

Event-related potentials to faces: the effects of priming and recognition

Sharon Hertz ^a, Bernice Porjesz ^{b,*}, Henri Begleiter ^b and David Chorlian ^b

*Departments of ^a Neurology and ^b Psychiatry, State University of New York Health Science Center at Brooklyn,
Box 1203, 451 Clarkson Ave., Brooklyn, NY 11203 (USA)*

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Summary Short-term visual memory, as in both implicit priming and explicit recognition tasks, can be demonstrated by decreased reaction times, the ability to preferentially select previously presented objects from lists and the ability to more readily complete previously exposed words from fragmented letters. The visual processing of faces occurs separately from the visual processing of non-face stimuli, within discrete areas of bilateral posterior inferotemporal cortices. While visual recognition and memory of faces are independent of those for non-faces, their processing appears to be similar. We have demonstrated an electrophysiologic correlate of short-term visual memory in a face-matching paradigm. We have observed a series of evoked potential components consisting predominantly of a C140, C180 and C240 with a posterior, bitemporal distribution. The priming effect is reflected by a diminution of C240 amplitude in the response to repeated pictures of faces compared to novel pictures of faces. These data reflect a previously unreported set of neurophysiological observations on short-term visual memory for faces.

Key words: Memory; Faces; Event-related potentials

Short-term visual memory has traditionally been assessed in healthy individuals and in amnesic subjects with the use of behavioral measures in a variety of memory paradigms (Graf and Schacter 1985; Shimamura 1986; Ellis et al. 1987, 1990; Gabrielli et al. 1990; Verfaellie et al. 1992). In recent years, a distinction between explicit memory and implicit memory has begun to emerge (Squire et al. 1985; Tulving and Schacter 1990). Explicit memory implies conscious recollection of facts or events, while implicit memory usually denotes some non-conscious ability reflected in priming, motor skills and various habits. It has been postulated that explicit and implicit memory reflect the operation of different brain systems (Squire et al. 1985).

Both recognition of familiar and unfamiliar faces and paired picture matching tasks of familiar and unfamiliar faces have been used successfully to produce priming effects as manifested by significant reductions in reaction time to primed stimuli (Bentin and Moscovitch 1988; Paller et al. 1992). An extensive behavioral literature exists on the use of face stimuli to study implicit and explicit memory (Bruce 1991).

As reviewed by Kutas (1986), the ERP changes that occur during the recall of studied words depend on the type of memory task, and the patterns of ERP changes

were not consistent between studies. Efforts to study memory for faces electrophysiologically have centered around the P300 component of the ERPs. In a study by Somer et al. (1991), unfamiliar faces were used as the stimuli. The encoding task was directed memorization of each face. The recognition task consisted of rating the studied and unstudied pictures as new or old. ERPs, recorded during the encoding phase and sorted by subsequent recognition of the faces, revealed anterior positivity and posterior negativity between the recognized and unrecognized faces persisting as long as 900 msec. No differences between old and new faces were elicited from ERPs recorded during the recognition phase of this study.

Recently, we have observed a novel ERP component, labeled a "visual memory potential" (VMP), which indexes short-term memory in a modified delayed matching to sample paradigm (Begleiter et al. 1993). This component of the ERP occurs between 170 and 240 msec and is generally located in the occipitotemporal region. Both the spatial and temporal characteristics of the VMP in humans are in general agreement with single cell studies in monkeys (Miller et al. 1991). Because the demand characteristics of this modified matching to sample paradigm involve both repetition priming as well as recognition, we could not determine if the VMP possesses features which distinguish priming from recognition.

* Corresponding author. Tel.: (718) 270-2911; Fax: (718) 270-4081.

In the present experiment we recorded ERPs to face stimuli. We used faces because they seemingly mediate a larger number of cognitive processes than any other type of visual stimulus. We used unfamiliar faces because recognition of such visual stimuli is of fundamental importance for all social interactions. In addition, face sensitive neurons have been localized in the temporal cortex of monkeys (Perrett et al. 1982), a region likely to have generated the VMP. We now report an ERP study using unfamiliar faces in two separate experiments in which we first assessed the effects of repetition priming and then studied recognition.

