

Long-Latency ERPs and Recognition of Facial Identity

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Abstract

■ N400 brain event-related potential (ERP) is a mismatch negativity originally found in response to semantic incongruences of a linguistic nature and is used paradigmatically to investigate memory organization in various domains of information, including that of faces. In the present study, we analyzed different mismatch negativities evoked in N400-like paradigms related to recognition of newly learned faces with or without associated verbal information. ERPs were compared in the following conditions: (1) mismatching features (eyes–eyebrows) using a facial context corresponding to the faces learned without associated verbal information (“pure” intradomain facial processing); (2) mismatching features using a facial context corresponding to the faces learned with associated occupations and proper names (“nonpure” intradomain facial processing); (3) mismatching occupations using a facial context (cross-domain processing); and (4) mismatching names using an occupation context (intra-

domain verbal processing). Results revealed that mismatching stimuli in the four conditions elicited a mismatch negativity analogous to N400 but with different timing and topographical patterns. The onset of the mismatch negativity occurred earliest in Conditions 1 and 2, followed by Condition 4, and latest in Condition 3. The negativity had the shortest duration in Task 1 and the longest duration in Task 3. Bilateral parietal activity was confirmed in all conditions, in addition to a predominant right posterior temporal localization in Condition 1, a predominant right frontal localization in Condition 2, an occipital localization in Condition 3, and a more widely distributed (although with posterior predominance) localization in Condition 4. These results support the existence of multiple N400, and particularly of a nonlinguistic N400 related to purely visual information, which can be evoked by facial structure processing in the absence of verbal–semantic information. ■

INTRODUCTION

The face is a practically omnipresent stimulus during human social interaction. The cognitive model proposed by Bruce and Young (1986) assumes that the recognition of a familiar face implies the access in long-term memory to visual and verbal–semantic codes. Visual face structure codes are related to the identity of features and verbal–semantic codes are related to data on the person’s occupation, other biographical information, and his or her name. This model hypothesizes the existence of face recognition units (FRUs) containing stored structural codes that describe each one of the faces known, whose activation precedes the retrieval of biographical semantic information and the verbal label representing the proper name. From a neuroscientific point of view, facial structure processing is thought to recruit brain mechanisms responsible for perceptual integration of invariant aspects of the individual face descriptions in memory (Haxby, Hoffman, & Gobbini, 2000). Haxby et al. (2000) have hypothesized the existence of a distributed human neural system in which a core system for the visual analysis of faces in the occipito-temporal visual extrastri-

ate cortex is distinguished from an extended system that processes the meaning of information extracted from faces. This latter system would include, among others, structures in the anterior temporal regions.

Single-unit recordings in nonhuman primates have found neuronal groups responsive to faces in the superior temporal sulcus and the inferior temporal gyrus (Hasselmo, Rolls, & Baylis, 1989; Perrett, Rolls, & Caan, 1982). In humans, intracerebral recordings have revealed neuronal groups that respond selectively to facial stimuli in the lateral fusiform and inferior temporal gyri (Allison, Puce, Spencer, & McCarthy, 1999), and functional brain-imaging studies have supported the role of the visual occipito-temporal cortex, either by applying behavioral paradigms in normal subjects or by analyzing brain-damaged individuals that present face-recognition deficits (prosopagnosics) (Dubois et al., 1999; George et al., 1999; Clarke, Lindemann, Maeder, Borruat, & Assal, 1997; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Clark et al., 1996). Other studies in nonhuman primates and humans using different recording techniques have reported the involvement of frontal regions in face-processing tasks (Katanoda, Yoshikawa, & Sugishita, 2000; Marinkovic, Trebon, Chauvel, & Halgren, 2000; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999; Scalaidhe, Wilson, & Goldman-Rakic, 1997), while

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the retrieval of semantic biographic information (and proper names) from familiar face recognition has been associated with activity in anterior temporal regions (Leveroni et al., 2000; Gorno Tempini et al., 1998).

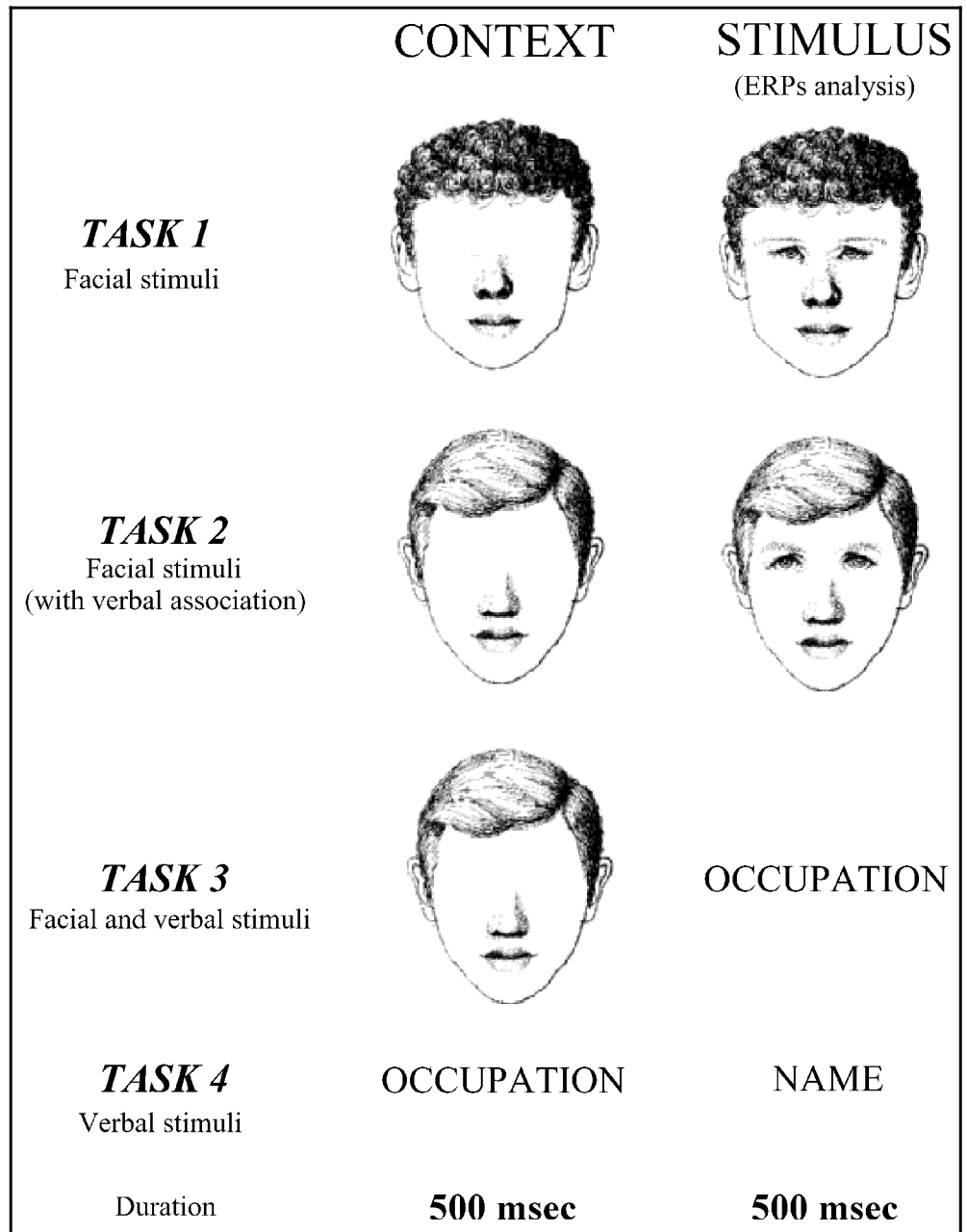
Event-related potential (ERP) studies have contributed to increasing knowledge of face-processing through experimental paradigms that reflect in real time the neural subroutines involved in the perception and recognition of visual facial structural information. The positive peak recorded at about 150–200 msec in mid-line electrodes has been described as a response characterizing the detection of faces as complex patterns, in comparison to other categories of stimuli for which the response was delayed or smaller (Bötzel & Grüsser, 1989; Jeffreys, 1989). A more posterior-located negative response, N170, reported by Bentin, Allison, Puce, Perez, and McCarthy (1996) was evoked preferentially by faces and with a maximum at right posterior temporal regions. The possible neural generators for these early responses have been presumed to be situated in the basal occipito-temporal regions (Bentin et al., 1996; Bötzel & Grüsser, 1989). Bentin et al. (1996) suggested that N170 could be representing the formation of face-specific representations necessary for subsequent face-recognition processes.

