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Research Report

"Did you see him in the newspaper?" Electrophysiological correlates of context and valence in face processing

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ABSTRACT

Face recognition emerges from an interaction between bottom-up and top-down processing. Specifically, it relies on complex associations between the visual representation of a given face and previously stored knowledge about that face (e.g. biographical details). In the present experiment, the time-course of the interaction between bottom-up and top-down processing was investigated using event-related potentials (ERPs) and manipulating realistic, ecological contextual information. In the study phase, half of the faces (context faces) were framed in a newspaper page entitled with an action committed by the person depicted; these actions could have a positive or a negative value, so in this way emotional valence could be manipulated. The other half was presented on a neutral background (nocontext faces). In the test phase, previously presented faces and new ones were presented on neutral backgrounds and an old/new discrimination was requested. The N170 component was modulated by both context (presence/absence at encoding) and valence (positive/ negative). A reduction in amplitude was found for context faces as opposed to no-context faces. The same pattern was observed for negative faces compared to positive ones. Moreover, later activations associated with context and valence were differentially distributed over the scalp: context effects were prominent in left frontal areas, traditionally linked to person-specific information retrieval, whereas valence effects were broadly distributed over the scalp. In relation to recent neuroimaging findings on the neural basis of top-down modulations, present findings indicate that the information flow from higher-order areas might have modulated the N170 component and mediated the retrieval of semantic information pertaining to the study episode.

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1. Introduction

Decades of research in the field of cognitive neuroscience have demonstrated that face recognition is probably one of the most complex skills of the human brain. The apparent social relevance of the capacity to recognize humans explains the development and specialization of the systems that accomplish this function. Recent functional imaging methods have

refined traditional models of face recognition (Bruce and Young, 1986; Burton et al., 1990) and extended knowledge about the functional anatomy of face processing originally drawn from neuropsychological patients. These have revealed a specialized brain region in the extrastriate visual cortex (Haxby et al., 2002), namely, the Fusiform Face Area (Kanwisher et al., 1997). Despite these advances in research techniques, some issues are still under debate. Experiments have generally

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employed stimuli presented in isolation, but in our everyday life we automatically process faces in complex visual scenes. There is no doubt that such contextual frames can strongly influence face perception in a top-down manner (Bar, 2004). A classic example is the "butcher-on-the-bus phenomenon" which has been recently investigated by Yovel and Paller (2004). This phenomenon occurs when an individual sees someone in an atypical context, and is experienced as a sense of familiarity while being unable to recall any specific detail about that person. The "butcher-on-the-bus phenomenon" clearly demonstrates that incoming information to the perceptual system can be influenced by what is already known about a stimulus. In other words, that visual perception is "cognitively penetrable" (Pylyshyn, 1999). Thus, what is the impact of context on face processing, and how does face perception interact with high-level, cognitive processing?

Numerous studies have focused their attention on local (intra-facial) context and have aimed to investigate how facial features are processed according to whole face (that is, context) manipulations. Results suggest an advantage of whole-face processing compared to parts processing (Tanaka and Farah, 1993) which would lead to an inhibitory influence of context on feature recognition both on normal (Leder and Carbon, 2005) and neuropsychological (Bousten and Humphreys, 2002) subjects. Other studies have focused on global (extra-facial) context to test how different elements associated with a face (semantic labels, background cues, scenes, co-presented stimuli) can influence its recognition. Behavioral studies show how changes in context decrease recognition accuracy (Thompson et al., 1982; Memon and Bruce, 1983). Moreover, it has been demonstrated that context affects visual search (Montoute and Tiberghien, 2001) and categorization (Rousselet et al., 2003) processes. These data account for the hypothesis of a contextual information effect on face perception.

In addition to behavioral data, findings from event-related potentials (ERPs) studies have substantially contributed to this area of research. Given its excellent temporal resolution, the event-related potentials technique provides a valuable means to investigate the time-course of face processing. Different ERP modulations for face stimuli have been investigated. N250r and N400 components have been elicited in short-term recognition and matching paradigms, showing larger positivities for repeated and matching faces respectively (Barrett and Rugg, 1989; Schweinberger et al., 2002). Starting around 300 ms and for a wide range of stimuli, including faces (Munte et al., 1998; Paller et al., 1999, 2000; Graham and Cabeza, 2001), ERP components elicited in long-term recognition paradigms are being identified in more positive-going waveforms for repeated, compared to new, items ("old-new effect", for a review see Friedman and Johnson, 2000). In-depth research on this "oldnew effect" has revealed spatio-temporal, functionally distinct subcomponents which have been linked to dissociable cognitive processes. For example, the parietal old/new effect is elicited over posterior areas between 400 and 800 ms, and is considered an index of recollection. That is, the remembering of an item together with the conscious retrieval of physical, contextual or other source-specific information related to its prior occurrence. Indeed, the parietal old/new effect in a Remember/Know paradigm is greater in magnitude when a Remember response is given (Duzel et al., 1997) and it is related