Methods

The subjects consisted of 25 men and 11 women recruited from the medical center population and from a local college. All subjects were right handed and their primary language was based on either a left to right or right to left alphabet, excluding any vertical pictorial languages. Subjects were excluded on the basis of any personal or family history of alcohol or drug abuse, or any history of neurologic, psychiatric or hepatic disease. The mean age of the subjects was 24.7 years (S.D. = 5.9). Visual acuity was equal to or greater than 20/30, tested by a hand-held Snellen card. Subjects who wore corrective lenses were tested wearing them. A Mini-Mental State examination was recorded for each subject and scores were greater than or equal to 27 (Folstein et al. 1975).

Subjects were seated in a sound attenuated room 1 m from a computer display with a fixation point taped to the center of the screen. A 31-lead electrode cap was applied and potentials were recorded from the full modified international 10/20 system along with one electrode above one eye. All electrodes were referenced to Cz. Impedances were kept below 5 k Ω . The signal was amplified with a gain of 10,000 by an Ep-A2 amplifier (Sensorium, Inc.) with 0.02 Hz high pass and 50 Hz low pass analog filters and digitally recorded on a Concurrent 55/50 computer (12-bit ADC) with subsequent 32 Hz low pass digital filtering. On-line rejection of eye movement and artifact greater than 73.3 μ V was utilized. The sampling rate was 256 Hz. The total length of the ERP epoch was 1600 msec including a prestimulus baseline of 180 msec.

The stimuli consisted of black and white pictures of faces and scrambled pictures of faces. The pictures were obtained from the medical center yearbooks from graduating classes, 5 and 6 years prior to the beginning of the study. There was a mixture of men and women of African American, Asian and Caucasian background. The individuals had pleasant expressions. Each picture subtended a minimum visual angle of 7° and a

maximum of 8°, depending on the shape and style of the hair. The scrambled pictures were the same face pictures divided into 64 sections randomly rearranged so that features were unrecognizable. The stimuli were otherwise of equal luminance and contrast to the face pictures. The interstimulus interval was 1.6 sec and the stimulus duration was 300 msec.

Eighty face and 80 scramble pictures were used. The pictures were arranged so that 6 combinations of stimuli were available for analysis: face followed by repeat face, face followed by different face, face followed by scramble, scramble followed by repeat scramble, scramble followed by different scramble and scramble followed by face. This resulted in a total of 240 stimuli. The pictures were presented in a continuous manner so that during the implicit task, the subject responded to each picture pressing button 1 under the left forefinger when a face appeared, and button 2 under the right forefinger, when a scramble appeared. No attention was drawn to the order or to the repetition of stimuli, and accuracy was stressed.

During the explicit task the pictures were again presented continuously, but the subjects were instructed to push button 1 when a face was followed by a repeat face or a scramble was followed by a repeat scramble and button 2 when a face or scramble was followed by a different type of picture. Subjects were told to respond to each picture relative to the preceding picture and not to separate them into pairs. Speed and accuracy were stressed during this task.

Immediately following the implicit task, recognition of faces was tested by showing the subjects 80 hand-held pictures, half of which were novel and half of which they had seen as part of the paradigm. The subjects were asked if they had seen the face before, and to rate their confidence in this decision on a 5-point scale. All subjects completed testing in one sitting and performed the tasks in the same order: implicit task, recognition testing and explicit task.

Evoked potentials were recorded to each picture stimulus and then sorted on the basis of the preceding stimulus for subsequent averaging. Only trials with correct responses and without excessive eye movement or muscle artifact were included in the averaging. The faces preceded by the same face are referred to as "repeat faces," while those preceded by a different face are referred to as "different faces." Similarly, scrambles preceded by the same scramble are referred to as "repeat scrambles" while those preceded by different scrambles are referred to as "different scrambles." The scrambles preceded by faces are referred to as "face/scrambles," while the faces preceded by scrambles are referred to as "scramble/faces."