Electrophysiological research on face recognition has been carried out by presenting famous or well-known faces (see, e.g., Bentin & Deouell, 2000; Jemel, George, Olivares, Fiori, & Renault, 1999; Barrett, Rugg, & Perrett, 1988). These studies demonstrate the existence of N400-like effects to mismatching faces (in two sequentially presented famous faces) or mismatching features (in face-feature-matching tasks for very familiar or famous faces), but with faces for which semantic verbal codes are easily available. Thus, an N400-like component elicited by faces as visual (nonlinguistic) stimuli has not been adequately demonstrated. To advance research in this area, we have analyzed long-latency ERPs during the recognition of newly learned (digitally created) faces without associated verbal information (Olivares, Bobes, Aubert, & Valdés-Sosa, 1994; Olivares, Iglesias, & Bobes, 1999). The procedure used in our experiments was a face-feature-matching task (see Olivares, Iglesias, Bobes, & Valdés-Sosa, 2000), similar to the original N400 paradigm from language studies (“I take coffee with cream and ‘socks’”; Kutas & Hillyard, 1980), and applied initially by Valdés-Sosa and Bobes (1990) with familiar natural faces. This face-feature-matching task is more likely to induce a feature-based, analytic type of processing that may avoid judgments about personality or other verbal–semantic information related to facial identity (Sporer, 1991). A mismatch negativity (analog to N400) was evoked in these experiments when mismatching features (inappropriate eyes–eyebrows fragments) were placed on an incomplete familiar (newly learned) face that served as context stimulus. However, although both the learn-

ing procedure and the recording task were designed in order to reduce the possible contribution of verbal–semantic information to the mismatch effect found, a critical point is the lack of within-subjects control conditions. Thus, subjects could have used covert verbal strategies to solve the face-feature matching, so that a cross-domain (verbal-to-facial) interference cannot be completely discarded. In other words, the presentation of a context face may activate in the memory some verbal information associated with that face, and the incongruent completion of that face may, in turn, generate a representation incongruent with this preactivated verbal information, giving rise to the mismatch negativity found.

In order to identify the role of verbal–semantic information in the N400-like component elicited by faces, it is essential to design experimental conditions that allow us to distinguish mismatch effects corresponding to mechanisms of access to and retrieval of the (visual) structural information from others related to the access to and retrieval of (verbal) biographical and proper-name information. This is crucial to a discussion of whether a visual long-latency ERP mismatch response is associated with cognitive and neural mechanisms different from the N400 obtained with verbal incongruences in the language domain (Bentin & Deouell, 2000; Jemel et al., 1999; Olivares et al., 1994, 1999). In the study reported here, we addressed this question by presenting subjects with faces newly learned with or without associated occupations and names in four N400-like matching tasks. These varied in their reliance on verbal information (see Figure 1). Task 1 was “pure” facial (visual only): A face presented without eyes–eyebrows was followed by the full face with the correct or incorrect eyes–eyebrows. Task 2 was “nonpure” facial (visual and irrelevant verbal): It was the same as “pure” facial except that the occupations and names of the faces had been learned. Task 3 was “cross-domain” (visual and verbal): A face was presented without eyes–eyebrows, followed by the correct or incorrect occupation. Task 4 was “pure” verbal (verbal only): A name was presented, followed by the correct or incorrect occupation. We supposed that N400-like effects associated with “pure” structural (visual only) face-processing would present shorter latencies and a scalp distribution analog to those (right occipito-temporal) responses described in other studies as more face-specific. On the other hand, incongruences presented with other material (visual and irrelevant verbal, visual and verbal, and verbal only) might elicit N400-like responses indicating to some extent the (overt or covert) availability of semantic information associated with facial identity. These N400 would show a longer latency and a different topographical distribution, more similar to those of the N400 from studies with famous faces or from linguistic studies (Bentin & Deouell, 2000; Jemel et al., 1999; Barrett et al., 1988;

Figure 1. The four ERP recording tasks: Task 1 (“pure” facial), Task 2 (“nonpure” facial), Task 3 (cross-domain), and Task 4 (verbal). Selection of the window for ERP analysis was synchronized with the items shown on the right of the figure. In half of the trials, stimuli were inappropriate, that is, they did not correspond to what participants had learned in the learning sessions.



Kutas & Hillyard, 1982, 1983; Kutas, Van Petten, & Besson, 1988).

RESULTS

Behavioral Data Corresponding to Learning Sessions

Subjects were trained over six sessions to learn a set of faces with or without associated occupations and names. In each session, after studying each subset of stimuli, they had to discriminate between correct and incorrect facial features displayed below an incomplete previously studied face (forced-choice discrimination task). In the case of the faces learned with verbal–semantic information, subjects were also required to provide the corre-

sponding names and occupations (see Methods section for details). In the forced-choice discrimination task for the “pure” facial subset (visual only), the d' (discrimination sensitivity) increased from 0.72 in Session 1 to 2.45 in Session 6, $F(5,70) = 10.92, p = .0000$. Similarly to that observed in the visual-only subset, the d' for the visual and verbal subset increased with successive learning sessions, $F(5,70) = 10.25, p = .0000$. The lowest d' , 0.68, corresponded to Session 1 and the highest value, 2.19, corresponded to Session 5. In order to compare the learning progression for the two subsets of faces, a repeated measures ANOVA was performed using as main factors subset (2) and sessions (6). The analysis showed that there were no significant differences either for the factor subset or for the interaction Subset \times Sessions.

Table 1. Windows Time throughout the Epoch (msec)

<i>Matching Task</i>	<i>Prenegativity Window 1</i>	<i>Negativity Window 2</i>		<i>Postnegativity Window 3</i>
	<i>From-To</i>	<i>From-To</i>	<i>Peak</i>	<i>From-To</i>
1. Face-feature “pure” facial	0–260	260–430	360	430–870
2. Face-feature “nonpure” facial	0–260	260–450	380	450–870
3. Face-occupation (cross-domain)	0–300	300–550	440	550–870
4. Occupation-name (verbal)	0–280	280–470	370	470–870

Window 1 = where we found no differences between “matching” and “mismatching” ERPs; Window 2 = where there was a mismatch negativity with a different peak in each task; Window 3 = where we observed a late positivity associated with mismatching completions in the four matching tasks.

The number of correctly reported occupations and of names both increased with successive learning sessions, $F(5,70) = 119.8, p = .0000$; $F(5,70) = 81.35, p = .0000$, respectively. In the case of occupations, the lowest average number of items remembered was 5.2, in Session 1, and the highest value was 19.8, corresponding to Session 6. Average number of names recalled in the first session was 8.6, and in the last session, 19.9.

Behavioral Data Corresponding to ERP Recording Session

The average d' for each matching task of the ERP recording session was 2.13 for Task 1, 2.11 for Task 2, 2.96 for Task 3, and 3.09 for Task 4. A repeated measures ANOVA, using as main factor the type of matching task, indicated that there were significant d' differences among the four tasks, $F(3,42) = 11.72, p = .0000$. Post hoc comparisons indicated that d' from Tasks 1 and 2 was lower than d' from Tasks 3 and 4 (d' from Tasks 1 and 2 did not differ, and nor did d' from Task 3 differ from that of Task 4). These differences will be discussed below, but in any case, d' in the four tasks showed that subjects efficiently discriminated matching stimuli from mismatching stimuli.