to correct source judgments (Wilding et al., 1995). Whereas the effect of higher-order processing on these memory-related components is relatively clear, the effect of the top-down information flow on earlier modulations is still a matter of debate. Converging evidence has shown that the N170, a negative component that peaks between 150 and 220 ms on occipitotemporal electrodes, is a specific electrophysiological correlate of face perception. Indeed it is significantly larger in response to faces than to other stimulus categories (George et al., 1996; Itier and Taylor, 2004a; Holmes et al., 2005). This component has traditionally been linked to structural encoding or initial categorization of face stimuli (Sagiv and Bentin, 2001). Although the N170 is considered to be insensitive to attentional modulations (Caquil et al., 2000) and repetition (Eimer, 1998; Bentin and Deouell, 2000), the cognitive impenetrability of N170 has been recently debated. Some studies have reported a reduced amplitude or latency for repeated compared to unrepeated faces (Campanella et al., 2000; Guillaume and Tiberghien, 2005; Itier and Taylor, 2004b; Jemel et al., 2005) and a modulation of N170 amplitude when ambiguous faces (Mooney or schematic faces) are primed with normally configured faces (Bentin and Golland, 2002; Jemel et al., 2003). Moreover, modulations of N170 according to expressional change (Guillaume and Tiberghien, 2005; Miyoshi et al., 2004) and spatial attention (Holmes et al., 2003) have been reported. Together, these findings are consistent with the hypothesis that some cognitive factors may somehow influence the N170 component.

It has been shown that context can modulate retrieval. Indeed, memory can be enhanced when the encoding context is reinstated at retrieval (Cutler and Penrod, 1988). The major goal of the present study is to verify whether contextual information associated with an unfamiliar face at encoding can improve its subsequent recognition, even if the contextual frames are not reinstated with the repeated original stimulus. We hypothesized that the association of perceptual/semantic context with an unfamiliar face in a study phase would affect the recognition of that same face when it is presented in isolation in the test phase. For this purpose, faces were presented either in a contextual frame (context faces) or in isolation (no-context faces) in the study phase. Context faces were embedded in a newspaper article, the headline of which specified an action committed by the actor depicted. Since the action could be positive or negative, emotional valence could be manipulated. In the test phase, context, no-context and new faces were presented in isolation, thus without a contextual cue. In this phase, reaction times and event-related potentials (ERPs) were recorded. We predicted that the effect of the encoding context on recognition would emerge at an early stage of processing, namely, at the N170 level. Indeed, although this component has been linked to structural encoding, recent evidences suggest that the N170 may be modulated both by memory-related factors, such as repetition (Eimer, 1998; Bentin and Deouell, 2000), and by contextual manipulations (Righart and de Gelder, 2005). As an index of the effect of context at encoding on later recognition, we used the comparison of ERPs elicited by the presentation of context, nocontext and new faces in the test phase. Instead, as an index of the effect of context valence on recognition, we used the comparison of ERPs elicited by the presentation of positive and

negative-context faces at test. Indeed, behavioral and ERP literature suggests that recognition is affected not only by the presence or absence of a given context, but also by its emotional valence. To our knowledge, emotionally valenced contexts associated with face stimuli have been studied exclusively with respect to facial expressions, which is considered an intrinsic context, that is, "an integral part of a face" (Guillaume and Tiberghien, 2001). Only one recent study manipulated extrinsic context and face emotional valence (Righart and de Gelder, 2005). However, in that study, the authors used a perceptual task. Thus, the effect of the encoding context on recognition was not taken into account. Consequently, our final goal was to assess the effect of an emotionally valenced context on face recognition.

Results¹

2.1. Behavioral data

2.1.1. Study-context

Behavioral performance for context, no-context and new faces is summarized in Table 1. Separate analyses for reaction times and accuracy were submitted to an analysis of variance with the factor Study-context with 3 levels (context, no-context and new). No differences were found in reaction times. For accuracy, the Study-context factor was significant [F(2,28)=21.85, P<0.0001]. Post hoc analyses revealed a higher percentage of correctly identified new faces compared to context and no-context faces (Ps<0.0001).

2.1.2. Study-valence

Table 2 provides a summary of behavioral performance for positive and negative-context faces.

Pairwise t-test comparisons on reaction times and accuracy were employed to compare positive and negative-context faces. Results showed a higher percentage of correctly identified negative faces as compared to positive-context faces $[t(14)=-2.98,\ P=0.01)]$. No reaction time differences were found.

2.2. Event-related potentials

ERPs analyses were performed on the N170 component and on five consecutive 100-ms-wide windows from 250 to 750 ms from stimulus onset.

N170 was identified as the most negative component, peaking between 150 and 200 ms after stimulus onset. This component was conspicuous at eight posterior electrode sites: T5, P3, Pz, P4, T6, O1, Oz, O2.

Separate analyses on ERP measures for Study-context and Study-valence conditions were performed. Huynh–Feldt correction was applied when necessary to compensate for the violation of the assumption of sphericity; the original degrees of freedom, the correction coefficient ε , and corrected P values

(significant at α =0.05) are reported. In the presence of significant interactions, Bonferroni-corrected pairwise comparisons were performed (and all reported P values are significant with respect to adjusted α levels).

2.2.1. Study-context

N170: A two-way repeated measure ANOVA was carried out with 3 levels of Study-context factor (context, no-context and new) and 8 levels of Electrode factor (T5, P3, Pz, P4, T6, O1, Oz, O2). For amplitude values, the interaction Study-context×-Electrode was significant $[F(14,196)=2.86, P<0.05, \varepsilon=0.35]$. Bonferroni-corrected t-tests at single electrode sites revealed that no-context faces elicited significantly larger (more negative) amplitudes than context faces at O1, Oz and O2 (Ps<0.01), Fig. 1. No latency differences were found.

