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Event-related potentials modulated by the perception of sexual dimorphism: The influence of attractiveness and sex of faces

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ABSTRACT

Sexual dimorphism has been proposed as one of the facial traits to have evolved through sexual selection and to affect attractiveness perception. Even with numerous studies documenting its effect on attractiveness and mate choice, the neurophysiological correlates of the perception of sexual dimorphism are not yet fully understood. In the present study, event-related potentials (ERPs) were recorded during visualisation of faces that had been previously transformed in shape to appear more masculine or more feminine. The participants' task consisted of judging the attractiveness of half of the total number of faces, and performing a sex discrimination task on the other half. Both early and late potentials were modulated by the sex of faces, whereas the effect of the sexually dimorphic transform was mainly visible in the P2 (positive deflection around 200 ms after stimulus onset), EPN (early posterior negativity) and LPP (late positive potential) components. There was an effect of sexual dimorphism on P2 and EPN amplitudes when female participants visualised male faces, which may indicate that masculinity is particularly attended to when viewing opposite sex members. Also, ERP results seem to support the idea of sex differences in social categorisation decisions regarding faces, although differences were not evident on behavioural results. In general, these findings contribute to a better understanding of how humans perceive sexually dimorphic characteristics in other individuals' faces and how they affect attractiveness judgements.

1. Introduction

The human face provides important social information to the observer, assuming an essential relevance in contexts of mate choice (Thornhill & Gangestad, 1999). One of the reasons why face perception may be so important in mate choice is because facial attractiveness may advertise mate quality (Little, Jones, & DeBruine, 2011). Therefore, the perception of facial attractiveness in opposite-sex faces is important for heterosexual individuals (Little & Jones, 2003). This assumption is supported by research on ERPs (event-related potentials) during face perception that investigated how women and men process opposite and same-sex faces. Results from such studies indicate the existence of specialised processing of faces of possible mates, reporting ERP modulations specifically when heterosexual individuals observe opposite-sex faces (Oliver-Rodríguez, Guan, & Johnston, 1999; van Hooff, Crawford, & van Vugt, 2011).

One of the variables that influence facial attractiveness is sexual dimorphism, i.e. the presence of secondary sexual characteristics in faces. The shape of mature men's and women's faces tends to be different, with men having larger jawbones, more prominent cheekbones and thinner cheeks (Enlow, 1990). The perception of sexually dimorphic traits is thought to influence mating preferences as they are honest signals of health and immunity in both sexes (Folstad & Karter, 1992) and/or intrasexual competitiveness, particularly in men (Puts, 2010; Scott, Clark, Boothroyd, & Penton-Voak, 2013; Swaddle & Reierson, 2002). Femininity in female faces is considered attractive by male counterparts (Perrett et al., 1998) possibly because it indicates health and fertility (Law Smith et al., 2006). Women with more feminine faces are believed to have better reproductive health (Baird et al., 1999; Thornhill & Gangestad, 1999) but also evoke positive attributions, such as warmth, honesty, cooperativeness and youthfulness (Law Smith et al., 2006; Perrett et al., 1998). Masculinity in male face shape

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is found to be attractive to women in some studies (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001) while others report a preference for more feminine male faces (DeBruine, Jones, Smith, & Little, 2010; Perrett et al., 1998). Although masculinity in males is expected to be attractive if it is associated with good genes and indirect benefits to the offspring (Kirkpatrick & Ryan, 1991; Zahavi, 1975), women's preference for a feminine shape in male's faces has been justified as a strategic trade-off when searching for a more co-operative partner (Gangestad & Simpson, 2000). Less masculine males are thought to be less aggressive, more honest, more cooperative and to have an increased parenting ability (Perrett et al., 1998). Less masculine males may, therefore, be perceived as more attractive, especially if women are considering long-term relationships (Little & Hancock, 2002). Given the importance of sexual dimorphism on mating decisions, its perception assumes a biological relevance that we expect to produce effects even at early stages of visual processing.

