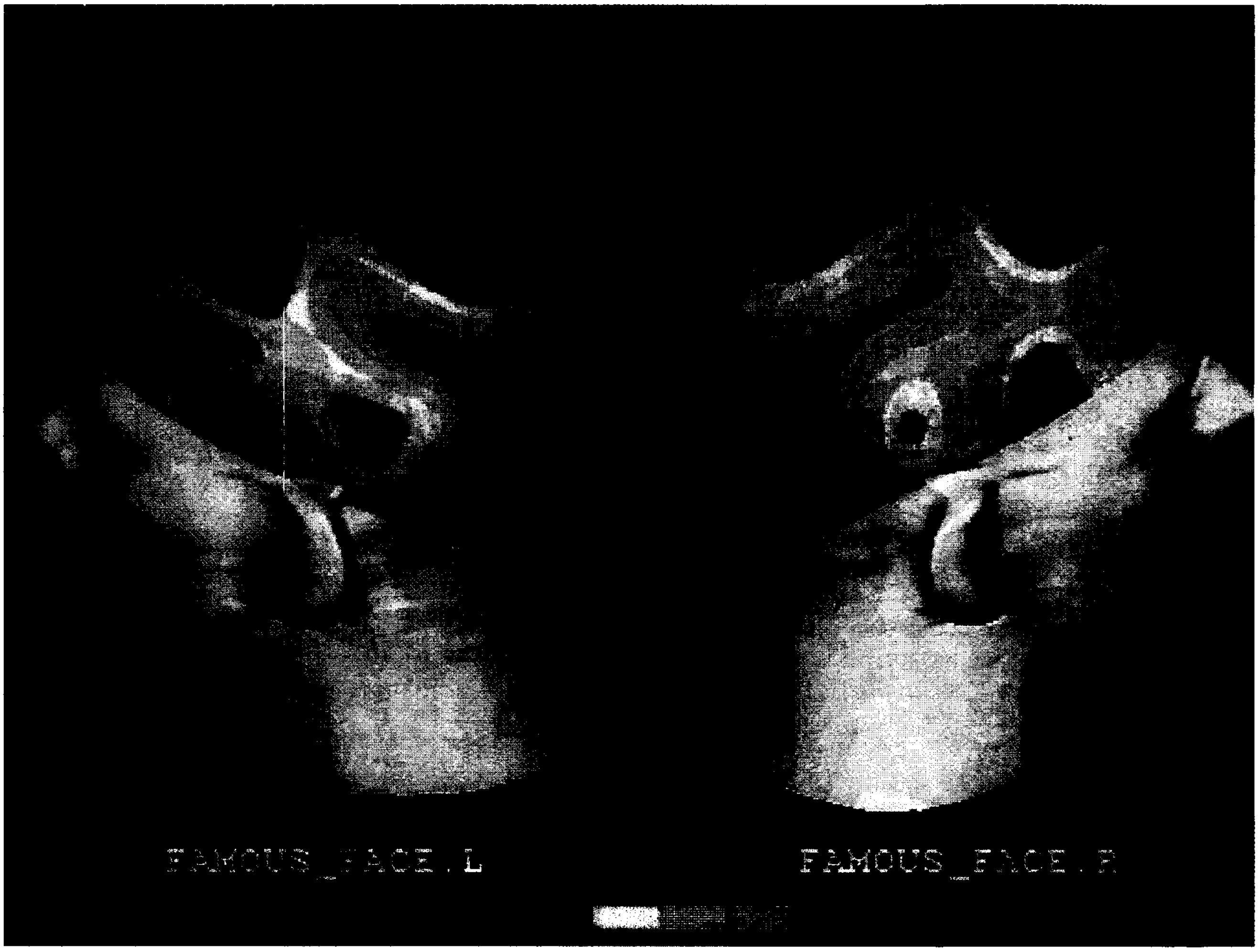


Fig. 5. Current source density map, VMP-C4 component. Source is represented by red, the sink by blue.

been demonstrated that IT neurons are not exclusively responsive to priming or recognition but participate in a variety of memory functions (Miller et al., 1993).

In addition to the reduction of the VMP to primed stimuli, we have also found that the latency of the VMP is significantly earlier to primed as compared to unprimed stimuli. This difference in processing time is consistent with response times obtained to famous faces. The VMP latency to the primed unfamiliar faces may be more sensitive than the response time measure. This finding in the current experiment is consistent with results obtained in a recent study from our laboratory (Hertz et al., 1994).

It should be noted that our findings in the present experiment are different from ERP results obtained to face stimuli by other investigators. Smith and Halgren (1987) reported that a posterior N445 component was significantly larger in amplitude to non-repeated faces. An ERP experiment reported by Sommer et al. (1991) noted that while ERP differences were predictive of subsequent face recognition, there was no ERP feature associated with recognition of face stimuli. Bötzel et al. (1989) recorded ERPs evoked by famous and unknown faces. The authors report no significant differences between the two classes of stimulus.

In our previous study (Begleiter et al., 1993) we investigated the effect of interstimulus interval and stimulus probability, two conditions which are known to influence the visual N2 component (Ritter et al., 1983) as well as the MMN component (Näätänen, 1992). We observed that both stimulus probability and interstimulus interval did not have a significant effect on the VMP. Moreover, because the VMP is larger to new unprimed events it may be argued that this ERP component is indeed identical to the N400 component. It should be noted that the topography of the N400 as assessed by sophisticated techniques was characterized by the lack of any topographical features (Curran et al., 1993). This is in sharp contrast to the topographical distribution of the VMP which manifests a scalp current density distribution specific to the occipito-temporal border (Begleiter et al., 1993; Hertz et al., 1994), as observed in the present study.

The high temporal resolution of ERPs coupled with the improved spatial resolution of current density maps indicate that recognition of faces occurs on or about 240 msec at approximately the occipito-temporal border as well as the frontal region. These results provide the opportunity to use these techniques to study the temporal resolution of sensory reception and recognition of faces and other complex visual stimuli in the human brain.

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