Mean amplitude values in the 250–350, 350–450, 450–550, 550–650 and 650–750 ms time windows were each subjected to a two-way repeated measures ANOVA with 3 levels of Studycontext factor (context, no-context and new) and 15 levels of Electrode factor (F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T6, P3, Pz, P4, T6).

As shown in Fig. 2, the effects of context on recognition were differently distributed over the scalp.

The overall ANOVA revealed no main effect for Study-context at any latency, whereas an interaction between Study-context and Electrode was found from 250 to 550 ms post-stimulus (Table 3). This interaction was clarified by means of pairwise comparisons at single-electrode sites. In the 250–350 and 350–450 time windows, the interaction was due to a greater positivity for context compared to no-context faces at F7 (250–350: P<0.01; 350–450: P<0.05), and to larger positivities for context and no-context faces as compared to new faces at Pz and P4 (in both time windows Ps<0.05 and 0.01, respectively). This latter effect at the parietal electrodes may be considered as an old–new effect. In the 450–550 time window, a larger positivity emerged for both kinds of old faces (context and no-context) as compared to new ones only at Pz (P<0.05).

2.2.2. Study-valence

N170: To investigate the distribution of ERP responses to differently valenced stimuli, a repeated measures ANOVA was carried out with 2 levels of Study-valence factor (positive and negative), two levels of Hemisphere factor (right and left) and three levels of Electrode factor (Temporal: T5/6, Parietal: P3/4, Occipital: O1/2). Fig. 3 shows the N170 at occipital sites. For amplitude values, a significant main effect for Study-valence

Table 1 - Mean response rates and reaction times for context, no-context and new faces

Stimulus type	Response category	Response rate (%)	RT (ms)
Context	Hits	71.5 (11.9)	953.1 (257)
	Miss	28.5 (11.9)	975.2 (241)
No-context	Hits	68.9 (14.5)	991.2 (294)
	Miss	31.1 (14.5)	995.7 (239)
New	Correct rejection	88 (1.2)	998.2 (237)
	False alarms	12 (1.2)	961.0 (210.1)

Values in parentheses display standard deviations.

¹ Preliminary ANOVAs were performed on behavioural and ERP data with sex as a between-subjects factor; because sex effects did not approach significance in any measure, subsequent analyses were performed on data collapsed over this factor.

Table 2 – Mean response rates and reaction times for positive and negative-context faces					
Stimulus type	Response category	Response rate (%)	RT (ms)		
Negative	Hits	74.4 (13.5)	952.5 (260)		
	Miss	25.6 (13.5)	967.1 (264)		
Positive	Hits	68.4 (11.7)	953.7 (266)		
	Miss	31.6 (11.7)	951.9 (256)		
Values in parentheses display standard deviations.					

was found: positive-context faces elicited greater amplitudes than negative-context faces [F(1,14)=4.86, P<0.05]. For latency values, a significant main effect for Study-valence was found: negative-context faces were processed faster than positive-context faces [F(1,14)=11.39, P<0.01].

ERP mean amplitudes for the following windows were analyzed: 250–350, 350–450, 450–550, 550–650, 650–750. A three-way ANOVA with repeated measures was carried out with 2 levels of Study-valence factor (positive and negative), 3 levels of anterior-to-posterior factor (frontal: F7, F3, Fz, F4, F8; central: T3, C3, Cz, C4, T4; posterior: T5, P3, Pz, P4, T6) and 5 levels of left-to-right factor (lateral left: F7, T3, T5; medial left: F3, C3, P3; middle: Fz, Cz, Pz; medial right: F4, C4, P4; lateral right: F8, T4, T6).

The main effect for Study-valence was significant from 250 ms post-stimulus (Table 4): larger amplitudes were observed for negative-context as compared to positive-context faces. Moreover, there was a significant interaction between Study-valence, posterior-to-anterior and left-to-right electrodes for all latencies (Fig. 4). This interaction was clarified by means of pairwise comparisons at single-electrode sites. In every time window, a significant effect for Study-valence was found at all midline electrodes (Fz, Cz and Pz: Ps<0.001) and at the anterior (F8, F4), central (T4, C4) and posterior (P4) leads of the right hemisphere (all Ps<0.01). On

the left hemisphere, Study-valence effects were significant only at central (C3) and posterior (P3) leads. These results show that the valence effect was rather broadly distributed, with a greater occurrence in the right hemisphere (Fig. 4a), especially at the anterior leads (Fig. 4b).

3. Discussion

In this study, we investigated whether face perception is modulated by higher-level processes and, if this is the case, at what stage of processing this modulation occurs. The association of realistic, ecological visual contexts with studied-face stimuli was considered to be a suitable means to accomplish this goal. Our primary interest was not only the absence/ presence of this context, but also its emotional valence. Our results demonstrate that this interaction starts at an early stage of processing, namely at the N170 level. Indeed, this component was sensitive not only to the face-context (presence/absence) but also to the contextual valence (positive/negative). These effects were also found on later, recognition-related modulations.

