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Following the time course of face gender and expression processing: A task-dependent ERP study.

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ABSTRACT

The effects of task demands and the interaction between gender and expression in face perception were studied using event-related potentials (ERPs). Participants performed three different tasks with male and female faces that were emotionally inexpressive or that showed happy or angry expressions. In two of the tasks (gender and expression categorization) facial properties were task-relevant while in a third task (symbol discrimination) facial information was irrelevant. Effects of expression were observed on the visual P100 component under all task conditions, suggesting the operation of an automatic process that is not influenced by task demands. The earliest interaction between expression and gender was observed later in the face-sensitive N170 component. This component showed differential modulations by specific combinations of gender and expression (e.g., angry male vs. angry female faces). Main effects of expression and task were observed in a later occipito-temporal component peaking around 230 ms post-stimulus onset (EPN or early posterior negativity). Less positive amplitudes in the presence of angry faces and during performance of the gender and expression tasks were observed. Finally, task demands also modulated a positive component peaking around 400 ms (LPC, or late positive complex) that showed enhanced amplitude for the gender task. The pattern of results obtained here adds new evidence about the sequence of operations involved in face processing and the interaction of facial properties (gender and expression) in response to different task demands.

Introduction

The issue of whether the processing of stable (e.g., gender and identity) and variable properties of faces (e.g., expression) takes place independently or interactively has been object of theoretical and empirical interest. For example, Bruce and Young´s classic model (1986) proposes two separate, non-interacting routes for the visual processing of identity and facial expression. On the other hand, Haxby, Hoffman and Gobbini´s (2000) brain systems model establishes a basic differentiation between processing of invariant and changeable aspects of faces that are supposedly performed by separate neural systems.

Though some results are consistent with independent processing for gender and expression (e.g., Le Gal and Bruce, 2002), evidence to the contrary also exists. In a study by Aguado, García-Gutierrez and Serrano-Pedraza (2009) symmetrical interaction between gender and expression was observed. For example, classification of faces as angry was faster when the face belonged to a male. Complementarily, faces were identified faster as females when they showed a happy rather than an angry expression. Other studies have reported asymmetrical interference, with only one of these properties influencing performance on the other (Atkinson, Tipples, Burt, & Young, 2005; Hess, Adams, Grammer & Kleck, 2009; Hugenberg & Sczesny, 2006). A plausible interpretation of these results is that gender and expression identification are based on at least a subset of common facial features, so that changes in one of those features have an influence on both tasks. For example, it is known that reducing the brow-to-lid distance makes a face look both angrier and more masculine (Becker, Kenrick, Neuberg, Blackwell & Smith, 2007; Burton, Bruce & Dench, 1993) and it has been suggested that expressive features characteristic of different emotions overlap with facial features that are markers for sex and that may thus bias gender classification (Hess, Adams, Grammer & Klek, 2009).

A different though related issue concerns the extents to which either gender or expression are processed when they are incidental for the task at hand. The evidence on interactive effects mentioned above would suggest that both facial properties are processed even when only one of them is relevant for the task at hand. Moreover, behavioral and neuroimaging studies have shown that facial expressions of emotion receive preferential processing even when they are task-irrelevant or are presented outside awareness (e.g., Calvo & Esteves, 2005; Vuilleumier, Armony, Driver & Dolan, 2001; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; see also Palermo & Rhodes, 2006 and Pessoa 2005, for reviews). Evidence of implicit processing of face gender is scarce, though some results suggest that the gender of faces can be processed in the near-absence of attention (Reddy, Wilken & Koch, 2004).

A key issue that remains largely unexplored is the time course of the interaction between the processing of stable and changeable properties of faces, such as gender and expression. Both theoretical models (e.g., Bruce & Young, 1986; Haxby et al., 2000) and empirical studies suggest that the interaction between facial properties is more or less probable at different stages of face processing. For example, in studies using the event-related potentials (ERP) technique, early visual components related to object identification and structural coding are usually sensitive to emotional expression but not to gender (see discussion below). Thus, one might reasonably infer from this that “pure” effects of emotional expression should be found on the earliest visual ERP components and that gender should influence expression processing only at later processing stages.

Previous research has investigated two main visual components over occipito-temporal sites in the latency range of 100-200 ms post-stimulus onset, the P100 and the so called “face-sensitive” N170 (Eimer, 2011). Effects of emotional expression on the P100 have been found as enhanced amplitudes in the presence of specific expressions such as fear (Pourtois, Dan, Grandjean, Sander & Vuilleumier, 2005; Rellecke, Sommer and Schacht, 2012) or as a general effect of expressive versus neutral faces (Batty & Taylor, 2003). The face-sensitive N170 component, with maximum amplitudes over occipito-temporal sites, has also been shown to be modulated by emotional expression, especially by faces showing negative emotions such as fear or anger (e.g., Aguado et al., 2012; Batty & Taylor, 2003), although effects of positive emotions have also been reported (Miyoshi, Katayama & Morotomi, 2004). However, it is fair to recognize that the response of the N170 to emotional expression is still a matter of debate as insensitivity to changes in expression has also been reported in some studies (e.g., Eimer & Holmes, 2002; Herrman et al., 2002; see Eimer, 2011 for a review).

Other ERP components appearing at later latencies have also been shown to respond differentially to faces showing emotional expressions. The EPN (Early Posterior Negativity), a negative potential measured over temporo-occipital sites within 200-300ms after stimulus onset, shows larger amplitudes in response to faces showing threat-related expressions (Rellecke, Palazova, Sommer & Schacht, 2011; Schupp et al., 2004a) and has also been reported to be sensitive to positive expressions (Holmes, Nielsen, Tipper, & Green, 2009; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001). Finally, effects of emotional expression have also been found on a late positive complex (LPC), with latencies around 300 ms (e.g., Schacht & Sommer, 2009; Schupp et al., 2004a). It has been suggested that the EPN and LPC components could reflect a sequence of differentiated operations in the processing of emotional stimuli (Schupp, Flaisch, Stockburger & Junghöffer, 2006).