To our knowledge, there are just two published studies that have investigated the neurophysiological correlates of the perception of sexual dimorphism in faces (Cellerino et al., 2007; Freeman, Ambady, & Holcomb, 2010). Cellerino et al. (2007) addressed facial sexual dimorphism by presenting participants with gender-ambiguous face stimuli which they had to classify as male or female. Although using event-related potentials (ERPs), they focused mostly on defining specific brain regions implicated in face gender and masculinity processing. Through independent component analyses, they found that the perceived facial masculinity correlated with one of the ERP components, that had a parieto-temporal source and latency of about 170 ms. The other study, from Freeman et al. (2010) used artificial face stimuli manipulated to appear "less gendered" and found that sex-typicality of faces modulated P1 latency and N170 amplitude. The results from this later study are difficult to interpret as the sex of participants was not described, especially taking into account the evidence that women and men respond differently to different sex faces (e.g. Godard & Fiori, 2010; Tiedt, Weber, Pauls, Beier, & Lueschow, 2013).

The present study aimed to investigate in detail the time course of the electrophysiological correlates of the processing of faces that vary in masculinity/femininity and define whether these correlates differ between male and female participants. Also, we investigated how this perception was modulated by the type of judgment, namely whether participants were making attractiveness judgments or sex discrimination judgments. To do so, we carried out an ERP experiment and analysed early and late potentials that are related either to more automatic or to more conscious mental processes during the perception of sexually dimorphic traits in faces, under different processing conditions (judge sex or judge attractiveness). To that end, we focused our analyses in the following potentials: P1, N170, P2, EPN, and LPP.

The P1 is an early visual ERP component, peaking around 100 ms at occipital electrodes, which is commonly thought to reflect the processing of low-level stimulus features and seems to be involved in early stages of attentional gain control (Hillyard, Vogel, & Luck, 1998). The P1 ERP component has also been shown to be linked to face perception (Itier & Taylor, 2004). Previous studies have reported modulations of the P1 component by the perception of sexual dimorphism in faces (Freeman et al., 2010) and by the participants' sex (Dzhelyova, Perrett, & Jentzsch, 2012; Hahn et al., 2016).

Temporo-occipital cortex responses occurring approximately 170 ms after stimulus onset (a component known as the N170) are thought to reflect the structural encoding stage in face perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000). According to Bruce & Young's (1986) model of face recognition, the direct encoding module, which is responsible for sex categorisation, follows the structural encoding of facial features. Accordingly, the N170 component should be insensitive to sex categorisation but several findings have challenged this idea reporting N170 modulations by face gender (Sun, Gao, & Han, 2010) and other high-level social features of faces, such as emotion (Frühholz, Jellinghaus, & Herrmann, 2011; Wieser, Pauli, Reicherts, & Mühlberger, 2010) and attractiveness (Hahn et al., 2016; Zhang & Deng, 2012).

The P2 is a visual potential that peaks around 200 ms after stimulus onset over parieto-occipital sites and has been associated with implicit selective attention to 'emotionally distinct' stimuli (Carretié, Martín-Loeches, Hinojosa, & Mercado, 2001). Enhanced P2 amplitudes were found in response to both attractive and unattractive opposite-sex faces (van Hooff et al., 2011). Larger P2 responses were also elicited for male compared to female faces in a sample of female participants (Ito & Urland, 2003).

The early posterior negativity (EPN) is an enhanced negativity at temporo-occipital electrodes, peaking approximately 260–280 ms after stimulus onset (Schupp, Öhman et al., 2004), although some studies have reported that the EPN peaks at 300 ms (e.g. Schupp, Junghöfer, Weike, & Hamm, 2004). It is suggested that EPN results from reflex-like visual attention to emotional stimuli, which facilitates sensory encoding processes. The amplitude of the EPN has been reported as more pronounced for stimuli of high evolutionary significance, namely erotic images and pictures of mutilations (Junghöfer, Bradley, Elbert, & Lang, 2001). Werheid, Schacht & Sommer (2007) revealed that attractive, as opposed to unattractive, faces elicited a larger EPN component.