Long-Latency Electrophysiological Data

Comparison between Match and Mismatch ERPs in Each Task

Before comparing the tasks with one another, we analyzed in each task the effect on the ERPs of the mismatching completions. The epoch was divided into three windows (Table 1): prenegativity, negativity (mismatch negativity), and postnegativity (late positivity). The prenegativity window began with the presentation of the stimulus and ended when the recordings corresponding to the matching versus mismatching completions started to differ. The negativity window comprised the period in which the recordings for the mismatching completions showed more negative amplitudes than those for the matching completions. The postnegativity window began when the recordings for the mismatching completions reflected more positive amplitudes than those for the

matching completions and lasted until the end of the epoch. We carried out an ANOVA for each window, comparing the amplitude between match and mismatch ERPs. The results confirmed that, in the prenegativity window, there were no differences between the two conditions in any of the tasks. It should be noted that this time window includes the latency corresponding to N170, so that it can be said that there was no modulation of this component in the present experiment. In the negativity window, significant differences were indeed found between conditions in each task, although in the case of Task 1 the difference was marginally significant (Table 2). The results of the ANOVAs carried out in the postnegativity (or late positivity) window showed significant differences between the two experimental conditions in the majority of the tasks, which will be referred to in the Discussion section. In each of the four tasks, there was, therefore, a different mismatch effect characterized by a negativity in the time window indicated for each task. To illustrate these results, both the difference (“mismatch” ERPs minus “match” ERPs) and a sample of the original waves are represented in Figure 2A and B, respectively (EOG waves, not included in the figure, showed no salient deviations from the isovoltaic line in the latency corresponding to N400).

Table 2. Results of the ANOVAs Comparing the Mean Amplitudes of Match (1) and Mismatch (2) ERPs in the Window Corresponding to the Mismatch Negativity (Window 2 in Table 1) Observed in Each Task

<i>Task</i>	<i>Match Condition</i>	<i>Average Amplitude</i>	<i>F(1,14)</i>	<i>p</i>
1	1	−1.429	3.73	0.074
	2	−2.776		
2	1	−0.269	15.76	0.001
	2	−2.271		
3	1	−4.793	9.63	0.008
	2	−6.502		
4	1	0.142	20.28	0.000
	2	−3.301		

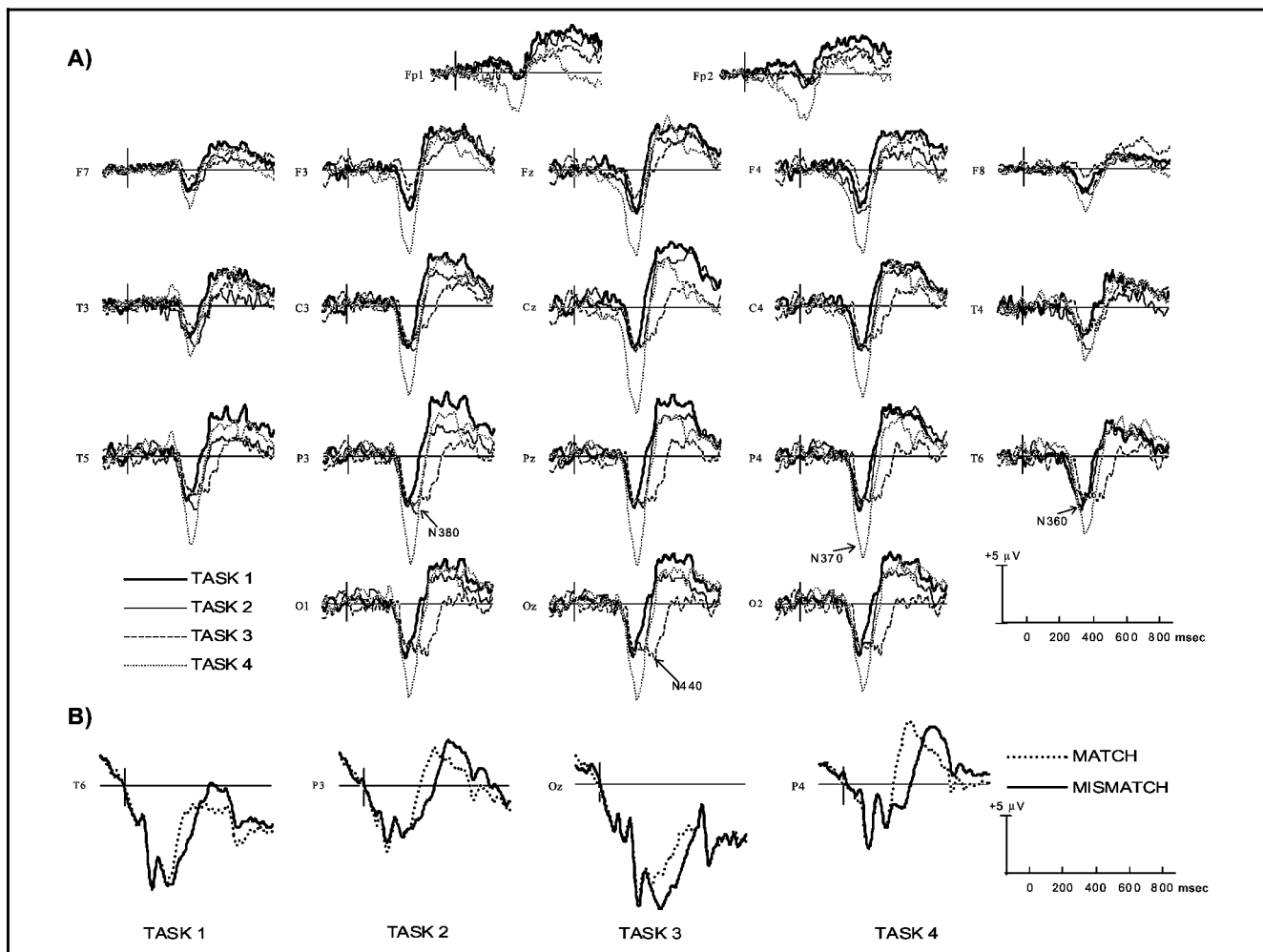


Figure 2. (A) Difference waves obtained by subtracting match ERPs from mismatch ERPs (mismatch minus match) in the four tasks. The peak of mismatch negativity in each task is indicated by an arrow (N360, Task 1; N380, Task 2; N440, Task 3; and N370, Task 4). (B) Original grand average ERPs for matching and mismatching stimuli at the site where the mismatch negativity was enhanced in each task. Curves are plotted with positive deflections pointing upwards.

With regard to latencies of the negativity, the mismatch effect followed a different time course in each task (see Table 1). It appeared earliest in Tasks 1 and 2, followed by Task 4, and then Task 3. It reached its peak (highest amplitude) earliest in Task 1 and Task 4, followed by Task 2, and finally Task 3. Effect offset also appears to vary across tasks, occurring in the following ascending order: Tasks 1, 2, 4, and 3 (the last one much later than the rest). In subsequent analyses, we compared the data corresponding to the difference waves, and the negativity epoch was divided into eight micro-windows of 40 msec each. The objective was to compare the latency, amplitude, and topographical distribution of the different mismatch negativities obtained.

Comparison of Latencies of the Negativity from Each Task

An ANOVA was performed for each task, taking window (the eight common preselected time microwindows,

from 260 to 580 msec, which included the onset, progression, and offset latencies of the mismatch negativity across all tasks) and site (which will be referred to below) as main factors. Figure 3 shows the average amplitude values (across sites) by window in the four tasks. Table 3 shows the results of the ANOVAs and the post hoc analyses carried out.

We performed a one-way ANOVA (factor task) to compare the latencies of the mismatch negativity peak between the four tasks. The results show significant differences between tasks, $F(3,42) = 9.8, p = .000$. Post hoc comparisons denoted that the latency of the peak in Task 3 was significantly different (later) from those of the other tasks.

Comparison of Amplitudes of the Most Negative Window in Each Task

An additional ANOVA (task as main factor) was carried out in order to make a comparison between the

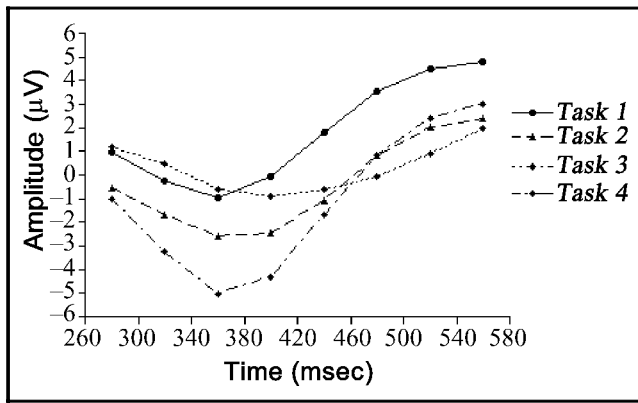


Figure 3. Average amplitude values (in μV) across sites for each time microwindow in each task.

amplitudes of the most negative window in each task (see Table 3). The analysis showed that there were significant differences between the amplitude values of the four tasks, $F(3,42) = 3.78, p = .017$, with average amplitude (across sites) in Task 4 (“pure” verbal task, $-5.01 \mu\text{V}$) being significantly higher than those of Tasks 3 (“cross-domain” task, $-0.9 \mu\text{V}$), and 1 (“pure” facial task, $-0.95 \mu\text{V}$), as confirmed by the post hoc Tukey HSD test. Average amplitude of the negativity in Task 2 (“nonpure” facial task, $-2.57 \mu\text{V}$) was not significantly different from those in the rest of the tasks.