In contrast to the effects of emotional expression, early visual components do not seem to be sensitive to face gender. No effects of face gender have been reported on the P100 and N170 components in studies that compared conditions that did or did not require explicit attention to this facial property (Mouchetant-Rostaing et al., 2000, Mouchetant-Rostaing & Giard, 2003). Moreover, attenuation of N170 amplitude by face repetition has not been found in a gender adaptation paradigm (Kloth, Schweinberger & Kovács, 2010), suggesting that the processes indexed by this ERP component are not related to the categorization of gender and thus that gender is still not processed or recognized at this latency. Interestingly, Kloth et al. (2010) did find specific gender-adaptation effects on a later (400-600 ms), central-parietal P3-like component. In fact, in the ERP studies by Mouchetant-Rostaing et al., (2000, 2003) gender effects in mid- and late components were also found. However, indirect evidence of gender-related modulations of the N170 was found in a study by Freeman, Ambady and Holcomb (2010). These authors observed enhanced N170 amplitudes in the presence of sex-typical, compared to sex-atypical faces.

The second issue of interest in the present study is the role of task demands in gender and expression processing. A few studies have compared brain activity associated to the perception of emotional expressions under different task conditions. Two neuroimaging studies found different activation patterns under implicit and explicit processing conditions (Gorno-Tempini et al., 2001; Straube et al., 2004). Evidence on the precise timing of these task effects comes from studies using the ERP technique. Wronka and Walentowska (2011) found enhanced N170 to expressive faces in an explicit emotion identification task but not in a gender task. Two additional studies (Knyazev, Slobodskoj-Plusnin & Bocharov, 2010; Van Strien, De Sonneville &

Franken, 2010) have also reported task-dependent modulation of brain activity in the presence of expressive faces. For example, in Van Strien et al.´s (2010) study, enhancement of the LPC by emotional faces was observed only in the explicit emotion task. The most complete ERP study to date comparing the effect of different tasks on facial emotion processing is that of Rellecke et al. (2012). Using happy, angry and neutral faces as stimuli, these authors compared five different task conditions requiring different levels of cognitive elaboration and attention to emotional expression. Two of the task conditions involved explicit instructions to categorize the faces (expression and gender identification), while the remaining three conditions (true passive viewing, passive viewing with attention oriented to expression and face/word discrimination) did not. Modulations by emotional expression that were independent of task demands were found on the P100, N170 and EPN components. Task-dependent effects were obtained on the EPN and LPC components for happy and angry faces, respectively. These latter effects were interpreted as indicative of the deeper perceptual analysis required by the more active tasks. The most interesting aspect of these results is that they reveal two different sets of processes in the analysis of facial expression. The first set of processes would correspond to early processing stages and appears to be largely automatic. The second set of processes would instead reflect more strategic processes adapted to task conditions that require an active response or demand explicit attention to emotional expression.

In the present study, interaction between face gender and expression was tested under three different task conditions. Two of these conditions (gender and expression tasks) were explicit face categorization tasks and involved differential allocation of attention to either the gender or the expression of the faces. In a third condition (symbol task), face processing was irrelevant as the task required only to discriminate between two simple symbols ($ vs £) that were placed over the nose region. In two task conditions only one of the facial properties, gender or expression, was relevant for the task, and in a third condition (symbol discrimination task) faces did not have to be attended at all. In this sense, this last condition is similar to the face/word task used in Rellecke et al.´s (2012) study. However, in that study the participants still had to identify the stimulus presented on the screen as a face or a word, thus requiring explicit attention to the faces on face trials.

Main analysis was focused on four ERP components that have been usually studied in relation to face perception and emotional expression (e.g., Rellecke et al., 2012) and that have been discussed in previous paragraphs, the P100, N170, EPN and LPC. Taking into account the evidence on emotional modulations described above and the results of the study by Rellecke et al. (2012) our prediction was that task-independent modulations by emotional expression would be more likely on the two components linked to the early stages of visual processing, the P100 and the N170. On the other hand, general effects of task demands should appear on the latter, EPN and LPC components.

Differential ERP modulations by specific combinations of gender and expression (for example, female-angry or male-angry) would be indicative of interactive processing of these facial properties. If the evidence discussed above on gender effects on different ERP components reflects the timing of gender processing by the visual system, then this interaction should not appear on the earliest, P100 and N170 visual components. However, early interaction effects might still be expected if some facial features with high diagnostic value for both gender and expression (for example, the brow-to-lid distance) are coded at these early latencies. Although these isolated features might not provide complete perceptual evidence conducive to gender coding, they might suffice to bias processing in the corresponding direction, for example making angry male and female faces be processed as if they were more and less angry, respectively.

Method

Participants

Thirty two undergraduate students from the Universidad Complutense de Madrid (aged from 18 to 22 years *M* = 18.79) participated voluntarily and were compensated with course credits for their participation. All of them had normal or corrected to normal vision, were right-handed and had no history of neurological disorders. Written informed consent was obtained from all participants. Seven subjects had to be excluded due to excessive signal artifacts. Therefore, 24 subjects (all females; right handed, aged from 18 to 22 years *M* = 19 *SD*=1.2) remained in the data analysis.

Materials

Stimuli were 48 black and white photographs of faces of sixteen models (eight male, eight female) taken from the Karolinska Directed Emotional Faces (KDEF) database (Lundqvist, Flykt, & Ohman, 1998). Three different pictures per model were used, one neutral and the other two showing a happy or angry expression. All images were cut to remove hair in order to avoid that attention was diverted to this feature and ensure that it was focused instead on internal facial features. The faces were presented centered on the screen of a CRT monitor, inside a 512 x 512 pixels square with a 50% gray background, subtending an area of 13.5 x 13.5 degrees of visual angle. In all pictures a symbol ($ or £) in white Verdana font size 20 was placed in the fixation position over the nose region. Images were equated in luminance and contrast (cRMS = .02). Half of the angry faces (4 male, 4 female) showed open mouth expressions with teeth clearly visible. All happy faces (16) showed open mouth expressions with teeth visible. In pictures of faces showing open-mouth expressions a semi-transparent mask was superimposed on the teeth with the aim of making white teeth less salient and reducing the difference between open and closed-mouth expressions. .