3.1. Context and valence effects on the N170 component

Although its neural generators and its cognitive penetrability are still debated, common opinion is that the N170 reflects structural encoding. Indeed, only a few studies report a modulation of this component according to memory or attentional factors (Campanella et al., 2000; Holmes et al., 2003; Itier and Taylor, 2004b). First of all, results reported here clearly demonstrate that the early stages of structural analysis, indexed by the N170 component, are influenced by the presence of context at encoding. Indeed, context faces elicited smaller negativities than no-context faces. This finding parallels the results of a recent ERP study (Righart

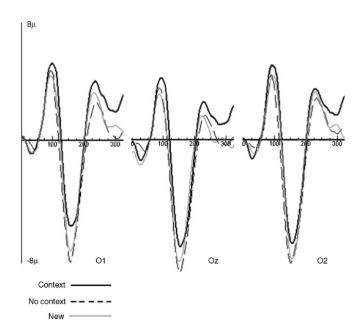


Fig. 1 - N170 amplitudes elicited by context and no-context faces at occipital sites.

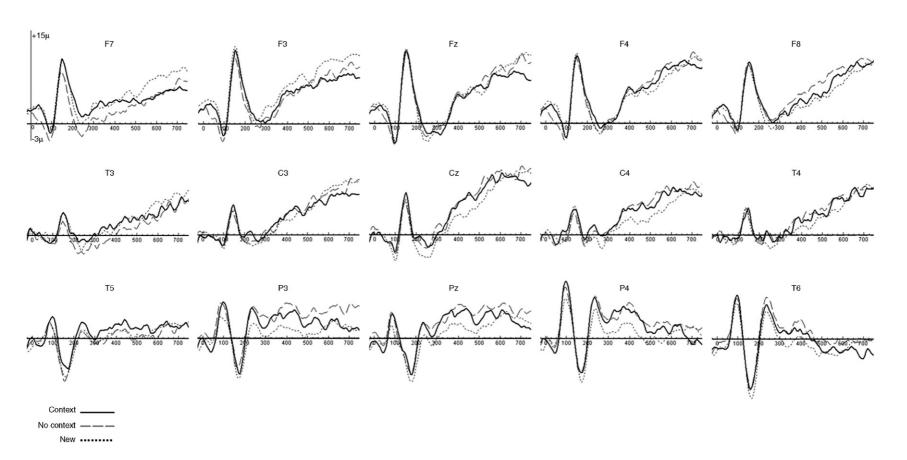


Fig. 2 - Grand-averaged ERP waveforms elicited by context, no-context and new faces at selected electrodes.

Table 3 – F ratios and Huynh–Feldt epsilon for main ERP context effects in consecutive time windows					
	250–350 ms	350–450 ms	450–550 ms	550–650 ms	650–750 ms
Context effects	F (ε)	F (ε)	F (ε)	F (ε)	F (ε)
Study-context	1.78 (0.92)	1.48	0.88 (0.86)	0.15 (0.89)	1.23 (0.8)
Study-context×Electrode	2.12* (0.23)	2.38 * (0.29)	2.22* (0.27)	1.97 (0.24)	0.37 (0.22)
e: Huynh_Feldt ensilon					

ε: Huynh–Feldt epsilon.

Uncorrected degrees of freedom: Study-context (2,28); Electrode (14,196); Study-context × Electrode (28,392).

and de Gelder, 2005), in which the presence of a contextual frame reduced the amplitude of the N170, compared to isolated faces. These data were interpreted as a function of the perceptual load of the context information, which may capture attention and thus decrease the N170 amplitude. In the Righart and de Gelder study, however, the context was perceptual information. Conversely, in the present experiment, context had to be retrieved from episodic memory. Hence, we believe that these results account for an early, topdown modulation on face processing. Several lines of evidence suggest that top-down knowledge is used to guide visual object recognition (Bar, 2004). It is commonly considered that top-down processes refer to contextual and knowledge-based factors such as expectation, selective attention, previous exposure, learning and so on. The top-down influence on face recognition in this work may be related to the formation of the episodic memory traces at study. These, in turn, may influence how the visual input was processed at retrieval. In other words, test faces may have benefited from the activation of the representation stored in memory which acted as a prime, at an early stage of processing. Recent theories have emphasized the role of feedback interactions in visual processing (Bar et al., 2006; Ranganath, 2006). These theories are supported by anatomical data from cell recording (Chelazzi et al., 1998; Hupe et al., 1998), neuroimaging (Miyashita and Hayashi, 2000; Murray et al., 2002) and MEG (Bar et al.,

2006) studies, as well as by computational models (Grossberg, 2004; Deco and Lee, 2001). Such findings provide evidence for a modulation of early visual areas and of category-responsive regions (such as the Fusiform Face Area) via a top-down information flow. This is thought to occur through a dense network of feedback connections which transmit signals from higher- to lower-order regions. For example, in a recent study by Bar et al. (2006) combining MEG and fMRI data, the activity of the orbitofrontal cortex preceded the activity of the fusiform gyrus by tens of milliseconds in a recognition task. Moreover, the orbitofrontal activity and the activity in the temporal (fusiform gyrus) and occipital (visual cortex) lobes were timelocked on a trial-by-trial basis. According to Bar's theory, recognition-related regions within the temporal cortex are modulated by coarse representations ("initial guesses") of the visual stimulus that are projected rapidly from early visual areas to the orbitofrontal cortex. Such a top-down mechanism may be particularly valuable in danger- and/or survivalrelated situations. Although not mentioned in Bar's theory, it is possible that similar top-down mechanisms have developed for highly socially relevant stimuli such as faces and, especially, when faces interact with emotional information. Accordingly, studies using face stimuli have also found that activity in the Fusiform Face Area was mediated by top-down feedback from prefrontal areas in working memory (Druzgal and D'Esposito, 2001) and visual imagery (Mechelli et al., 2004)

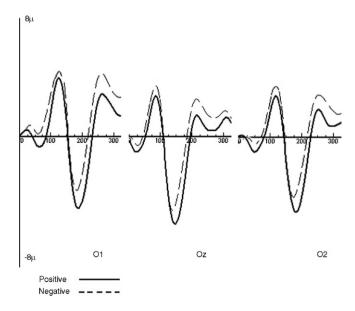


Fig. 3 - Amplitude and latency differences between positive and negative-context faces at occipital sites.