Scalp Topography of the Negativity in Each Task

Tables 4–7 show the amplitude values of the difference waves at each recording site for the four matching tasks. To describe the recording sites characterizing the specific scalp distribution in each task, we chose the site showing the most negative amplitude value across all windows, and then looked for the sites with similar (not significantly different) values using the Tukey HSD test (subsequent to the ANOVA mentioned above). Amplitude values in Table 4, corresponding to difference waves from Task 1 (“pure” facial), show that, systematically (across all windows), the most negative sites were T6, P4,

Fz, P3, and O2. Effect onset appears to be situated at the right posterior sites T6, P4, and O2, and the effect reaches a peak (360 msec, window 340–380 msec) at T6, P4, and P3. In the window in which offset occurs, the most negative sites are T6, F8, and Fz. In general, T6 was the most negative site and the sites P4, P3, and Fz were systematically not significantly different from T6 across all windows. Data in Table 5, corresponding to difference waves from Task 2 (“nonpure” facial) show that, systematically, the most negative sites were P3, F4, F8, and Fp2 (left frontal sites Fp1, F7, and F3 were similar to these in the final windows). In sum, the most negative site, P3, was similar to F4, F8, and Fp2 in most of the windows. Data from Task 3 (“cross-domain”) are shown in Table 6. Post hoc comparisons showed that the most systematically negative site, Oz, was similar to P3, Pz, and P4 in most of the windows. Data corresponding to Task 4 (“pure” verbal) are shown in Table 7. Post hoc analysis showed that P4, the most systematically negative site, did not differ from Pz, Oz, O2, and P3 in any of the windows. Furthermore, nor did other sites, such as C3 and C4, differ from P4 in most of the windows in this task. Figure 4 shows voltage maps representing the scalp topography of the mismatch negativity in each task.

Pairwise comparisons were carried out between all the recording sites of the different tasks in each window. The data were previously scaled following the procedure of McCarthy and Wood (1985), in order to avoid confusing amplitude differences with topographical differences. The significant differences found between sites confirmed that the mismatch negativity in Task 2 was more frontally distributed than in Tasks 1 and 3, that the negativity in 3 was more occipital than that of 1 and that the mismatch negativity of 4 was more center-right and in general more dispersed than that of 1 and 2.

DISCUSSION

The main purpose of this study was to verify the possible existence of an N400-like ERP component elicited by faces as a nonlinguistic analog of the N400 observed for

Table 3. Results of the ANOVAs (First Two Columns) and of the Post Hoc Analyses Carried Out for Comparing the Amplitude of the Eight Microwindows of 40 msec (Each Corresponding to the Negativity in the Four Tasks)

	$F(7,98)$	p	1 (260–300)	2 (300–340)	3 (340–380)	4 (380–420)	5 (420–460)	6 (460–500)	7 (500–540)	8 (540–580)
Task 1	19.2	0.000	×	×	×	×				
Task 2	14.74	0.000	×	×	×	×	×			
Task 3	5.7	0.000		×	×	×	×	×	×	
Task 4	36.8	0.000		×	×	×				

××× = where the most negative values were found; ×× = where the second most negative values were found; × = where the values closest to (not significantly different from) the previous ones were found. Note how these analyses show an earlier onset for the mismatch effect in Tasks 1 and 2, a shorter duration of this effect in Tasks 1 and 4 and a longer duration of it in Task 3 (higher number of microwindows with similar amplitudes). The concentration of the most negative values (××× and ××) was somewhat earlier in Task 1 than in Tasks 2 and 4, and much later in Task 3.

Table 4. Mean Amplitude Values (in μV , DC Corrected) of the Difference Waves (Mismatch ERPs minus Match ERPs) for Task 1 at Each Site (Columns) and in Each of the Eight Consecutive Time Windows (Rows) Corresponding to the Latencies with Which the Mismatch Negativity Appeared

Window	Fp1	F3	F7	C3	T3	P3	T5	O1	Fz	Cz	Pz	Oz	Fp2	F4	F8	C4	T4	P4	T6	O2
260-300	2.464	1.868	3.135	0.394	3.080	-0.118	1.404	0.617	-0.122	1.060	0.283	0.423	3.100	1.861	0.671	0.392	2.611	-0.741	-2.141	-0.354
300-340	2.095	0.706	2.439	-1.004	2.123	-1.728	-0.105	-0.995	-1.251	-0.358	-1.302	-1.159	2.658	0.678	-0.064	-1.033	1.567	-2.384	-3.579	-1.932
340-380	1.619	-0.222	1.778	-1.949	1.257	-2.674	-1.178	-1.761	-2.221	-1.155	-2.182	-1.762	2.159	-0.044	-0.568	-1.693	0.969	-3.109	-3.997	-2.322
380-420	1.911	0.677	2.065	-0.961	1.616	-1.554	-0.439	-0.667	-1.313	0.178	-0.965	-0.531	2.449	0.947	-0.302	-0.487	1.456	-1.799	-2.768	-0.918
420-460	3.024	2.958	3.144	1.425	3.034	0.935	1.537	1.333	1.117	2.858	1.446	1.491	3.456	3.028	0.373	1.813	2.698	0.637	-0.736	1.159
460-500	4.000	4.729	4.191	3.559	4.542	3.356	3.503	3.163	2.980	5.063	3.729	3.399	4.244	4.561	1.088	3.703	4.041	2.843	1.005	3.089
500-540	4.407	5.397	4.799	4.635	5.553	4.781	4.727	4.387	3.619	6.215	5.176	4.799	4.549	5.121	1.741	4.608	5.037	4.115	2.038	4.465
540-580	4.611	5.573	5.030	4.960	5.998	5.266	5.205	4.892	3.796	6.706	5.734	5.406	4.706	5.205	2.040	4.789	5.277	4.427	2.140	4.891

Values in **boldface** are those found to be not significantly different from the most negative value (corresponding in this task to T6) in each time window.

Table 5. Mean Amplitude Values (in μV , DC Corrected) of the Difference Waves (Mismatch ERPs minus Match ERPs) for Task 2 at Each Site (Columns) and in Each of the Eight Consecutive Time Windows (Rows) Corresponding to the Latencies with Which the Mismatch Negativity Appeared

Windows	Fp1	F3	F7	C3	T3	P3	T5	O1	Fz	Cz	Pz	Oz	Fp2	F4	F8	C4	T4	P4	T6	O2
260-300	-0.545	-0.750	-0.009	0.493	0.219	-2.565	1.767	1.024	-1.171	-0.302	0.044	-0.316	-1.904	-1.956	-1.716	-0.594	-0.424	-1.123	0.200	-0.874
300-340	-1.069	-1.732	-0.621	-0.809	-0.671	-4.128	0.270	-0.358	-2.281	-1.581	-1.599	-1.723	-2.368	-3.084	-2.331	-1.897	-1.421	-2.631	-1.175	-2.181
340-380	-1.534	-2.556	-1.315	-1.908	-1.628	-5.379	-0.999	-1.393	-3.086	-2.509	-2.869	-2.691	-2.770	-3.834	-2.934	-2.855	-2.314	-3.822	-1.998	-3.016
380-420	-1.424	-2.323	-1.445	-1.896	-1.992	-5.450	-1.278	-1.408	-2.691	-2.152	-2.784	-2.581	-2.627	-3.444	-3.012	-2.507	-2.400	-3.582	-1.459	-2.686
420-460	-0.735	-0.856	-0.835	-0.383	-1.364	-3.826	-0.160	0.047	-0.904	-0.132	-0.910	-1.000	-1.868	-1.894	-2.392	-0.595	-1.407	-1.481	0.371	-0.891
460-500	0.142	1.014	0.167	1.870	0.009	-1.332	1.790	2.260	1.217	2.504	1.780	1.302	-0.983	-0.122	-1.534	1.745	-0.048	1.190	2.316	1.401
500-540	0.761	2.118	0.844	3.378	1.158	0.348	3.283	3.706	2.344	4.103	3.525	2.730	-0.487	0.743	-0.866	3.083	0.980	2.777	3.366	2.719
540-580	0.977	2.265	0.921	3.733	1.589	0.841	3.867	4.169	2.502	4.492	4.076	3.105	-0.306	0.792	-0.421	3.424	1.569	3.254	3.684	3.097

Values in **boldface** are those found to be not significantly different from the most negative value (corresponding in this task to P3) in each time window.