Procedure

Participants sat in front of a 17” PC monitor in a soundproof room. All participants completed three blocks of 32 trials each that were assigned to one of three discrimination tasks. In all task conditions a neutral, happy or angry male or female face was presented on each trial. Superimposed on the face, a symbol (pound or dollar) appeared over the nose region. Participants were successively tested under three different conditions, all of which involved a binary discrimination task. In Task 1 (symbol discrimination) the participants had to discriminate between the pound and dollar symbols. In Task 2 (expression discrimination) the participants were asked to discriminate between expressive (happy or angry) and non-expressive (neutral) faces. This task was selected to keep constant the binary discrimination requirement across all task conditions. An emotion discrimination task would have required discriminating between three different alternatives (neutral, happy and angry), thus increasing the difficulty of the task and introducing variations that might complicate interpretation of the results. Finally, in Task 3 (gender discrimination) participants had to discriminate between male and female faces. Participants had to respond pressing one of two keys (“c” or “m”) on the keyboard to respond. The order of blocks and the response key assignment were counterbalanced across participants. Each specific stimulus (for example, model “a” showing a happy expression) was presented four times in each block, thus making 192 trials per block and a total of 576 trials. There were 32 samples corresponding to each condition of the 3 (Task) x 3 (Expression) x (Gender) design.

Participants were given 36 practice trials with a different set of faces at the beginning of each block. Each trial began with a fixation cross (+) presented during 500 ms. Fixation was immediately replaced by a target face that remained on the screen for an additional 500ms. Finally, the target face was replaced by a blank screen that stayed on until participants responded or 3000 ms had passed. In order to prevent the contamination of the EEG signal by response-related activity, participants were instructed to respond once the stimulus had disappeared.

EEG signal acquisition and analysis

Electrical brain activity was measured from 30 monopolar electrodes placed on an elastic cap (32 Electrode Cap, Quick-Cell system, NeuroScan Inc.) and distributed according to the 10-20 system. Electrical signal was amplified and recorded using a 16 bit amplifier (Synamps; NeuroScan Inc.) set with a band-pass filter from DC to 200 Hz and a sampling rate of 1000 Hz. All impedances were kept below 5 kΩ. Online recording was referenced to the vertex (Cz). Vertical eye movements were also recorded using a bipolar channel with electrodes 1cm below and above the left eye.

EEG signal was re-referenced offline with an average reference and filtered using a zero-phase band pass filter from 0.1 to 30Hz. Eye-blink artifacts were removed using a regression-based algorithm (Semlitsch, Anderer, Schuster, & Presslich, 1986). EEG epochs were created from -100 to 500 ms locked to stimulus onset and then averaged for each experimental condition, having Task (Symbol/ Expression/ Gender), Gender

(Male/Female) and Expression (Angry, Happy, Neutral) as factors, thus completing a total of 18 ERPs per participant. EEG epochs containing ±50µv were excluded from the averages. Percentage of rejection mean was 2,1% (*SD* = 3.6). A mean of 31.6 sweeps per condition were used for the ERP averaging.

Results

Behavioral Results

For all analyses reported in this paper, the Greenhouse-Geisser (GG) correction was applied to adjust the degrees of freedom of the *F*-ratios when the sphericity assumption was violated. Post-hoc comparisons to determine the significance of pairwise contrasts were made using the Bonferroni procedure ($\alpha = 0.05$). Effect sizes were computed using the partial eta-square (η^2_p) method.

Accuracy was the critical behavioral variable. Given that participants were instructed to withhold their response until stimulus termination and that reaction times were locked to the onset of the blank screen that acted as a response prompt, response speed could not be taken as a reliable measure of performance. Accordingly, this variable was not considered for analysis. The results of the accuracy measure are presented in Figure 1in terms of error rates. These data were submitted to a 3 x 3 x 2 ANOVA with Task, Expression and Gender as repeated measures factors. The analysis gave significant main effects of Task, $F(2, 46) = 34.726$, $\eta^2_p = 0.6$, Expression, $F(2, 46) = 16.65$, $\eta^2_p = 0.42$ and Gender, $F(1, 23) = 61.03$, $\eta^2_p = 0.72$, (all $p_s < .001$). Analysis of the Task effect revealed significantly lower error rates in the symbol and expression tasks than in the gender task (*M* = .026, *SEM* = .010, *M* = .046, *SEM* = .006 and *M* = .115, *SEM* = .010, respectively).

All the interactions were also significant: Task x Expression, *F*(2.51,57.8) = 14.57, η^2_p = .38; Task x Gender, *F*(1.24,28.6) = 42.04, η^2_p = .64; Expression x Gender, *F*(2,46) = 30.91, η^2_p = .57; and Task x Expression x Gender, *F*(2.78,64.14) = 23.16 , η^2_p = .5, (all $p_s < .001$). Further analysis of this three-way interaction revealed a significant Gender x Expression interaction only in the gender task. More specifically, higher error rates in the categorization of female faces were committed with those faces that showed an angry expression than neutral or positive faces. Conversely, in the case of male faces identification of gender was less accurate with happy than with angry faces (both p <.05).

<<INSERT FIGURE 1 ABOUT HERE>>

ERP results

As can be seen in Figure 2, four clearly identifiable components appeared, corresponding to the P100, N170, EPN –early posterior negativity- and LPC –late positive component-. Analysis of the ERP data was performed on the individual mean amplitude values obtained from ±10 ms around the maximum peak of the components identified by visual inspection of the Mean Global Field Power (Lehman & Skrandies, 1980). For the last component this window was established at ± 50 ms.

Visual inspection of topographic distribution led to the selection of the electrode sites included in the analyses. For the first three components the electrodes included were O1, O2, P7 and P8. The electrodes selected for the LPC were P3 and P4 (see Figure 2). The data corresponding to each component were submitted to separate ANOVA analyses with Task, Expression, Gender and Channel as repeated measures factors. In order to keep constant the number of trials across conditions both correct and incorrect trials were included in the analyses.

<<PLEASE INSERT FIGURE 2 HERE>>

P100 (90-110 ms)

A 2 (Gender) x 3(Task) x 3(Expression) x 4 (Channel) repeated measures ANOVA over mean amplitude values revealed amplitude modulation of the P100 component by emotional expression at occipital sites. A significant Expression x Channel interaction F (6, 138) = 5.78, $p < .001$ $\eta^2_p = 0.201$ showed effects of expression under all task conditions at occipital electrodes. Specifically, angry and neutral faces elicited higher amplitudes than happy faces (all $p < .05$). No other significant effects or interactions were found.