^{*} P<0.05

Table 4 – F ratios and Huynh-Feldt epsilon for main ERP valence effects in consecutive time windows					
	250–350 ms	350–450 ms	450–550 ms	550–650 ms	650–750 ms
Valence effects	F (ε)	F (ε)	F (ε)	F (ε)	F (ε)
Study-valence Study-valence×AP×LR	10.57** 3.69** (0.67)	9.2** 3.5** (0.68)	10.29 ** 3.06 ** (0.76)	8.96** 2.52* (0.8)	9.81** 2.43* (0.89)

ε: Huynh–Feldt epsilon; AP: Anterior-to-posterior electrodes; LR: Left-to-right electrodes.

Uncorrected degrees of freedom: Study-valence (1,14); AP (2,28); LR (4,56); Study-valence × AP × LR (8,112).

tasks. Given that the fusiform gyrus is supposed to be the neural generator of the N170 component, these patterns of activation are of particular interest with respect to the results of the present study. Finally, Henson et al. (2000) demonstrat-

ed that the face-specific activity in the fusiform gyrus increases when unfamiliar faces are repeated, generating a "repetition enhancement effect". Taken together, these data allow us to speculate that repetition-related modulations on

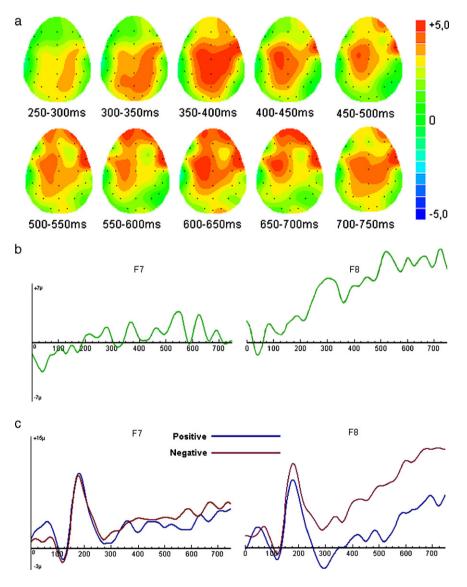


Fig. 4 – Brain potentials to negative and positive-context faces. (a) Topographical maps in the time windows of maximal difference between conditions: strongest color intensity corresponds to maximal amplitude difference. (b) Corresponding differential waveforms (negative-context faces minus positive-context faces). (c) ERP waveforms elicited by positive and negative-context faces at F8 and F7 electrodes. Note that this difference was more prominent on right electrode.

^{*} P<0.05.

^{**} P<0.01.

the N170 occur through top-down connections from prefrontal areas to the FFA.

Secondly, our results indicate that the N170 component is not only affected by the presence/absence of a contextual frame, but also by its emotional valence. Overall, negativecontext faces were processed faster, and elicited smaller N170 amplitudes, than positive ones. This finding is in line with recent ERP studies which have found an early emotional discrimination for face stimuli (Eimer and Holmes, 2002; Pizzagalli et al., 2002; Eger et al., 2003). Although this effect was mainly frontally distributed, some studies have also found an emotion-related N170 modulation. For instance, Batty and Taylor (2003) and Righart and de Gelder (2005) found a longer N170 for negatively, as compared to positively, valenced expressions. It is interesting that, in the latter study, faces embedded in negative contexts elicited larger N170 amplitudes as compared to faces embedded in neutral contexts. This result is inconsistent with our N170 amplitude decrease for faces embedded in negative contexts at encoding. As previously mentioned, however, this difference may be due to the fact that immediate perception of contextualized faces occurred in the Righart and de Gelder study, whereas context retrieval took place in the present experiment. Moreover, a "negativity bias" was shown in several behavioral, ERP and neuroimaging studies. For example, negative stimuli evoked significantly larger P100 (Smith et al., 2003) and P200 (Carretié et al., 2001) than arousal-equivalent positive stimuli in attentional paradigms. From an evolutionary perspective, a processing advantage for negative stimuli may be considered adaptive - in terms of "chances of survival" - as it facilitates rapid responses to aversive events. It is noteworthy that in the aforementioned studies emotional valence is triggered by immediate perception. In our study, emotional information must be retrieved from episodic memory, since all the stimuli were neutral in the test phase. It is reasonable to suppose that a strong faceemotional valence association was formed in the study phase. This representation was sufficiently strong to endure until the successive exposure of the face and thus to affect the N170 elicited by the neutral stimulus in the test phase. A possible explanation for this early effect for negative-context faces could be modulations from higherorder areas to visual cortex and category-specific areas within the temporal lobe. As previously stated, such topdown mechanisms could have developed by virtue of evolutionary pressures to assure rapid responses to danger. Of course, it is very tentative to assume that faces associated with negative contexts in the present study may have such survival or danger-related value. Nonetheless, impressive, negative information is surely closer to danger than neutral or positive information, and specialized brain circuits may have evolved to process this kind of input. The prefrontal cortex possibly subserves this circuit. Indeed, some studies have reported an earlier activation (beginning 100-150 ms poststimulus) of the prefrontal cortex for emotionally negative as compared to emotionally positive or neutral stimulation (Northoff et al., 2000; Kawasaki et al., 2001; Carretié et al., 2005). In a recent study, Smith et al. (2006) found that emotional discrimination enhanced orbitofrontal activity, which in turn increased activity in the hippocampus. As reported by the authors, these neuroimaging findings suggest a top-down modulation which might strengthen the association between emotion and memory.