Finally, the LPP (late positive potential) occurs around 350–400 ms at centro-parietal sites, lasting for several hundred milliseconds, in response to emotionally arousing pictures (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000) and aesthetically pleasing images (Höfel & Jacobsen, 2007). Augmented LPP amplitudes have been reported, particularly to faces expressing anger or fear (Schupp, Öhman et al., 2004). Enlarged LPP amplitudes have also been identified as indices of selective attentional processing in the domain of explicitly directed attention, that is, when subjects are instructed to selectively attend to certain stimulus features (Schupp, Junghöfer et al., 2004).

The aim of this study was to explore the electrophysiological correlates of the perception of both female and male faces that were masculinised or feminised, focusing on the previously mentioned ERP components, which have been associated with sex and/or attractiveness processing. Participants performed two different tasks: in the attractiveness task, participants were asked to evaluate each face as attractive or unattractive; in the sex discrimination task, they were asked to indicate if the presented face was male or female. Regarding the attractiveness task, we expected participants to consider feminised female faces more frequently as attractive since femininity has been clearly shown to enhance attractiveness in female faces (Law Smith et al., 2006). Given the inconsistency in previous studies regarding the influence of shape masculinity on men's facial attractiveness, we did not hold a specific prediction on how sexual dimorphism would affect attractiveness evaluations of male faces. Regarding the sex discrimination task, although studies have shown that humans are very proficient at recognising the sex of faces (Bruce et al., 1993), we expected participants to perform slightly worse when judging feminised male faces and masculinised female faces (as these could be considered as sex incongruent stimuli). Considering the effects on the ERP components, we expected to observe specific modulations by sexual dimorphic differences in faces, especially towards opposite-sex stimuli, which may indicate the presence of attentional mechanisms related to mate choice.

2. Methods

2.1. Participants

Detailed written informed consent was obtained from all participants prior to enrolment, and all aspects of the study were performed in accordance with the Declaration of Helsinki for experimentation with human subjects. The study was part of a project that was approved by the Scientific Council of the University of Aveiro, which assesses its ethical, formal, and scientific aspects. Forty-four participants took part in the experiment but four were excluded from the analyses as they did not fulfil the criterion of 5% maximum of omissions (no responses) in both experimental tasks or the criterion of 10% maximum of bad channels during EEG (electroencephalography) recording (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007). Another five were excluded for being left-handed. The remaining 35 right-handed participants (M_{age} = 22.94, SD = 3.93, Range: 18–31), 18 men and 17 women, were included in the analyses. All participants reported being Caucasian and exclusively or predominantly heterosexual (≤ 2 in a scale from 0 as "exclusively heterosexual" to 6 as "exclusively homosexual").

2.2. Stimuli

Sixty facial photographs selected from a database of Portuguese young adult faces, 30 male, and 30 female, were delineated with 192 points (with X and Y coordinates) using Psychomorph software (Tiddeman, Burt, & Perrett, 2001). This delineation intended to delimit the different face areas, a process which is required prior to averaging processes and sexually dimorphic transformations. For each sex of faces, groups of four different facial photographs were averaged together to create 121 composite male faces and 121 composite female faces. Composite faces were used in preference to the original individual faces since composites are not recognisable as familiar individuals and assure lower levels of inter-individual differences (namely in attractiveness). Also, such procedure ensures that the stimuli have average levels of sexual dimorphism, allowing subsequent standardisation of shape manipulations.

The facial shape of each of the 242 composite faces was manipulated towards higher masculinity or higher femininity according to the shape difference between the male and female prototype faces. Each of the two prototypes consisted of the average of all same-sex faces of the original set. Although faces vary in several traits besides sexual dimorphism, when averaging all of them according to sex, the final appearance will contain the mean structural features that represent each sex, with all other variations being lost as noise during the averaging process. Using these face prototypes, we created a feminised version (−50% masculinity) and a masculinised version (+50% masculinity) of each composite face (see Fig. 1). The hair, neck, ears and background were occluded with an oval black mask. Each of the 484 images was converted to greyscale and resized to 719 × 1200 pixels, with a resolution of 300 × 300 dpi.