Amplitudes of the first 3 major components at 140, 180 and 240 msec were measured from baseline to peak. The response at P8 was most consistent in mor-

phology and, therefore, was used as a template to identify the components at the other electrode sites. An upgoing wave form represents relative positivity at the recording electrode compared to the reference at Cz, but there was no determination of absolute polarity. The first 3 components (C) will be called C140, C180 and C240 on this basis. Latencies were measured from the time of the stimulus onset to the peaks of

each component. The results were measured for each condition at each electrode and for each component, and these were organized into groups by region, prior to measurement, for the purpose of analysis by MANOVA. The frontal group (FP1, FP2, AF1, AF2, F7, F8, F3, F4, Fz) was excluded due to a marked inconsistency in wave form morphology both between subjects as well as within the same subject when com-

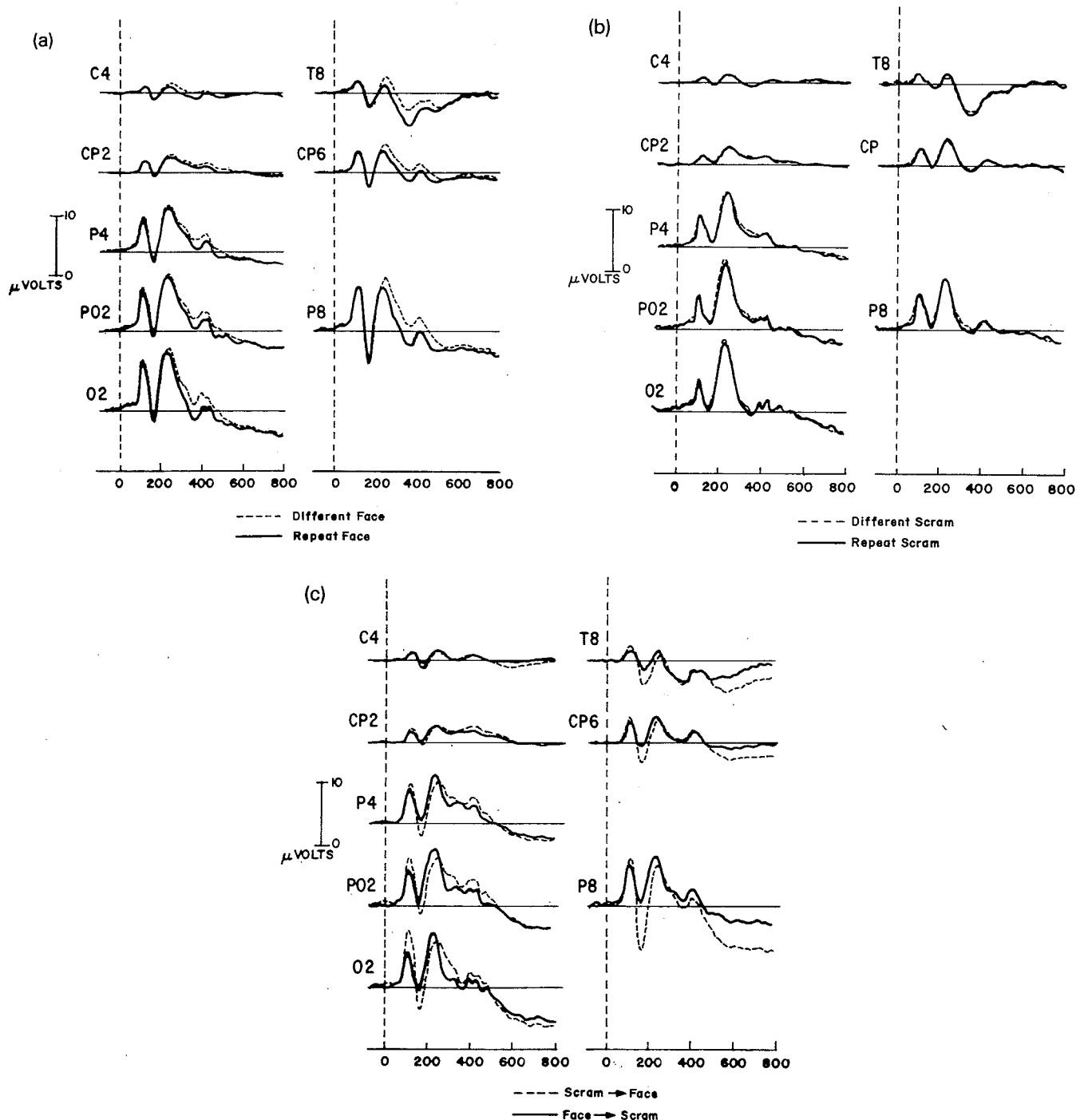


Fig. 1. Grand mean wave forms, implicit task. a: repeat face and different face. b: repeat scramble and different scramble. c: scramble/face and face/scramble.