N170 (150-170 ms)

A significant four-way, 2 (Gender) x 3(Task) x 3(Expression) x 4 (Channel) interaction, was found on the N170 amplitude values, *F* (12, 276) = 2.49 $p = .004$, η^2_p = .098. Separate analyses of the Gender x Task x Expression interaction at each channel showed a significant effect at P8, *F* (4, 92) = 4.83, $p < .01$, η^2_p = .173. A significant Gender x Expression interaction appeared in the symbol and expression tasks, *F* (2, 46) = 6.7, $p = .002$, η^2_p = .226 and *F* (2, 46) = 7.28, $p = .001$, η^2_p = .241, respectively. Planned comparisons revealed differences between female faces in the symbol task, with happy faces eliciting more negative amplitudes than angry and neutral faces. However, in the expression task differences appeared in the case of male faces, with happy and angry faces eliciting larger amplitudes than neutral ones (see Figure 3.). The Gender x Expression interaction was also significant at occipital sites: O1, *F* (2, 46) = 3.88, $p < .05$, η^2_p =.145; O2, *F* (2, 46) = 8.71, $p < .001$, η^2_p = .275. More negative amplitudes were observed in response to female happy, compared to female angry and neutral faces; moreover, male neutral and angry faces produced more negative amplitudes than the corresponding female faces (all $p < .05$; see Figure 4).

<<INSERT FIGURES 3 AND 4 ABOUT HERE>>

EPN (220-240)

A 2 (Gender) x 3(Task) x 3(Expression) x 4 (Channel) repeated measures ANOVA over mean amplitude values showed a significant main effect of Expression, F (2, 46) = 6.82, $p < .01$, $\eta^2_p = .23$, with less positive amplitudes in the presence of angry faces ($p < .05$). A significant Task x Channel interaction was also obtained, F (6, 138) = 3.53 $p < .01$, $\eta^2_p = .13$. Analysis of this interaction showed an effect of task demands at electrodes O2 and P8, with less positive amplitudes in the expression and gender tasks than in the symbol task. The corresponding waveforms can be seen in Figure 5.

<<INSERT FIGURE 5 ABOUT HERE>>

LPC (350-450)

A 2 (Gender) x 3(Task) x 3(Expression) x 2 (Channel; P3 and P4) repeated measures ANOVA revealed a main effect of Gender, F (1, 23) = 5.08 $p <.05$ $\eta^2_p = .18$ and a significant Task x Channel interaction (2, 46) = 5.88, $p <.01$ $\eta^2_p = .20$. Female faces produced larger amplitudes than male faces. Further analyses of the two-way interaction showed a significant effect of Task only at P4, where the larger LPC amplitudes corresponded to the gender task (see Fig. 6).

<<INSERT FIGURE 6 ABOUT HERE>>

Discussion

Behavioral and ERP measures were obtained under different task demands that directed the attention of the participant to the gender or the expression of faces. A third condition was included that did not require explicit attention to the faces, as the participant only had to identify a symbol superimposed on the face. While the expression and gender tasks are appropriated to detect possible variations in face processing under different task demands we assumed that the symbol task would be ideal to study automatic and non-strategic processes involved in face perception.

The behavioral data showed a significant interaction between gender and expression in the gender task. Specifically, participants committed more errors with female angry than with female happy faces. Conversely, male faces were identified more accurately when they showed an angry expression. These results are consistent with those from previous studies that have also shown an influence of emotional expression on gender categorization (Aguado et al., 2009; Atkinson et al., 2005; Hess et al., 2009).

The analysis of electrophysiological data revealed amplitude modulations of ERP components at different post-stimulus onset latencies. These modulations showed different types of effects. First, at latencies corresponding to the visual P100 and the EPN components we obtained task-independent effects of expression that can be considered as manifestations of automatic processing of facial expression. In the case of gender, similar effects were obtained at a later latency corresponding to the LPC component. Second, modulations showing an interaction between gender and expression at the stage where the stimulus is identified and categorized as a face were observed in the face-specific, N170 component. Finally, modulations associated to the manipulation of task demands started around 220-240 ms post-stimulus onset. More specifically, effects that can be related to differences in task difficulty or attentional demands were observed in the EPN and LPC components. These three types of effects are discussed below in more detail.

Modulations related to the emotional expression of faces under task conditions that do not require explicit attention to expression have been reported previously (e.g., Batty & Taylor, 2003; Pourtois et al., 2005). However, a more convincing demonstration that these effects are task-independent requires an explicit comparison between different task conditions. Such comparison has been made by Rellecke et al. (2012) using a design similar to that employed in the present study. These authors found P100 modulations in the presence of expressive faces under different task conditions that required different levels of attention to emotional expression. We also found in our study a task-independent effect of emotional expression on the P100 component that showed more positive amplitudes to angry than to happy faces. An unexpected result was that enhanced amplitudes were also observed in the presence of neutral faces. This is at odds with results such as those by Batty and Taylor (2003), where all expressive faces (except those showing surprise) produced larger P100 amplitudes than neutral and Rellecke et al.´s (2012),where angry faces produced larger P100 amplitudes than happy and neutral ones. One possible explanation for this discrepancy is that in our study the neutral faces were perceived as relatively cold or unfriendly and that consequently they were treated as more similar to the angry faces. In fact, the results of a previous study on face evaluation with a larger set of KDEF faces (Aguado et al., 2011) indicate that the neutral faces used in the present experiment were perceived as relatively untrustworthy. A reanalysis of the evaluations obtained in that study including only the faces used in the present study gives an average evaluation of 4.61 on a continuous 1 to 9 scale from minimum to maximum trustworthiness. It is important to point out that early visual components such as the C1 and N170 have been shown to be modulated by the trustworthiness of faces and that less trustworthy faces produce enhanced amplitudes of these components (Dzhelyova, Perrett & Jentzsch, 2012; Yang, Ding & Song, 2011). Thus, it seems reasonable to assume that the increased P100 amplitudes we observed in the presence of neutral faces might have been due to their relatively low trustworthiness.