Table 6. Mean Amplitude Values (in μV , DC Corrected) of the Difference Waves (Mismatch ERPs minus Match ERPs) for Task 3 at Each Site (Columns) and in Each of the Eight Consecutive Time Windows (Rows) Corresponding to the Latencies with Which the Mismatch Negativity Appeared

Windows	Fp1	F3	F7	C3	T3	P3	T5	O1	Fz	Cz	Pz	Oz	Fp2	F4	F8	C4	T4	P4	T6	O2
260-300	0.486	2.589	2.100	0.331	1.609	-0.159	2.626	0.864	0.987	0.182	-0.017	-1.213	2.094	0.741	0.936	1.410	2.572	-0.059	4.617	1.342
300-340	0.509	2.132	1.983	-0.557	1.076	-1.300	1.701	-0.234	0.454	-0.769	-1.199	-2.314	1.951	0.114	0.603	0.524	1.869	-1.251	3.607	0.235
340-380	0.431	1.316	1.511	-1.805	0.150	-2.777	0.419	-1.705	-0.334	-2.071	-2.811	-3.694	1.697	-0.661	0.219	-0.741	0.920	-2.794	2.326	-1.126
380-420	0.608	1.330	1.456	-2.134	-0.241	-3.402	-0.276	-2.405	-0.354	-2.417	-3.454	-4.300	1.797	-0.582	0.288	-1.100	0.538	-3.394	1.688	-1.721
420-460	0.981	2.043	1.795	-1.679	0.044	-3.269	-0.250	-2.538	0.366	-1.923	-3.309	-4.424	2.248	0.059	0.672	-0.700	0.762	-3.209	1.728	-1.774
460-500	1.318	2.705	2.041	-0.982	0.692	-2.711	0.319	-2.275	1.330	-1.055	-2.727	-4.161	2.739	0.738	1.159	0.060	1.437	-2.554	2.286	-1.427
500-540	1.591	3.320	2.241	0.043	1.548	-1.513	1.408	-1.192	2.350	0.265	-1.386	-3.008	3.130	1.522	1.778	1.279	2.565	-1.231	3.495	-0.265
540-580	1.867	4.023	2.605	1.196	2.332	0.051	2.705	0.337	3.170	1.666	0.402	-1.415	3.341	2.267	2.271	2.510	3.585	0.250	4.844	1.222

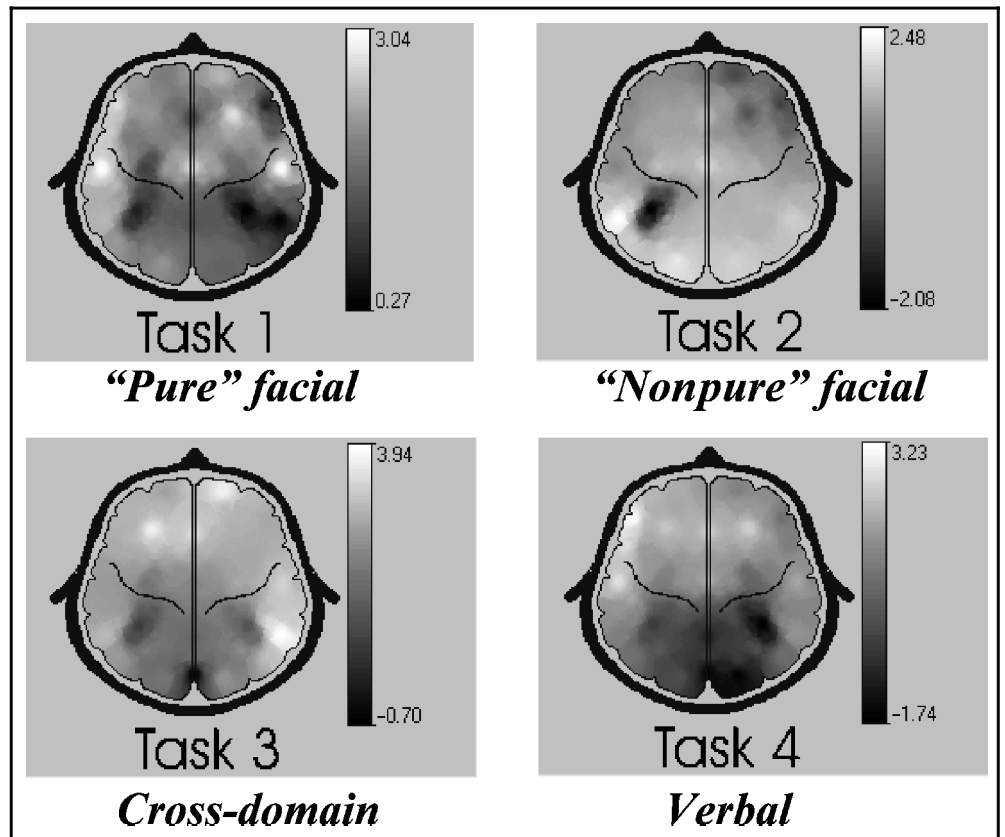
Values in **boldface** are those found to be not significantly different from the most negative value (corresponding in this task to Oz) in each time window.

Table 7. Mean Amplitude Values (in μV , DC Corrected) of the Difference Waves (Mismatch ERPs minus Match ERPs) for Task 4 at Each Site (Columns) and in Each of the Eight Consecutive Time Windows (Rows) Corresponding to the Latencies with Which the Mismatch Negativity Appeared

Windows	Fp1	F3	F7	C3	T3	P3	T5	O1	Fz	Cz	Pz	Oz	Fp2	F4	F8	C4	T4	P4	T6	O2
260-300	-1.176	-1.227	2.419	-1.817	2.264	-1.802	0.242	-0.508	-2.710	-2.491	-2.669	-2.544	-1.913	-0.910	0.231	-2.202	1.830	-2.980	0.661	-2.377
300-340	-2.017	-3.644	1.228	-4.638	0.576	-5.113	-2.581	-3.399	-4.878	-5.454	-5.932	-5.390	-2.740	-2.998	-0.785	-4.727	0.331	-5.959	-1.702	-5.099
340-380	-2.493	-5.195	0.099	-6.777	-1.323	-7.842	-5.381	-5.814	-6.101	-7.337	-8.559	-7.694	-3.067	-4.203	-1.530	-6.489	-1.126	-8.298	-3.826	-7.270
380-420	-1.574	-3.668	0.492	-5.720	-1.413	-7.076	-5.377	-5.351	-4.364	-5.792	-7.739	-7.177	-2.183	-2.788	-1.195	-5.415	-1.263	-7.587	-3.808	-6.779
420-460	0.059	-0.433	1.798	-2.366	0.166	-3.524	-2.631	-2.459	-0.743	-1.808	-4.186	-4.293	-0.662	0.188	-0.086	-2.305	0.098	-4.423	-1.507	-4.058
460-500	1.218	1.971	2.781	0.674	1.909	-0.076	0.370	0.561	2.117	1.786	-0.612	-1.160	0.447	2.579	1.011	0.703	1.963	-1.121	1.384	-1.023
500-540	1.817	3.215	3.439	2.383	3.231	1.960	2.131	2.443	3.554	3.690	1.519	0.858	1.026	3.904	1.841	2.654	3.539	0.940	3.306	0.962
540-580	2.009	3.764	3.890	3.035	4.048	2.732	2.725	3.133	4.010	4.111	2.207	1.585	1.285	4.354	2.346	3.439	4.548	1.719	4.076	1.710

Values in **boldface** are those found to be not significantly different from the most negative value (corresponding in this task to P4) in each time window.