pared with the wave form at other regions. The central group consisted of FC1, FC2, FC5, FC6, C3, and C4. The parietal group consisted of CP1, CP2, P3, P4 and Pz. The temporal group consisted of T7, T8, CP5, CP6, P7 and P8. The occipital group consisted of PO1, PO2, O1 and O2.

MANOVAs were run according to the generalized linear method. A conservative level of significance,

based on Bonferroni corrections, was used for the dependent t test comparisons.

Current source density topography was based on the entire ERP data set using the grand mean of spline-Laplacian transformations (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. it is a spatial filter that

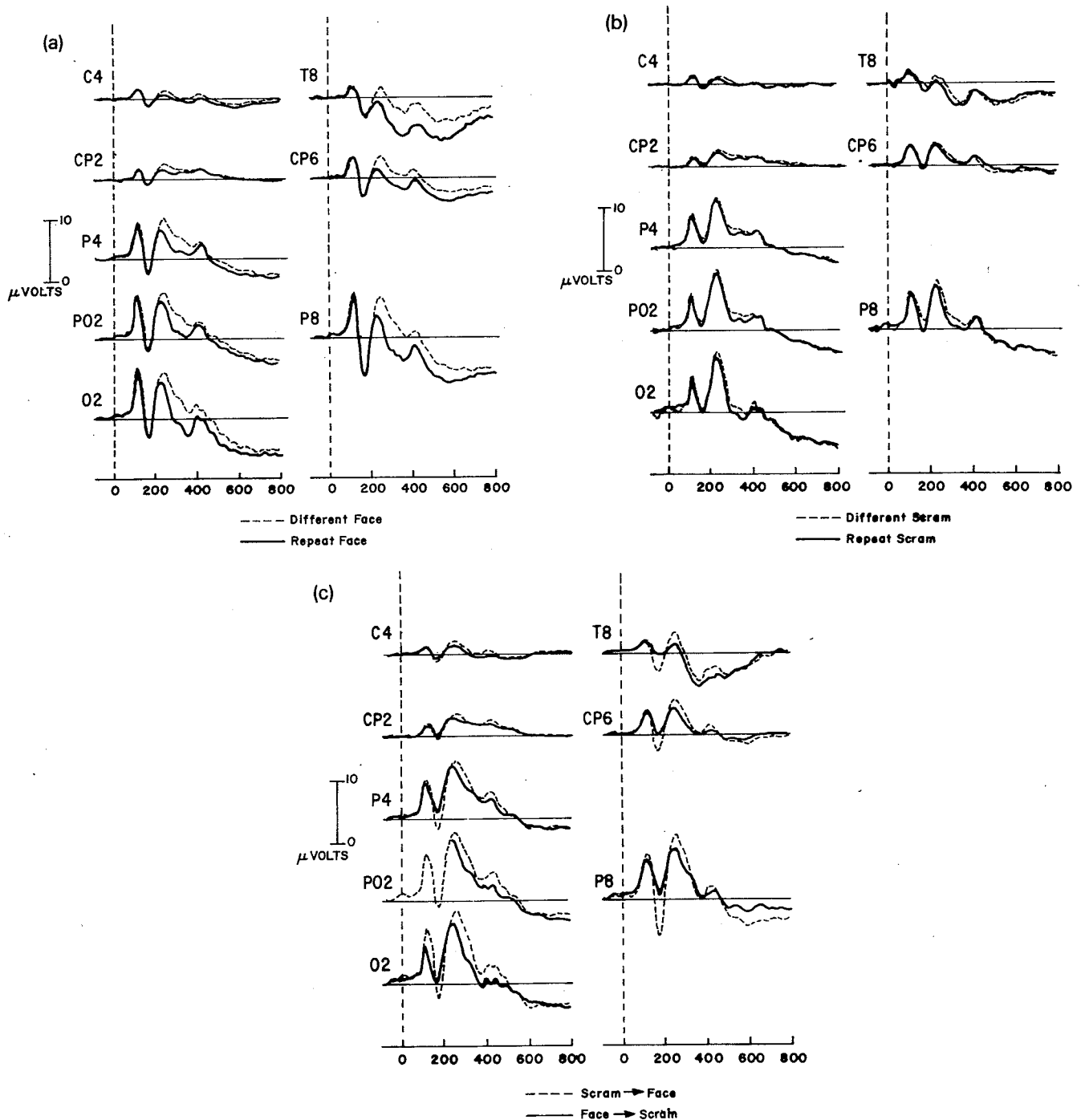


Fig. 2. Grand mean wave forms, explicit task. a: repeat face and different face. b: repeat scramble and different scramble. c: scramble/face and face/scramble.

TABLE I

Behavioral measures.

	Repeat face	Different face	Repeat scramble	Different scramble	Scramble/face	Face/scramble
<i>Mean number of correct responses</i>						
Implicit	30	29	29	30	27	31
Explicit	29	27	24	17	32	29
<i>Mean reaction time (msec)</i>						
			Implicit (S.D.)		Explicit (S.D.)	
Repeat face			365.0 (71.1)		547.3 (99.1) *	
Different face			393.1 (69.6)		613.9 (99.9) *	
Repeat scramble			393.1 (72.1)		629.1 (139.6)	
Different scramble			386.3 (71.1)		662.1 (132.4)	
Face/scramble			419.8 (59.4)		599.3 (111.9)	
Scramble/face			414.7 (59.4)		652.8 (105.5)	

* *t* test comparison, $P < 0.005$.

emphasizes local sources over distant sources. The Laplacian is a model-free and reference-independent technique which improves spatial resolution. Positive values of the current source density indicate local current flow out of the skull, whereas negative values indicate current flow into the skull.