Main effects of expression in all task conditions were also obtained within the 220-240 latency window corresponding to the EPN component. In this case, less positive amplitudes were observed in the presence of faces showing angry expressions. This result replicates previous evidence showing modulation of the EPN by threatening faces under conditions where explicit expression categorization was not required (Frühholz, Jellinghaus & Herrmann, 2011; Rellecke et al.,2012; Schupp, Öhman, Junghöfer et al., 2004b). The task-independent nature this effect replicates previous results (Rellecke et al., 2012). Sensitivity of the EPN component to the affective properties of stimuli has been attributed to the ability of emotional or highly arousing stimuli to engage attentional resources (Schupp et al., 2006). Likewise, the task independent modulation of EPN by angry faces in our study can be related to the ability of threatening social signals to capture attention in an automatic fashion.

A main effect of face gender was observed on the LPC component as enhanced amplitudes in the presence of female faces. It might be that the fact that the final sample was composed only of female participants influenced this result. Previous studies have shown that females (Cellerino, Borghetti & Sartucci, 2004; Lewin & Herlitz, 2002) perform at a higher level than males in the recognition of female faces. Although the explanation of this finding is not known, it probably reflects differences in the depth or level of detail with which faces of either gender are processed by males and females. In the present case, the enhanced LPC amplitude observed in the presence would reflect a deeper or more detailed processing of female faces.

The interaction of gender and expression has not been taken into account as a relevant factor in previous ERP studies on face perception. The main contribution of our study is precisely to provide new evidence on ERP component modulations driven by the interaction between gender and expression. The interaction effects found in the N170 component have important implications for the debate on the time course and independence of different face processing operations, as proposed by cognitive and brain-systems models of face perception (Bruce and Young, 1986; Haxby et al., 2000). Previous studies have not showed evidence of main effects of gender on the N170 to male and female faces (Kloth et al., 2010; Mouchetant-Rostaing and Giard, 2000, 2003). This result would indicate that gender is still not coded at the stage of face processing that is indexed by the N170 component. However, the interaction effects observed in the present study seem to contradict this claim. One possible interpretation of this interaction is that the processing operations indexed by the N170 involve the coding of features that have diagnostic value for both gender and expression identification, such as the reduced brow-to-lid distance characteristic of both angry and male faces or the increased roundness of the face typical of female and smiling faces. The perceived intensity of different emotions would then be influenced by gender due to the additive perceptual effect produced when gender-typical features coincide with expression-typical features. For example, this could make angry male faces look more threatening than angry female faces and happy females look more approachable than happy males. Larger amplitudes of the N170 component would thus reflect enhanced processing of faces presenting these particular combinations of gender and expression due to their superior emotional and social relevance.

Modulations associated to the different task demands were observed in the two later ERP components, the EPN and the LPC. Significant task effects started around 220 ms post-stimulus onset. Specifically, gender and expression tasks showed less positive amplitudes at the EPN latency (220-240 ms) in right hemisphere electrodes. At the LPC time window (350-450), larger amplitudes at right parietal sites (P4) were observed in the gender task. This LPC effect replicates previous findings by Sun, Gao and Han (2010) and probably reflects the greatest difficulty of the gender task. The higher error rates observed in this task revealed indeed that gender categorization was the more difficult task. Thus, the task effect observed on the LPC can be interpreted as reflecting the increased attentional demands and deeper processing of faces required by this task. As to the effects obtained on the EPN component, it might seem contradictory that task effects appeared on a component that was also sensitive to emotional expression in a task-independent fashion. However, it should be noted that while the effect of expression did not interact with electrode channel, that of task was significant only on right hemisphere electrodes. Differences in the precise functional meaning of specific components depending on lateralization are common. Current interpretations of the

EPN in connection to emotional stimuli consider that modulations of this component reflect enhanced perceptual processing of highly arousing stimuli (Schupp et al., 2004, 2006). This would be the appropriate explanation for the above mentioned effects of emotional expression observed on this component. The lateralized effect of task demands, with less positive EPN amplitudes in the two face discrimination tasks, could instead be interpreted as reflecting enhanced perceptual processing of faces in general in the task conditions where explicit attention to the faces was required.

Finally, we must recognize that the generalizability of our conclusions might be limited due to the fact that only females participated in the study. We have already mentioned the finding of superior gender identification performance in female participants. Of direct relevance for the present study, an effect of participant´s gender on the modulation of ERP components in gender categorization has been described previously (Sun, Gao & Han, 2010). For example, although in the mentioned study the gender task was associated to enhanced amplitudes of the P300 , this effect was stronger in female than in male participants. This last result is especially relevant as it suggests that the enhancement of the LPC that we observed in the gender task might have been due to the characteristics of our sample, composed exclusively of females. However, we do not know of any other evidence from previous ERP studies that would suggest that participant´s gender might have had a significant influence on other results from the present study.

Conclusions

The results reported in the present study replicate some previous findings from ERP studies of face perception and also provide new evidence on two theoretically relevant issues. The task-independent effects of emotional expression observed at different post-stimulus onset latencies replicate previous findings that have also shown that early visual ERP components can be modulated by facial expression. Our results also show new evidence on the interaction between gender and expression in face perception using the ERP technique. Given that previous evidence on this issue comes exclusively from studies using behavioral measures that only provide a rough estimation of the end result of basic processing operations, our main contribution in this respect is to provide new evidence based on electrophysiological measures that allow precise tracking of the early stages of visual information processing. Specifically, we have shown that interactive effects of gender and expression appear already at the processing stage indexed by the face-sensitive N170 component. A second relevant issue is the influence of task demands on the modulation of ERP components by the emotional expression of faces. In the present study, these effects appeared at later latencies corresponding to the LPC and EPN components. Together, these results reveal the operation of multiple processing operations taking place at different post-stimulus onset latencies. ERP components indicative of these operations show both simple and interactive effects of gender and expression and react differentially to the specific demands of the task at hand.

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FIGURE CAPTIONS

Figure 1. Mean percentage of errors in each experimental condition.

Figure 2. Mean global field power for all conditions showing the topographical distribution for the four components identified.