Figure 4. Voltage maps obtained from the difference waves representing the mismatch negativity in each task (average amplitude of the epochs corresponding to each mismatch effect: Window 2 in Table 1). The darkest regions were the most negative.



words. With this aim, we presented subjects with a face-feature-matching task using newly learned faces with no associated verbal information related to identity. In addition, as within-subjects control conditions, we presented the same matching task using other faces learned with associated verbal information (occupation and proper name) and another two similar matching tasks that used the learned verbal material in different ways. A first step was therefore to ensure that subjects became familiar with two subsets of faces (with and without associated verbal information) and the verbal stimuli (occupations and proper names related to the subset of faces with associated verbal information). Behavioral results obtained across learning sessions revealed progressive learning of both faces and verbal stimuli presented. No differences were observed between faces with and without associated verbal information in the forced-choice discrimination task of learning sessions. A very high level of recognition, and thus of familiarization, was obtained for both facial and verbal materials by the end of the training sessions. In accordance with this, in the four matching tasks of the ERP recording a good level of performance was also found, the subjects being capable of recognizing efficiently matching and mismatching stimuli in all tasks. Considering the d' values, subjects demonstrated better recognition in the face-occupation and occupation-name matching than in the face-feature matching, due probably to the fact that verbal stimuli were easier to learn. Subjects fared no

better in matching features with faces when these were associated with occupations and names (Task 2) than when the task involved “pure” faces (Task 1). According to priming studies, in which presentation of the name as verbal information related to the face does not facilitate the decision on whether or not a face is familiar (a task dependent on access to FRUs; Bruce & Young, 1986), in our face-feature-matching tasks (1 and 2) face structural recognition seemed not to be influenced by the verbal information associated with the face (even when verbal information could be activated in conjunction with the facial structure).

Electrophysiological results obtained show that mismatching stimuli evoked different N400-like effects in all tasks. This negativity was followed by a late positivity also associated with mismatching stimuli. In a previous study (Olivares et al., 1999), we suggested, following Halgren (1990), that the negativity evoked by mismatching completions may reflect a more difficult retrieval from long-term memory when mnemonic representations are incompatible with the stimuli displayed (an explanation commonly proposed for N400), whereas the consecutive positivity would denote an integratory process in working memory that is also more difficult for this type of completion. Here, the negativity associated with mismatch stimuli is conspicuous when match ERPs are subtracted from mismatch ERPs (Figure 2A). Amplitude was significantly greater in Task 4 (verbal) than in Tasks 1 (“pure” facial) and 3

("cross-domain"). Given that there were differences in performance between the four matching tasks, we considered first of all whether task difficulty might be related to amplitude differences. However, although the best performance was found in Tasks 3 ("cross-domain") and 4 ("pure" verbal), in these tasks significantly different amplitudes were recorded (the N400 of Task 4 was that with the highest amplitude, and that of Task 3 was among the two with the lowest amplitudes). Also, we found that there was greater similarity between the training and recording tasks for the facial stimuli than for the verbal ones, with the latter perhaps being at a disadvantage in terms of priming effects. This should have been reflected also in Task 4, both in a higher amplitude of the mismatch negativity and in a poorer performance. Nevertheless, a greater amplitude associated with a better performance were found in this task. We might ask ourselves, therefore, whether the greater amplitude (or the very existence) of an effect such as the N400 is necessarily associated with the processing of verbal information. If this was the case, we would expect to find greater amplitude of the effect in Task 3, in which the associated verbal information is of special relevance, compared to Tasks 1 and 2. This was not the case, and we shall therefore discuss the intervention of different processes of domain-dependent codification and retrieval related to each task.

Examination of the timing differences between tasks shows that the onset of the mismatch negativity occurred 20 msec earlier in Tasks 1 and 2 (face-feature matching, 260 msec) than in Task 4 (occupation-name matching, 280 msec). These differences could be determined by timing differences for accessing facial (structural) and verbal codes when the stimuli are presented visually and all are related to the person's identity. Timing differences in accessibility to structural and verbal codes related to face recognition have been confirmed in psychological studies on face-name interference. In a study by Young, McWeeny, Ellis, and Hay (1986, Experiment 1), for example, faces could be categorized as familiar or unfamiliar (which depends on access to FRUs) more quickly than they could be named. Of particular interest is that the onset of the mismatch negativity in Task 3 ("cross-domain") occurred about 20 msec later than that evoked by mismatching names (Task 4). The contextual information related to a face—the person's occupation, for example—is commonly supposed to be accessed before or in parallel to the name codes (de Haan, Young, & Newcombe, 1991; Bruce & Young, 1986). However, in Task 3 of this study, the underlying processes are somewhat special, since the occupation is primed by an incomplete face, a type of (visual) code (of a structural nature) that is supposedly activated first, after which the subject must access another type of (verbal) code related to an occupation, and match it with the face presented. This domain shift may there-

fore determine the time delay observed, compared to tasks in which information relative only to a single domain is processed. In support of this interpretation, the peak latency of the mismatch negativity in Task 3 permits us to compare it with the mismatch negativity described by Barrett and Rugg (1989) in a task in which subjects had to decide whether two consecutively presented faces belonged to the same occupational category. This negativity peaked around 450 msec, later than the classic N400 described for the verbal domain. In relation to the timing in Tasks 1 and 2, it should be stressed that the most negative values (including the peak) tended to have shorter latencies for Task 1 (windows 300–340 msec and 340–380 msec, peak at 360) than for Task 2 (windows 340–380 and 380–420 msec, peak at 380). Moreover, in Task 1, the similar (negative) amplitude values were observed to be slightly more concentrated in time (260–420 msec) than in Task 2 (260–460 msec). Although we have stressed that verbal information was not decisive in the recognition of facial identity in Task 2, these differences in latencies of the peak and duration of the negativity between these two tasks may suggest a more verbal-independent effect in Task 1.

Concentrating on the scalp topography, a general result across all tasks is that parietal sites P3 and P4 appeared among the most negative, which may reflect common domain-independent attentional and visual processes required in matching tasks involving faces seen beforehand or recently learned (Katanoda et al., 2000; Haxby et al., 1996; Grady et al., 1995). We discuss first the results from Task 1, the task most independent of verbal-semantic information. As mentioned above, in Task 1, the mismatch effect was observed to peak at about 360 msec (N360). N360 had a predominant right posterior temporal localization, since T6 appeared as the most negative site. In addition to T6, the right occipital site O2 was among the most negative. This predominant right temporal posterior distribution of N360 in Task 1 is clearly congruent with results from studies by other authors (those quoted in the Introduction section). Interestingly, a predominant right occipito-temporal localization at T6 has also characterized the N170 reported by Bentin et al. (1996). N170 has been associated with early structural encoding mechanisms that may be not specifically involved in face identification but associated with a mechanism providing a sensory facial representation to a higher level perceptual system. Although N170 and N360 might share some neural generators, unlike N170, N360 would be preferentially associated with mechanisms involved in further processing of information related to structural descriptions of familiar faces in long-term memory. In relation to long-term memory, Eimer (2000) described an N400 for faces distinguishable from the classic N400 for words, which was greater for the first presentation of a familiar face when

compared with that of unfamiliar faces. This author attributed the modulation of this long-latency component to the activation of stored representations of familiar faces and the subsequent activation of representations in semantic memory (a similar interpretation to that postulated in studies with famous faces). In our experiment, we think N360 may reflect a different process. Studies on imagery reveal that the representation and/or perceptual analysis of facial stimuli is accompanied by the activation of the ventral occipito-temporal cortex (O'Craven & Kanwisher, 2000), with a notable activation of regions devoted to early visual processing when subjects form images in anticipation of answering questions about concrete details (Klein, Paradis, Poline, Kosslyn, & Bihan, 2000). In accordance with Damasio (1989), early visual structures support the processes of perception and computation of facial elements and hold the records for such computations in functional mappings dedicated to different visual properties. In the present study, when variations are introduced in the facial structure (through the insertion of mismatching features), the activity of these early visual structures may be necessary for the top-down "reconstruction" of the stored face representations in long-term memory. Thus, although no modulation of the N170 was produced (until 260 msec no differences were observed between the two experimental conditions, and this was corroborated statistically), some neural mechanisms related to the "structural encoder" could have been recruited in order to resolve the matching task in the present experiment.