Results

The grand mean wave forms from the right temporal, parietal and occipital electrodes for each stimulus category are presented in Fig. 1 (implicit task) and Fig. 2 (explicit task). The mean numbers of correct, artifact-free responses for each of the tasks and stimulus categories are presented in Table I.

Subjects were only confident of their decisions on the recognition questionnaire following the implicit task on an average of 49 out of 80 responses. The

confident correct and incorrect responses were subjected to a χ^2 analysis which revealed that subjects were as likely to rate a previously seen face incorrectly as correctly.

The mean reaction times for each stimulus category are presented in Table I. The reaction time for the repeat face was significantly shorter than for a different face for the explicit task ($P < 0.005$) but was not significantly different for the implicit task, although the difference was in the right direction. There were no significant differences in reaction times between repeat and different scramble stimuli for either implicit or explicit tasks.

Priming was studied by comparing the ERPs to the repeat and to the different faces. By MANOVA there

Repeat Face vs Different Face Explicit

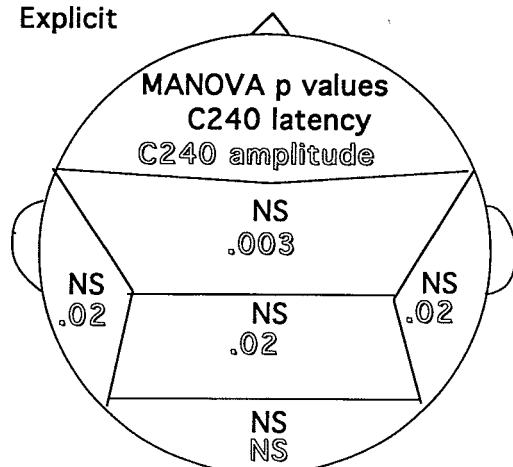
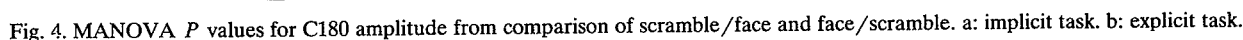


Fig. 3. MANOVA P values for C240 amplitude from comparison of repeat face and different face, explicit task.

TABLE II

Repeat face vs. different face, paired *t* test P values.