A final observation regarding the modulation of the N170 component concerns the time lag between the study and the test phase. Indeed, previous studies on the effects of stimulus repetition on the N170 mainly used short-repetition or matching paradigms. In our experiment, the interval between the first exposure to the stimulus and the repetition is relatively large (approximately 20 min). This probably indicates that the effect of context manipulations is long-lasting and exerts top-down effects, despite long intervals and many intervening stimuli.

3.2. Context and valence effects on recognition-related ERPs

One of the first results that emerges from this study is a larger positivity for both kinds of old faces (context and no-context) compared to new ones until 550 ms after stimulus presentation. This modulation resembles the parietal old-new effect, which has been extensively reported in recognition memory research (Friedman and Johnson, 2000). This effect is linked to correct source retrieval and it is thought to reflect recollection (i.e. the remembering of an item together with the conscious retrieval of physical, contextual or other source-specific information related to its prior occurrence). Hence, in the present study, the parietal old-new effect might be considered an index of successful recognition of studied faces, regardless of the encoding context. The scalp distribution of the parietal effect can vary as a function of the stimuli used (Mecklinger, 1998). In our study - as well as in others using face stimuli (Munte et al., 1998) – prominent parietal old–new effects were found in the right hemisphere, whereas this effect is typically elicited on left-parietal electrodes with word stimuli (Friedman and Johnson, 2000). Although the parietal modulation did not discriminate between the two types of old faces, a left frontal, positive going waveform, starting at 250 ms after stimulus onset, differentiated between context and no context faces. We argue that this ERP difference is only attributable to the contextual manipulation at encoding, since there were no systematic physical stimulus differences in the recognition phase (by virtue of a counterbalanced design and context absence for all tested faces). Hence, this modulation may be considered an index of context effects. It is noteworthy that two kinds of contextual information were associated with faces at encoding: a perceptual context – that is, the newspaper article - and a semantic context - that is, an action committed by the person depicted. To facilitate deeper encoding, the semantic context was of great importance, as the actions had a high-arousal, impressive value, and were presented twice as the title of the article in the newspaper and as an isolated statement in the preceding slide. One might argue that our frontal modulation was elicited by the mere sense of having previously seen a face within a contextual frame, without being able to retrieve any precise detail about that specific context. However, the strong valence effect indexed by early and late ERP modulations, including the parietal effect, suggests that some kind of semantic, person-specific contextual information was retrieved. In fact, frontal lobe activation for semantic information associated with faces has been extensively documented. As has emerged from ERP research, the comparison between the electrophysiological correlates elicited by the presentation of familiar and unfamiliar faces (Bentin and Deouell, 2000; Nessler et al., 2005) has demonstrated that left frontal lobe activation is related to semantic familiarity. In the aforementioned study by Paller et al. (2000), the retrieval of biographical information associated with faces at study elicited a priming effect on frontal electrodes. These data have been recently confirmed by neuroimaging and neuropsychological findings. Leveroni et al. (2000) found greater activation in the left inferior temporal cortex for newly learned faces as compared to famous faces; Papagno and Muggia (1999) reported the case of a patient with a left frontal lesion who was unable to recall any biographical information about people she could name and recognize. However, the early onset of our frontal effect suggests that it probably does not reflect the retrieval of specific face-context associations, but rather that it may trigger the search for temporarily stored contextual, person-specific representations, facilitating the subsequent recognition of (especially negative) context faces.

Context valence manipulation elicited different effects on memory-related modulations: negative-context faces elicited larger amplitudes than positive ones, being prominent at right-anterior lateral electrodes. Emotion-induced memory enhancements are frequently reported. ERP research has shown an effect for emotion on recollection-related components (Maratos and Rugg, 2001; Johannsson et al., 2004; Smith et al., 2004b). Maratos and Rugg (2001, Experiment 1) found larger parietal old/new effects for neutral words that had been studied in negative sentences compared to neutral words studied in neutral sentences. In that study (as in the present one), the retrieval of the emotional context was not a task requirement, since participants had to perform an old/new discrimination task. Thus, the findings indicate that incidental retrieval of emotional context elicits a greater activation in neural systems supporting recollection than does retrieval of nonemotional context. A similar interpretation is suggested by Smith et al. (2004b, Experiment 1), in which emotionrelated memory enhancements took the form of an earlier temporal and a later temporo-frontal modulation for items encoded in emotional contexts compared to those encoded in neutral contexts. As evidenced by neuropsychological and neuroimaging studies, emotion-related memory enhancements are likely to be subserved by the amygdala. Patients with amygdala lesions do not show performance enhancement with emotional material (Phelps and Anderson, 1997). Additionally, neuroimaging research demonstrates a crucial role of the amygdala for encoding (Cahill et al., 1996; Canli et al., 2000) and retrieval (e.g. Hamann et al., 1999; Maratos et al., 2001, Smith et al., 2004a). It has been proposed that the amygdala exerts its influence on memory through the modulation of hippocampal activity and via interactions with prefrontal regions crucial for memory-related processes and for higher-order emotional evaluation processes (Dolan, 2002). For instance, recent data by Smith et al. (2006) show that increased levels of recollection for emotional material are