Figure 3. N170, Gender x Task x Emotion interaction in P8. a)Task 1 (Symbol discrimination): Effect of Emotion in Female faces, b) Task 2 (Expression discrimination): Effect of Emotion in Male faces. Effects of gender only in Happy: Females > Male.

Figure 4. Gender x Expression interaction at occipital electrodes: a) Female happy faces had more amplitude than Female angry and neutral faces. b) Male neutral and angry faces showed more amplitude than female angry and neutral faces.

Figure 5. Task x Channel: Effects of Task in EPN at P8 and O2: (T1>T2/T3) at O1 and O2

Figure 6. Task effects in LPC significant only at P4.

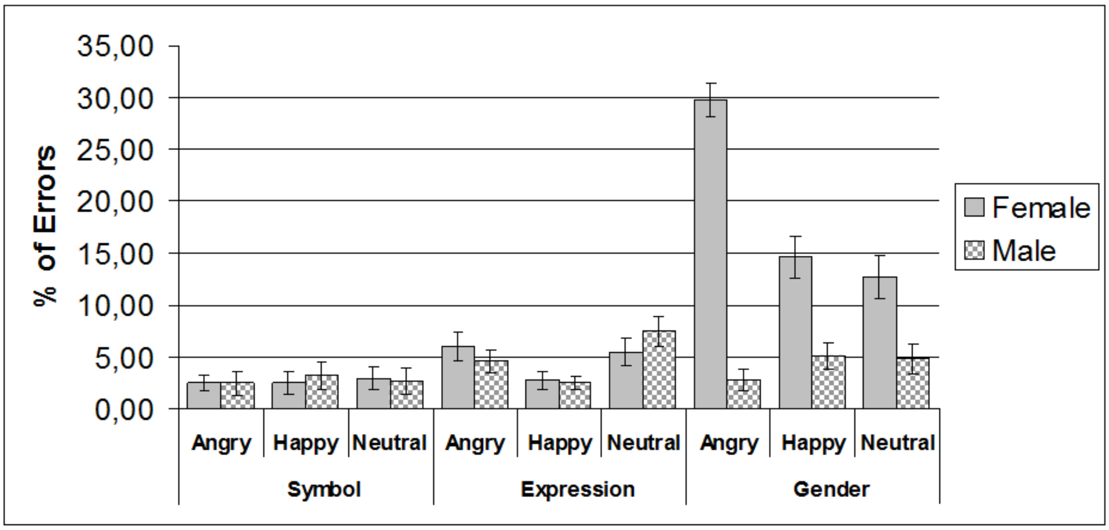

% of Errors
35,00
30,00
25,00
20,00
15,00
10,00
5,00
0,00
Angry
Happy
Neutral
Angry
Happy
Neutral
Angry
Happy
Neutral
Symbol
Expression
Gender
Female
Male

Figure 1

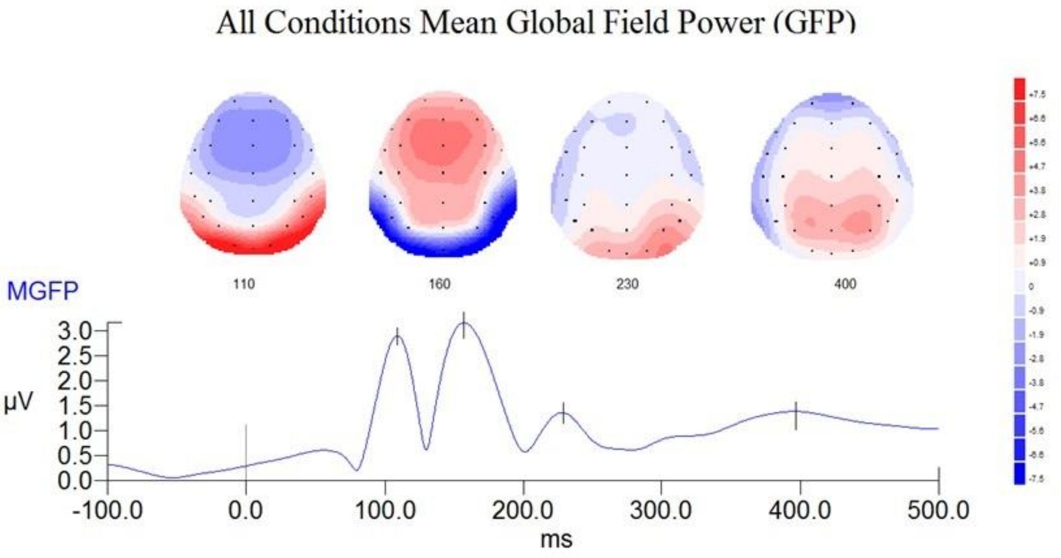

All Conditions Mean Global Field Power (GFP)
110
160
230
400
+7.5
+6.6
+5.6
+4.7
+3.8
+2.8
+1.9
+0.9
0
-0.9
-1.9
-2.8
-3.8
-4.7
-5.6
-6.6
-7.5
MGFP
µV
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-100.0
0.0
100.0
200.0
300.0
400.0
500.0
ms