	Implicit	Explicit
<i>Temporal electrodes</i>		
<i>Amplitude</i>		
C140	NS	≤ 0.007 (CP5, T7, T8)
C180	NS	NS
C240	≤ 0.01 (P7, T8)	≤ 0.006
<i>Latency</i>		
C140	0.0001	NS
C180	0.0001	≤ 0.007 (P7, P8, T7)
C240	0.0001	≤ 0.003 (P7, P8, T7, T8)
<i>Occipital electrodes</i>		
<i>Amplitude</i>		
C140	0.0001	0.0001
C180	0.0001	0.0001
C240	< 0.01 (O2, PO1)	0.0001
<i>Latency</i>		
C140	0.0001	0.0001
C180	0.0001	0.0001
C240	0.001	0.0001

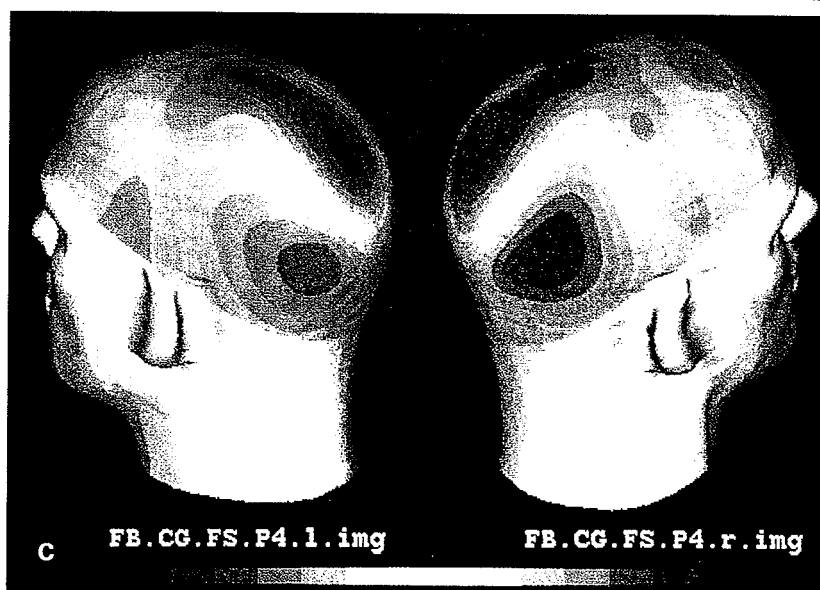
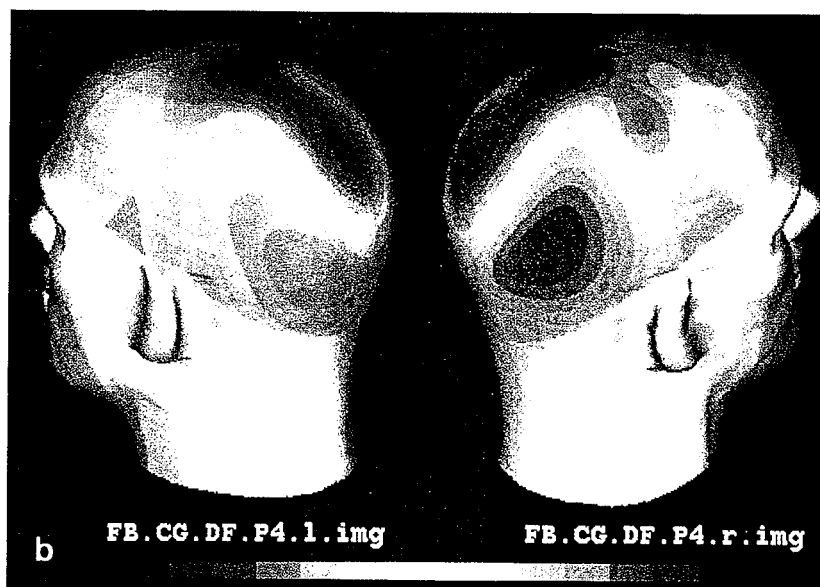


The results of comparisons between individual electrodes made by dependent t tests are presented in Table II and demonstrated priming, as a significantly smaller C240 amplitude, for all of the temporal and occipital electrodes in the explicit task. However, for the implicit task there were also significant findings at the temporal electrodes at T8, with T7 approaching

The comparisons by MANOVA between repeat scramble and different scramble did not yield any significant difference in amplitude or latency between

Face/scramble vs. scramble/face, paired *t* test *P* values.