correlated with stronger connectivity between the hippocampus and amygdala. Selective amygdala and medial temporal lobe activations were not exclusively found in relation to material that was emotional per se. Of particular interest with respect to the results of the present study was the fact that even neutral stimuli which were previously presented in emotional contexts elicited strong hippocampal and amygdala modulations (Maratos et al., 2001). More specifically, a recent study by Medford et al. (2005) showed literalized patterns of activity as a function of emotional content vs. context retrieval. Whereas the right amygdala and right hippocampus were activated by emotional material (content) per se, left parahippocampal activations were found with (neutral) material that was emotive only by virtue of an association with an emotional context at encoding. These data partially conflict with our findings, which show prominent right hemisphere activations for neutral material associated with emotional contexts at study. It should be noted, however, that the Medford et al. study used verbal material. The use of face stimuli in the present experiment may have activated right hemisphere regions to a stronger degree. Although it is relatively clear that emotional and nonemotional stimuli produce different patterns of activation, the effect of emotional valence (positive or negative) is still under debate. This is mainly because most studies have compared emotional vs. neutral, or negative vs. neutral stimuli, thus bypassing a direct comparison between positive and negative valence. ERP results are controversial. As previously stated, negative stimuli generally elicit larger amplitudes than positive stimuli in a variety of (non memory-related) paradigms (Ito et al., 1998; Orozco and Ehlers, 1998; Dolcos and Cabeza, 2002; Holmes et al., 2003). Nevertheless, considering the effect of emotionally valenced stimuli at encoding on recognition performance, only Johannsson et al. (2004), who employed face stimuli, have reported an ERP effect for negative information. In our study, context valence at encoding elicited conspicuous processing differences in the recognition phase. Therefore, it is possible to assume that the negative context associated with face stimuli had a more ecological and hence impressive value compared to previous studies (which have extensively used words as stimuli). This probably resulted in enhanced encoding and retrieval processes. A final noteworthy result concerns the distribution of ERP differences to negative and positive stimuli. Indeed, valence effects were prominent on right electrodes, confirming the important role of the right hemisphere in emotional processing. Additionally, it is remarkable that negative-context faces elicited larger amplitudes on F4. This result is in line with recent neuroimaging findings, indicating the dominant role of right PFC in the processing of negative information (Davidson and Irwin, 1999).

The present study has some limitations. In particular, two methodological issues must be noted. In this exploratory study, the authors were not specifically concerned with disentangling perceptual context from semantic context effects. Rather, the main question of interest was to assess if any context effect (either perceptual or semantic) at encoding would affect recognition, even if faces were presented without contextual frames at test. Our experimental design, however, makes it difficult to discern between the effect of the semantic and perceptual context. Indeed, the newspaper article for

context faces provides both a perceptual and a semantic (the headline specifying the action committed by the actor) context, whereas no-context faces lack any kind of contextual information. In this sense, an improved design would have required the addition of two conditions: firstly, faces without the newspaper context, preceded by a sentence, and, secondly, faces without the sentence, embedded in a newspaper context. A related issue is that the results may be due to a difference in cognitive load at encoding for context faces rather than to context effects per se. Specifically, presenting a slide with a sentence prior to the context face may have caused a deeper encoding of that face, and this may have, in turn, facilitated retrieval. Creating a richer encoding context was a goal of the present study and, simultaneously, a methodological limit. This is because it is not possible to disentangle the effects of context per se from the effects of cognitive load at encoding without matching the presentation of context and no-context faces perceptually and semantically. Evidently, follow-up studies with more comprehensive experimental designs are necessary to further address these issues.

Despite the aforementioned methodological limits, several important conclusions can be drawn from the results of the present research. The contextual information associated with a face at the time of its first encoding is salient enough to guide subsequent recognition, even if those contextual cues are absent when a face is seen for the second time. Most importantly, this effect takes place at an early stage of processing, namely at the N170 level. Thus, face recognition is a complex process that relies on a network of multiple brain regions associated with different processes, from structural analysis to the retrieval of person-specific information. These processes are not activated in a strictly serial manner, as posited by influential models of face recognition (Bruce and Young, 1986). Rather, early visual analysis of faces can be modulated by the information flow from higher-order areas which may mediate the retrieval of biographical, contextual and emotional information pertaining to the study episodes.

4. Experimental procedures

4.1. Participants

Fifteen students at the University of Florence (ten females and five males, mean age = 23.2) participated in the study. All were right handed and reported normal or corrected-to-normal vision, and had a poor or absent English language knowledge.

4.2. Stimuli

One hundred and ninety greyscale pictures of unfamiliar faces were selected from the "Extended Multimodal Face Database-XM2VTSdb" (Messer et al., 1999). Stimuli were of approximately equivalent luminance and contrast and had no distinct facial expressions. A set of 120 faces was used in the study phase: 60 faces framed on a white background (no-context faces) and 60 faces superimposed in a newspaper article on a newspaper page (context faces). For this purpose, 60 different newspaper scenarios were created using the following steps.