Figure 2

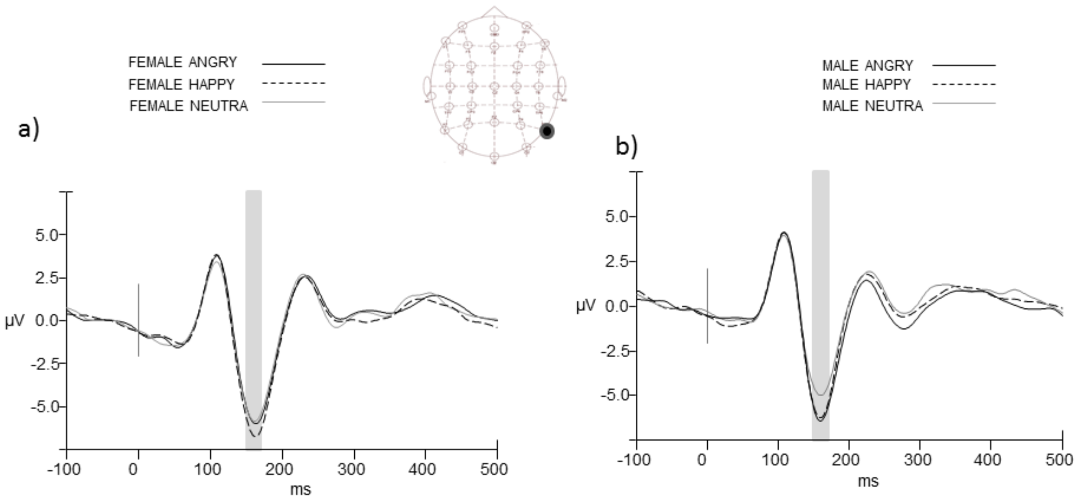

a)
FEMALE ANGRY
FEMALE HAPPY
FEMALE NEUTRA
5.0
2.5
µV 0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms
b)
MALE ANGRY
MALE HAPPY
MALE NEUTRA
5.0
2.5
µV 0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms

Figure 3

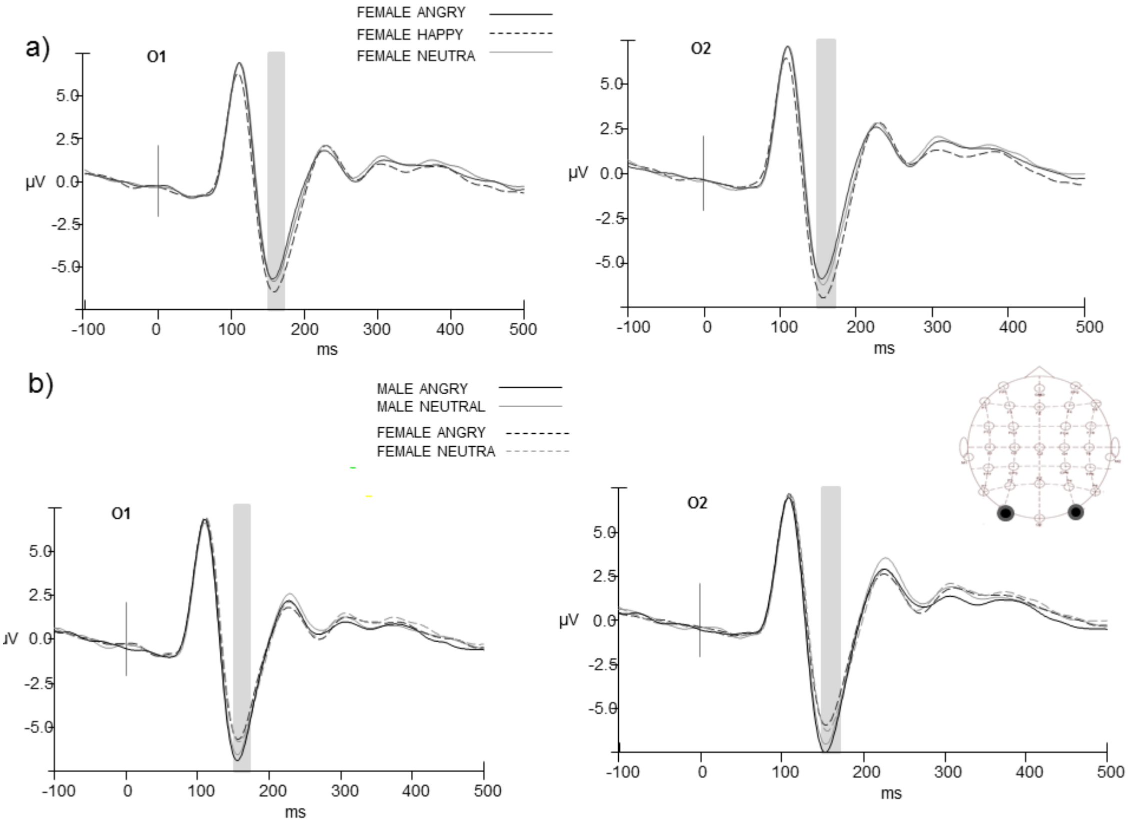

a)
FEMALE ANGRY
FEMALE HAPPY
FEMALE NEUTRA
O1
O2
µV
5.0
2.5
0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms
b)
MALE ANGRY
MALE NEUTRAL
FEMALE ANGRY
FEMALE NEUTRA