* Numbers in parentheses represent the number of electrodes in that group with *P* values indicated, i.e., 1/6 = 1 of the 6 temporal electrodes.



the two stimuli. In contrast, the results from dependent *t* tests revealed significantly smaller C140 and C240 amplitudes and shorter C140, C180 and C240 latencies from the repeat scrambles at the occipital electrodes ($P < 0.0001$) only, for both implicit and explicit tasks.

Differences between implicit and explicit memory were evaluated by contrasting the results of the implicit and explicit tasks. Comparisons by MANOVA using the electrode groups were performed for each stimulus category. The C240 amplitudes from the scramble/face stimuli were significantly smaller from the explicit task than from the implicit task at all electrode groups ($P < 0.004$). There were no significant findings with the other components.

To evaluate differences in the electrophysiologic response to the visual image of a face compared with a meaningless stimulus such as the scramble, the ERPs to the scramble/face pictures were compared with those to the face/scramble pictures. The MANOVA comparisons between scramble/face and face/scramble demonstrated several differences. The C180 amplitude was significantly greater at all but the central group for the scramble/face from implicit task (Fig. 4a) and at all electrode groups from the explicit tasks (Fig. 4b). The C240 latency was significantly longer for the scramble/face at all electrode groups from the implicit task ($P < 0.03$) and the parietal and occipital electrode groups from the explicit task. C240 amplitude was larger for the scramble/face at the central and temporal electrode groups from the implicit task ($P < 0.03$), but smaller at the temporal group from the explicit task ($P < 0.03$). C140 amplitude was just significantly greater for scramble/face from the explicit task ($P < 0.05$), but only approached significance from the implicit task.

The results of dependent *t* tests comparing scramble/face and face/scramble are presented in Table III and show trends similar to the MANOVA but are much more variable. The most consistent findings were larger C140 amplitude and longer C140, C180 and C240 latencies for scramble/face at the temporal and occipital electrodes for both implicit and explicit tasks, with C240 latency longer for scramble/face at the central and parietal electrodes as well. C240 amplitude for scramble/face was larger for the implicit and smaller for the explicit tasks at the temporal and occipital electrodes.

A spherical surface spline interpolation using the entire electrode montage was performed, followed by computation of the spatial derivatives on the spherical spline functions to obtain current density distributions. In contrast to the dipole localization method, the cur-

rent density distribution or Laplacian is independent of any volume conduction model of the head. The spline method uses data obtained at all electrodes to estimate Laplacians at all locations within the electrode montage. The current density maps for C240 amplitude are presented in Fig. 5. The predominant field was over the posterior temporal/occipital region, right greater than left. In the implicit task, the responses to repeat face and different face stimuli did not appear to differ, but the different face yielded a greater response than the repeat face in the explicit task. There were no differences between the repeat face stimuli from the implicit and explicit tasks. The scramble stimuli had a somewhat stronger posterior left field than the face stimuli for both implicit and explicit tasks.

Discussion

We have demonstrated an ERP correlate of short-term visual memory for faces manifest as a significantly smaller visual memory potential (VMP), C240 in this case, to a primed (repeated) face as did Begleiter et al. (1993) using line diagrams without apparent semantic representation. This occurred in the absence of a behavioral correlate in our first, implicit task. The ERP difference was even more pronounced when the task required explicit recognition of the repeated faces and, under these conditions, a behavioral correlate was also manifest as a shorter reaction time. We are confident that our implicit task was in fact implicit, and that the subjects directed their attention toward the category decision and not toward the unique features of the faces, as demonstrated by the lack of recognition of faces presented after the implicit ERP task. The ERP finding of an amplitude reduction is in agreement with Ojemann et al. (1992), who recorded from intracellular electrodes in the anterior temporal lobes of humans undergoing surgery for epilepsy during a face-matching task. They found there was an overall pattern of decreased neuronal firing during the first 1.3 sec of recording, while there was generally an increased firing rate during tasks of identifying facial expression and naming objects. Electrophysiologic studies of inferior temporal gyrus and superior temporal sulcus cells in the brains of non-human primates have demonstrated cell populations, some of which are maximally sensitive to the visual presentation of faces. Similar to the configuration of neurons in sensory cortex, these populations tend to be located in clumps from 3 to 5 mm across, interspersed with clumps of cells maximally sensitive to other stimuli (Perrett et al. 1982, 1984;

Fig. 5. Current source density maps, C240 component, explicit task. The source is represented by red, the sink by blue. a: repeat face. b: different face. c: face/scramble.