First, the pages of English newspapers were digitally scanned and edited so that the face was centered on the computer screen and the title of the article was clearly visible. The original headline was then replaced by an invented headline which specified an emotional action committed by the person depicted. Half of the headlines were emotionally positive (positive-context faces: "Taxi-driver saves a child") and half were emotionally negative (negative-context faces: "Hooligan rapes a girl"). Each context face was preceded by a slide reporting the Italian translation of the headline.² It is noteworthy that unlike previous studies, in this case the emotional valence was not provided by the facial expression (all faces being neutral with respect to facial expression), but rather by the action associated with the stimulus. For the test phase, 70 additional faces were framed on a white background and used as new faces. In summary, there were 60 context faces (30 positive and 30 negative), 60 no-context faces and 70 new faces. Each set of faces included an equal number of men and women. All stimuli were processed by Adobe Photoshop graphics software.

4.3. Procedure

Participants were seated in a dimly lit room and a computer screen was placed at a viewing distance of 57 cm. Following electrode application, they received general instructions for the experiment. They were told to remain as still as possible and to reduce eye blinks to a minimum. Participants were also instructed to carefully pay attention to the faces presented in the first phase, because later they were to be involved in a memory task. The experimental procedure included a study phase and a test phase. In the study phase (Fig. 5a), 60 context and 60 no-context faces were presented. Each trial began with a 250 ms fixation point, followed by a 1000 ms presentation of the sentence indicating the Italian translation of the newspaper title. The face was then presented for 700 ms and was followed by a blank screen that lasted until the response was collected. For each presented face, subjects were required to perform a gender discrimination task: they were instructed to press a response key if a man was presented, and another response key if a woman was presented. The aim of this task was to ensure that attention was directed to the stimuli. In the test phase, all 120 faces from the study phase (60 context and 60 no-context) and 70 additional new faces were presented. In this phase, all faces (including those that were embedded in contexts at study) were presented on a white background (see

² There are two main reasons for using English, instead of Italian, articles and headlines. First of all, we supposed that if Italian headlines were presented in close physical proximity to the face, then excessive attention might be directed to the headline. In other words, the emotional sentence might have been more salient than the unfamiliar face, and therefore subjects may have automatically read the sentence without paying attention to the actor's face. Moreover, subjects were told that the newspaper articles and pages were real and that the articles referred to actual events. Accordingly, the news had to be as credible as possible. If the article was in Italian, participants might have doubted its authenticity because it is unlikely that they would not have heard about major news items.

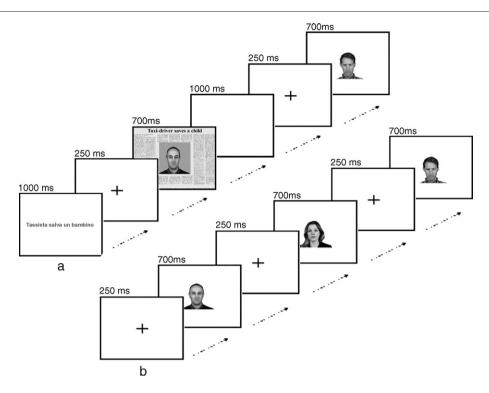


Fig. 5 – Schematic representation of the procedure. (a) In the study phase, context and no-context faces were presented to subjects, who performed a gender discrimination task. (b) In the test phase, previously presented faces were presented along with new ones, and participants had to perform old/new discriminations task.

Fig. 5b). Each test trial began with a 250 ms fixation point, followed by the onset of the face which was presented for 700 ms. After picture offset, the screen went blank until the response was collected. Subjects were instructed to use their left and right index fingers to indicate whether the faces were previously studied ("old") or not ("new"). The presentation order of the stimuli was randomized across participants. Response hand and old–new status were counterbalanced.

4.4. Event-related potentials recording

EEG was recorded from 18 tin electrodes embedded in an elastic cup (ElectroCup International, Eaton, OH): F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O2, Oz, O1. The electrodes location was based on an expanded version of the international 10-20 electrode placement system. Three additional electrodes were used for EOG recording. Specifically, two electrodes on the outer canthi of both eyes for horizontal eye movements monitoring, and one electrode below the right eve for vertical eve movements and blinks recording. A linkedearlobe reference was used. Impedances were kept below 5 k Ω at all sites. Electrical activity from the scalp and eyes was continuously recorded and amplified by a Neuroscan NuAmps amplifier, which applied a band pass filter between 0.10 and 100 Hz and a sampling rate of 500 Hz. The continuous recording was segmented off-line into epochs of 950 ms commencing 200 ms prior to stimulus onset. Drifts were corrected by applying a high pass filter of 0.01 Hz with a zero phase shift. Trials containing artifacts were excluded with an automatic artifact rejection on ocular channels if their voltage exceeded $\pm\,50\,\mu\text{V}.$ Moreover, all trials were visually scanned for

further artifacts (percentage of rejected trials was approximately 11% for each condition). ERPs were then aligned to a 200 ms baseline before stimulus onset, averaged separately for each channel and experimental condition, and low-pass filtered at 30 Hz. Only correct responses were averaged.

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