2.3. Procedure

Participants were seated in a dimly lit and sound-attenuated room, at a distance of 80 cm from the computer screen. Initially, participants performed a training block with four trials in which they were instructed to press one of the two mouse buttons to judge the attractiveness of faces. They were told to follow their first impression and respond quickly. The instruction was to press one of the buttons if the face was judged as attractive and the other button for unattractive evaluations. It was stressed that during the training block, responses would not be considered for further analyses and that EEG recordings were still inactive. The faces presented during the training block (two male and two female faces) were different from the ones presented in the experimental phase.

In the experimental phase, participants were asked to perform a similar attractiveness judgment task and also a sex discrimination task in separate blocks. EEG recording was carried out during this phase. In the attractiveness task, it was explained that there were no right or wrong answers as it depended on their own judgment. Two blocks of 120 face images (60 female faces and 60 male faces), making a total of 240 face images, were presented in each of the experimental tasks (attractiveness and sex discrimination tasks). Half of the faces were masculinised versions of the composite faces, and the other half were feminised versions of the same faces. Task, block and image order were randomised, and response key mapping was counterbalanced across participants. Participants were allowed to take a break of fixed duration after each block. Each trial started with a fixation cross (500 ms) followed by the face image (250 ms) and then participants were instructed to respond (2000 ms maximum time allowed). Answers were only allowed after the face disappeared from the screen. Responses were followed by a 1000 ms blank screen (see Fig. 2). Each face was presented only once.

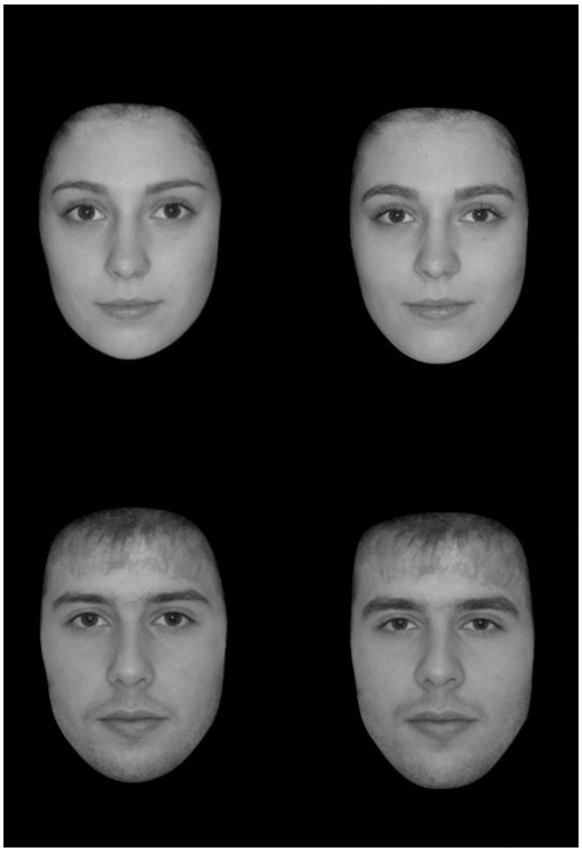

Fig. 1. Examples of the sexually dimorphic shape transforms applied to the faces. The left images represent increased feminisation (-50% masculinisation) and the right images represent increased masculinisation (+50% masculinisation).

2.3.1. EEG recordings

EEG activity was recorded using *Neuroscan* software (Scan 4.3) and a Quick-cap with 64 Ag/AgCl electrodes located according to the 10/10 International System. Signals were amplified with a SynAmps2 system.