Perrett and Mistlin 1990; Harries and Perrett 1991). While no particular cell is responsive exclusively to faces, these populations of cells increase their firing rates from 2 to 10 times over their spontaneous rate when the subjects are presented with the image of a face and with minimal changes to non-face stimuli (Bruce et al. 1981; Perrett et al. 1982, 1984; Yamane et al. 1988; Perrett and Mistlin 1990). Some of these face sensitive populations, as well as other populations, undergo a reduction in response rate after repeated exposures to the same visual stimuli including faces (Mikami and Kubota 1980; Rolls et al. 1989; Miller et al. 1991). The results of these studies with non-human primates also correlate well with the amplitude reduction we recorded with the C240 (VMP) component.

Furthermore, the findings from this study are in agreement with prior behavioral work. Bentin and Moscovitch (1988) demonstrated a reduction in reaction time to explicit recognition of familiar and unfamiliar faces, but did not record a change in reaction time to an implicit task requiring structural decisions of faces. Paller et al. (1992) also produced a priming effect with familiar and unfamiliar faces in a paired picture-matching task. Ellis et al. (1990) demonstrated reduced reaction times to familiar faces as long as subjects made decisions on familiarity during the testing phase, regardless of whether the decision task during the study phase was a sex, facial expression or familiarity decision. Another study revealed priming to semantic decisions (occupation) of familiar but not unfamiliar faces, regardless of prior familiar or semantic decisions about the same faces (Young et al. 1986). Earlier work demonstrated a failure to prime to faces after exposure to the names of famous faces, but did reveal the presence of priming to different photographs of the same person, the extent of which was proportional to the degree of similarity of the two pictures (Ellis et al. 1987). Our results indicate that reaction time is not sensitive enough to demonstrate the presence of a priming effect for unfamiliar faces under implicit conditions, while ERP differences between primed (repeated) versus unprimed (different) faces can reveal that priming has taken place. Under explicit conditions, priming is demonstrated by even larger VMP differences in conjunction with a reduction in reaction time.

The most consistent ERP changes were present at the occipito-temporal area. These results are similar to those of Begleiter et al. (1993), who also found a major effect at the occipito-temporal area for their VMP using line diagrams. These areas approximate the visual association cortex in the human brain and correlate with the inferior temporal gyrus and superior temporal sulcus in the monkey brain which are active in both visual memory paradigms as well as in response to face stimuli. Studies in humans using PET scans

during face-matching tasks have demonstrated significantly increased regional cerebral blood flow in bilateral, occipito-temporal regions (Haxby et al. 1991; Sergent et al. 1992). Clinical correlation exists in patients with prosopagnosia who have a deficit in the ability to recognize faces and at times even match pictures of faces. The lesions responsible for this condition typically occur in the inferior temporal visual association cortex or the anterior connections of occipito-temporal white matter (Meadows 1974; Damasio et al. 1982).

Short-term visual memory and, in particular, short-term memory of the visual image of a face, appears to take place in a system which is functionally separate, although not anatomically distinct, from more general, visual processing systems. Our results demonstrated differences in the ERPs from faces and meaningless stimuli, manifesting predominantly as a larger potential (C180) from the meaningful face stimulus.

It is remarkable that these ERP changes, demonstrated to implicit and explicit priming and recorded with surface electrodes from human subjects, are in close agreement with the studies of single cell recordings from analogous areas in humans and in non-human primates performing similar tasks. The PET studies provide a consistent set of data for the localization of areas active during face matching, although they cannot provide the extraordinary time resolution of ERPs. These findings open the possibility for further study of visual memory processes, as well as additional definition of the differences in visual processing of faces as compared to other meaningful and non-meaningful stimuli using surface ERP recordings and current source density determinations in human subjects.

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