It is also necessary to point out that in Task 1, together with T6 and O2, Fz appeared among the most negative sites, as did to a lesser extent F8. Furthermore, the scalp distribution of the mismatch effect (N400) was frontally characterized in Task 2, where subjects performed the same face-feature matching, but for faces with associated semantic verbal information. In our study, effects on ERPs at frontal sites do not necessarily indicate frontal cortex involvement. However, the involvement of frontal sites in face-processing tasks has been described in various functional brain imaging and deep recording studies (Katanoda et al., 2000; Marinkovic et al., 2000; Vignal, Chauvel, & Halgren, 2000; McDermott et al., 1999; Scalaidhe et al., 1997). In particular, a right frontal (together with a parietal) activation has been described by Katanoda et al. (2000) as associated with the detection of new faces and retrieval effort. Thus, in Task 1, placing incongruent features on a familiar face can lead to the perception of new stimuli, and this novelty could elicit the participation of (right) frontal regions in the mismatch effect obtained. Moreover, in Task 2, a (greater) frontal modulation may reflect at the scalp the activity of neural systems in the frontal and anterior temporal cortex that are responsible for processes that bring together several sources of infor-

mation (Leveroni et al., 2000; Gorno Tempini et al., 1998). Covert updating of information related to biographical knowledge, associated with this subset of faces, may have led to a widespread activation across these areas. In accordance with this, a similar frontal modulation partially characterizing mismatch negativities has been described as reflecting the activity of neural systems that are sensitive to "semantic" relationships between pictorial stimuli (Barrett & Rugg, 1990). Thus, in Task 2, the mismatch negativity may be mainly reflecting mechanisms that relate (in a covert way) facial structural descriptions (or FRUs) with personal identity and name codes (Bruce & Young, 1986). The peak latency of 380 msec in this task suggests a certain delay with respect to the mismatch effect in Task 1 (N360), thus reflecting an incipient participation of mechanisms corresponding to stages of face recognition of a higher order. Failures in this kind of link have been described in individuals with "amnesic associative" prosopagnosia following damage in anterior temporal regions, including limbic and paralimbic structures and near-associative cortices (Damasio, Tranel, & Damasio, 1990). Concentrating on the ERP studies using highly familiar faces as stimuli, the negativity obtained by Barrett et al. (1988) for nonmatching second faces in a same-different task between approximately 250 and 600 msec was greater at frontal and temporal sites for a large part of its duration. Especially interesting was the result from Jemel et al. (1999), who found, applying the same face-feature-matching task as in the present study, but with famous faces as stimuli, an N400-like effect in which two components could be distinguished: The first, an N350, was associated with occipito-temporal and parieto-occipital activity (probably corresponding to the N360 of Task 1 in the present study); the second, an N380, with the same latency as the negativity of Task 2 in the present study, was related to activity in right infero-frontal regions. Furthermore, Bentin and Deouell (2000) found a negativity between 250 and 500 msec with a maximum in frontal and central areas when subjects carried out a task of counting faces of famous politicians in a sequence of stimuli in which these were mixed with faces of famous nonpoliticians and unfamiliar faces. All of these findings suggest that access, covert or otherwise, to verbal identity codes, such as those related to occupation and name, is commonly linked to the involvement of frontal or anterior areas.

In Task 3, a mismatching negativity (N440) was evoked when mismatching occupations were presented after a facial context (incomplete face). Interestingly, the scalp distribution of the mismatch effect in this task, which has been characterized as a cross-domain task, was almost exclusively parieto-occipital. If it is assumed that in this task codes of different kinds, including those related to biographical verbal knowledge, must be activated in parallel in order to

carry out the cross-domain matching, a more extensive frontal (or anterior) distribution should be expected. The almost exclusive posterior distribution of the mismatch effect in this task, however, points to the possible involvement of other psychophysiological mechanisms. It may be that the presentation of a stimulus prime from a different domain leads the subject to maintain active a facial representation in order to facilitate the cross-domain matching. Furthermore, displaying an incomplete face may evoke a sort of covert face completion, thus facilitating the matching of face representation and associated verbal information. ERP modulations in occipital regions related to facial image reconstruction have been described by Uhl et al. (1990), who found slow DC shifts to be enhanced in occipital sites when subjects were required to imagine famous faces. Studies using functional brain-imaging techniques have also noted the activation of the areas involved in earlier visual processing in tasks requiring visual–mental imagery (Klein et al., 2000; Kosslyn et al., 1999).

The most negative sites were posterior in Task 4, although in this task we also found central sites to be among the systematically most negative. If we bear in mind, moreover, that a certain lateralization of the mismatch effect towards the right was observed (P4 and O2 were two of the four most systematically negative sites), we can consider that it was in this task where we obtained, as expected, a scalp distribution similar to that of the N400 of language. Thus, it could be said that a linguistic N400 may also be elicited by verbal stimuli that are closely related to knowledge about a familiar face.

In summary, it is quite remarkable that an N400 mismatch effect can be elicited even by “pure” facial stimuli (with associated verbal information unavailable or difficult to access), as in Task 1. Moreover, addition of verbal–semantic information to faces affected the latency and topography of the N400. It should be stressed that latencies were usually shorter when intradomain processing was required, and that access to verbal semantic codes in this type of task appears to occur later than access to structural facial codes. The mechanisms underlying an N400 nonlinguistic component seem to rely, like those related to the codification of the face as a complex visual pattern, mainly on occipito-temporal structures, and appear to function at stages of processing subsequent to such codification but before verbal biographical data processing. Access to and retrieval of the latter type of data, where available, seems to involve mainly fronto-temporal structures, the activity of which may characterize the topographical distribution of electrophysiological responses, even in tasks where subjects are required to carry out processing of a structural type. The mismatch response evoked in Task 1 appeared even when subjects had no verbal information about the face. However, without testing visual stimuli other than faces,

face specificity cannot be assumed from this work. Recent studies using neuroimaging techniques (see, e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000) have found an activation in areas involved in face processing when expert subjects carry out tasks of detection of nonface objects (e.g., cars and birds). According to Adolphs (2001), face-responsive regions in the fusiform gyrus have evolved as a part of a distributed neural system for processing faces; however, this system does not distinguish between stimuli that actually are faces and those that are nonface stimuli making similar computational demands. Thus, both perspectives (domain-specificity and expertise) may have some claim to validity.

In conclusion, our data support the existence of an N400 component in response to visual stimuli, and which seems to be related to facial structural information processing. Further research is necessary to solve the face-specificity question and to identify the degree and type of knowledge an individual possesses about previously seen faces. It is reasonable to expect that future ERP research, in conjunction with other techniques with high spatial resolution (such as magnetoencephalography or functional magnetic resonance) and suitable experimental designs, may permit us to determine the neural bases of such processes, giving rise to important applications, for example, in criminological investigations. For the time being, ERPs constitute good indicators in real time of the codification and retrieval processes involving multiple codes, and are a useful tool for investigating the cognitive and neural bases of face recognition.

METHODS

Subjects

The subjects include 15 healthy (8 women and 7 men), right-handed volunteers (although one claimed to be ambidextrous, he was included in the sample because he used his right hand and his electrophysiological recordings were quite similar to those of the other subjects). Ages ranged from 20 to 38 years (mean age 25.3 years). All had normal or corrected vision and university-level education. No subject was informed about the specific aims of the experiment.

Stimuli

Facial Stimuli

Forty artificial (digitized) faces with neutral expression served as learning faces. These faces were created by combining selected male Caucasian features from a catalogue (Identikit gallery) used in criminological investigations. Also used, in the learning sessions and ERP recording session, were 40 context (incomplete) faces, that is, the original 40 faces of the learning set without

the eyes–eyebrows region. Another 320 faces served as mismatching features–faces stimuli, of which 240 were used in the learning sessions and 80 in the ERP recording session. All of these incongruent faces were created by completing the eyes–eyebrows region of each context face with features (eyes–eyebrows) that were different from the original ones (for a detailed description of the construction of these faces, see Olivares et al., 2000). The size of each face (presented on a white background 15 cm high \times 15 cm wide) on the computer screen was 14 cm high \times 10 cm wide (approximately half natural size). In the recording session, each subject sat 108 cm from the screen, and the faces subtended an approximate vertical visual angle of 3.7° and an approximate horizontal visual angle of 2.65° .