Figure 4

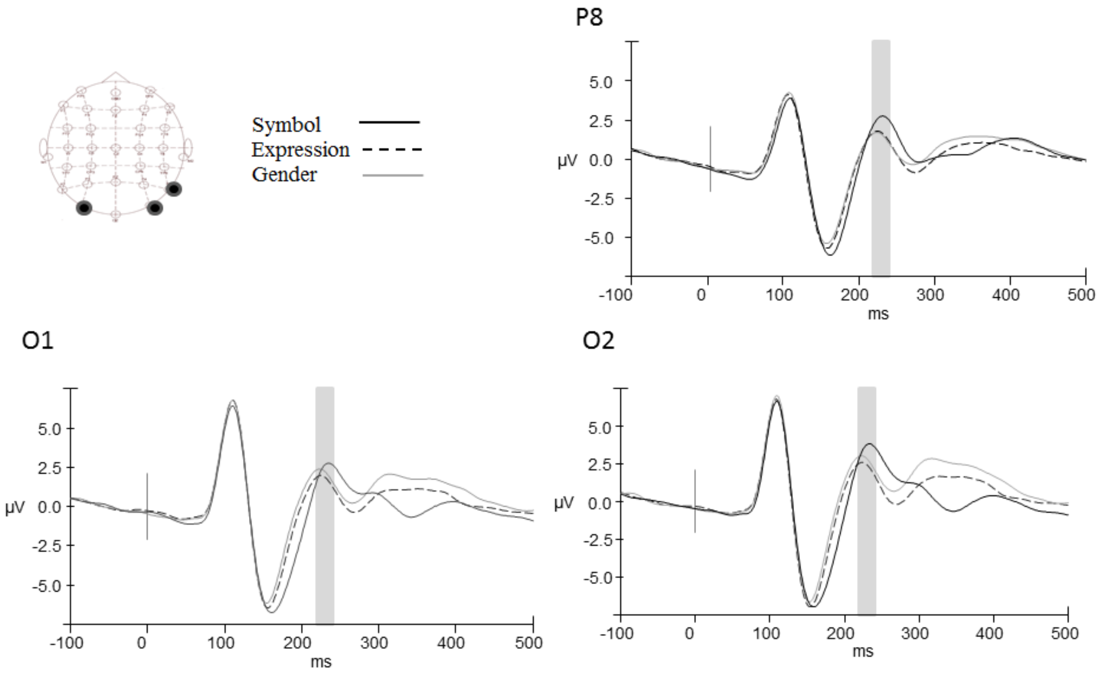
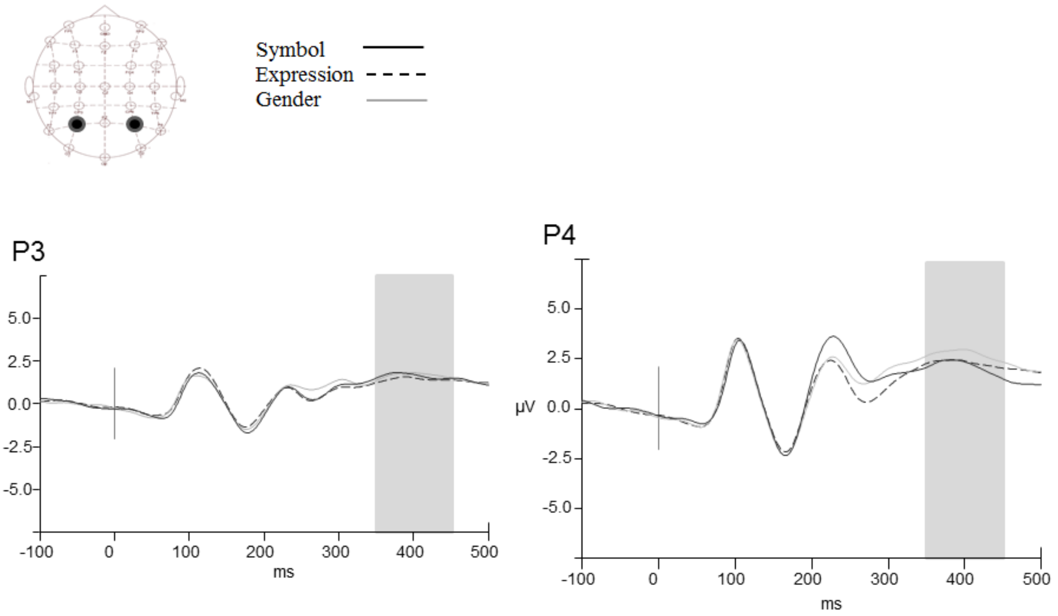

P8
Symbol
Expression
Gender
5.0
2.5
µV 0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms
O1
O2

Figure 5


Symbol
Expression
Gender
P3
5.0
2.5
µV 0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms
P4
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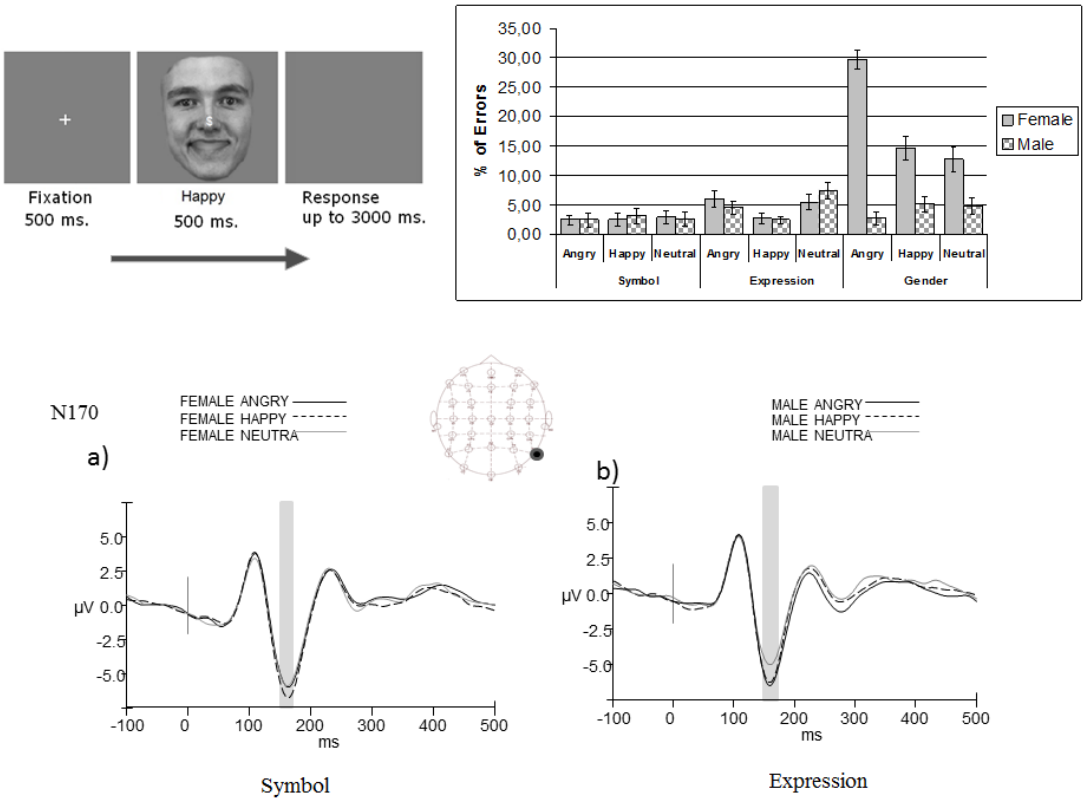
2.5
µV 0.0
-2.5
-5.0
-100
0
100
200
300
400
500
ms

Figure 6



Graphical abstract

Highlights

- We recorded EEG during 2 tasks involving facial features (gender and expression).
- A third implicit task is introduced to locate attention to non-facial features.
- We describe the time course for implicit and explicit ERP effects.
- We replicate early implicit effects of expression in the ERP waves.
- Results provide new evidence about the interaction of facial properties.