Verbal Stimuli (Occupations and Proper Names)

Verbal stimuli were obtained by asking 20 judges (average age 28.2 years and with university-level education) to write down 20 names of occupations and 20 male proper names, all commonly used in real life. The 40 most-repeated items from each set (occupations and names) were selected, of which 20 were used as a learning set of verbal stimuli and the remaining 20 as mismatching stimuli in the ERP recording session. The combinations of faces, occupations, and names, which would be learned as associated stimuli, were random. Word length in the total set of occupations varied from 6 to 14 letters (average 8.4 letters) and in the set of names, from 4 to 8 letters (average 5.75 letters). In the recording session, both occupations and names appeared, as in the case of the facial stimuli, in the center of a white background 15 cm high \times 15 cm wide. Occupations subtended approximate vertical and horizontal visual angles of 0.29° and 1.51° , respectively. Names subtended approximate vertical and horizontal visual angles of 0.29° and 1.16° , respectively.

Procedure

A first training part consisting of six learning sessions was carried out over three days (two sessions per day).

Learning Sessions

To familiarize subjects with the faces, occupations, and proper names, the original learning set of 40 faces was divided into two subsets of 20 faces each. The first subset was presented to half of the subjects without associated verbal information, while the second subset was presented to the same subjects with an occupation and a proper name associated with each face. Subsets of faces with and without associated verbal information were counterbalanced across subjects. Each learning session was made up of two phases, the study phase

and the test phase, which were carried out separately for each subset of faces.

Study and test phases for faces learned without associated verbal information. During the study phase, subjects were required to pay close attention to each one of 20 faces that appeared on the computer screen when they pressed the spacebar of the keyboard. Their task consisted in memorizing the structure of each face, paying special attention to the eyes and eyebrows belonging to it, and avoiding making verbal associations. The test phase consisted in a forced-choice discrimination task between matching and mismatching features for each face studied. In this task, subjects again pressed the spacebar to see each face, which was displayed on the computer screen without the eyes and eyebrows. Simultaneously, below this incomplete face were shown two numbered combinations of eyes and eyebrows (one of them belonging to the face). Subjects had to decide (and indicate their decision by pressing a particular key) which one completed the face appropriately. Once they had made their choice, the selected combination was superimposed automatically on the face, completing it. Subjects could then verify the fit of the selected features on the face and, if not satisfied, rectify their decision. Feedback (by means of a sound from the computer) on mistakes was provided (for a detailed explanation, see Olivares et al., 2000).

Study and test phases for faces learned with associated occupations and proper names. In this case, the study and test phases were quite similar, but subjects were required to familiarize themselves, in addition to the faces, with occupations and names associated with each face. In the study phase, when a face appeared on the screen, subjects pressed the spacebar again so that the labels of an occupation and a proper name, both corresponding to the face presented, were displayed below it (e.g., Carpenter, John). Subjects were permitted to make any kind of verbal association between the face and the verbal labels, since the main purpose of this phase was to facilitate associative learning between facial and verbal stimuli. In the test phase, subjects carried out the forced-choice discrimination task for the faces studied from this subset, but were also asked to tell the experimenter the occupation and name that had been presented previously (in the study phase) as associated with the displayed face. These verbal reports were recorded by the experimenter. In cases in which subjects could not produce the occupation or name (or made mistakes), the experimenter told them the correct response, in order to facilitate the association between facial and verbal stimuli. Even if the subject did not remember the occupation, the experimenter provided it, after which the subject was permitted to say the associated name. The order of presentation of each subset of faces varied across sessions, so that in one session, the faces with associated verbal information were studied

and tested first, and in the following session, it was the set of faces without associated verbal information that was presented in first place. Subjects' performances were evaluated, in the forced-choice discrimination task, using the d' of signal detection theory (Swets, 1964), which verifies the subject's ability to discriminate correct from incorrect features. In the case of occupations and names we used the number of items recalled (as reported verbally by subjects) in each session. Subjects were shown their performance results at the end of each session.

ERP Recording Session

ERP recording was carried out the day following the end of the learning sessions. Subjects sat in a comfortable chair in front of the computer monitor and were asked to minimize eye and body movements. Before the recording, they reviewed the learned faces, occupations, and names in a similar way to that used in the study phase of the learning sessions. Subsequently, the ERP recording was carried out, with subjects being required to perform four matching tasks (Figure 1).

Task 1: Face-feature matching task ("pure" facial task, using as stimuli the faces without associated verbal information). In this task, each one of the 20 faces was presented (by the subject pressing a key) four times as a context stimulus without the eyes-eyebrows fragment for 500 msec. In half of the trials (40), each context face was completed automatically with the correct features (eyes and eyebrows belonging to the face), as they had been learned; in the other half of the trials, the face was completed with mismatching features (not belonging to the face). The complete face was displayed for 500 msec. In each trial, subjects had to decide whether the completion was the correct one or not.

Task 2: Face-feature matching task ("nonpure" facial task, using as stimuli the faces with associated verbal information). This task was identical to Task 1, except that the subset of faces was different. In this case, the faces used as stimuli were those that had been learned with associated occupations and names.

Task 3: Face-occupation matching task ("cross-domain" task). For this task, the context stimulus used was the same as in Task 2 (the incomplete face), but once it had been displayed for 500 msec, it disappeared and was replaced by an occupation (which was also displayed for 500 msec). In half of the trials (40), the occupation displayed corresponded to that learned in the learning sessions as associated with the face presented; in the other half, the occupation was incorrect. In each trial, the subject had to decide whether the occupation displayed was correct or not.

Task 4: Occupation-name matching task ("pure" verbal task). In this task, only verbal stimuli were presented. The stimulus used as context was an occu-

pation belonging to one of the 20 faces from the subset with associated verbal information. The occupation was presented for 500 msec (by the subject pressing a key), after which it disappeared and was replaced by a name, which was also displayed for 500 msec. In half of the trials (40), the name presented was that learned (in the learning sessions) as associated with the occupation presented; in the other half, the name presented did not correspond to the occupation.

In each task, once the second stimulus disappeared, the screen went black for 700 msec before the word "respond" appeared, so that the subject could give his/her response (left mouse key for correct and right mouse key for incorrect). Presentation of stimuli was randomized. The order of presentation of the four matching tasks was rotated across subjects, so that a subject began with Task 1, moving onto Task 2, and so on, and the following subject began with Task 2, went on to Task 3, and so on. Behavioral data were also analyzed using d' . In this case, we evaluated subjects' capacity for discriminating matching from mismatching second stimuli (features, occupations, and names).

ERP Recording Technique and Analysis

EEG was recorded with Ag/AgCl disk electrodes from 20 recording sites: Fp1-2, F3-4, C3-4, P3-4, O1-2, F7-8, T3-4, T5-6, Fz, Cz, Pz (10/20 International System) and Oz. The tip of the nose was used as reference. Impedance was below 5 k Ω . EOG was recorded from electrodes placed just above the right supraorbital ridge (vertical EOG) and on the right outer canthus (horizontal EOG). EEG and EOG signals were filtered on-line between 0.05 and 30 Hz (3 dB down). A notch filter for 50 Hz was also used. ERPs were calculated off-line, averaging segments of 256 points of digitized EEG (12-bit A/D converter, sampling rate of 250 Hz). These segments covered 1024 msec, comprising a prestimulus interval of 148 msec and a poststimulus onset interval (presentation of the complete face in Tasks 1 and 2, presentation of the occupation in Task 3, and presentation of the name in Task 4) of 876 msec. Before averaging, EEG was visually inspected and those segments with excessive EOG artifacts eliminated. Only trials with correct responses were considered for averaging. Correction of DC level was carried out by subtracting the average prestimulus amplitude value. Data were submitted to repeated measures ANOVAs, where the Greenhouse-Geisser procedure was applied when appropriate (Keselman & Rogan, 1980). Post hoc analysis using the Tukey HSD test and pairwise comparisons were carried out.

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