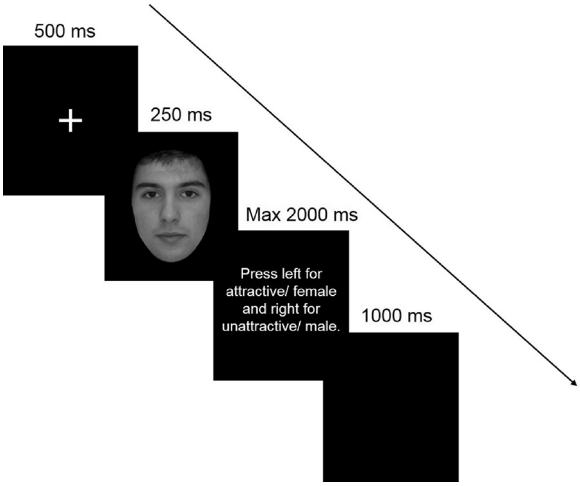

Fig. 2. Representation of the sequence of events in both tasks.

Vertical eye movements were recorded using two electrodes placed above and below the left eye. Two electrodes placed in the external corner of each eye were used to record horizontal eye movements. The EEG signals were measured relative to a reference electrode positioned on the tip of the nose and a notch filter for 50 Hz was applied online. For all electrodes, impedance was kept under 5 kΩ, and EEG was sampled with a digitization frequency of 1000 Hz.

2.4. ERP analyses

Offline analyses included a band-pass filtering from 0.1 to 30 Hz. Offline epochs were generated lasting 1050 ms and starting 150 ms before stimulus onset. Baseline correction was carried out by subtracting the average pre-stimulus amplitude value. EEG data were analysed only for correct response trials in the sex discrimination task and for all the answered trials in the attractiveness task. EEG waveforms were averaged separately for all conditions (masculinised female face, feminised female face, masculinised male face, feminised male face) of each task (attractiveness and sex discrimination tasks). Considering the topographical characteristics of the grand average waveforms and the locations and latencies where the components were more conspicuous, each of these potentials was analysed in the following electrodes and time windows: P1 (90–140 ms; electrodes O1, OZ and O2); N170 (140–200 ms; electrodes P7, P8, PO7, PO8, O1, OZ and O2); P2 (200–260 ms; electrodes PO3 and PO4); EPN (260–340 ms; electrodes P7, P8, PO7 and PO8); LPP (330–430 ms, 430–530 ms, 530–630 ms, 630–730 ms; electrodes CP1, CPZ, CP2). For early components (P1, N170, and P2), peak amplitude was analysed within the respective time window, while mean amplitudes in specific time windows were computed for EPN and LPP components. The peak amplitudes of early components were taken when the peak was maximal at each individual electrode within the corresponding time interval.

3. Results

3.1. Behavioural data

After performing tests of normality and visual inspection of Q-Q plots of behavioural data, most of the conditions appeared to have non-normal distributions. Therefore, in order to guarantee uniformity in the analyses, we opted to use non-parametric tests in all conditions. For all tests, we report the Vovk-Sellke Maximum p-Ratio (e.g., Bayarri, Benjamin, Berger, & Sellke, 2016), and the Rank-Biserial Correlation as an estimate of effect size (e.g., Tomczak & Tomczak, 2014). Descriptive data for all analyses are presented in Figs. 3–6. For easiness of interpretation, the graphs represent means and standard errors of the mean.

3.1.1. Attractiveness task

3.1.1.1. Percentage of faces evaluated as attractive. The mean percentage of faces in each condition that were evaluated as attractive was analysed. In order to analyse the effect of sex of the face, we calculated the overall mean percentage of attractive evaluations for male faces and female faces. Wilcoxon signed ranks tests revealed that female faces were associated with a higher percentage of attractive evaluations compared to male faces, $Z = -4.55$, $p < .001$, VS-MPR = 5195, Rank-Biserial Correlation = .787, 95% CI for Rank-Biserial Correlation [.594, .895] (see Fig. 3). We also calculated the overall mean percentage of attractive evaluations for masculinised faces and feminised faces to analyse the effect of sexually dimorphic transform. Feminised faces were overall associated with a higher percentage of attractive evaluations compared to masculinised faces, $Z = -3.02$, $p = .003$, VS-MPR = 22.04, Rank-Biserial Correlation = .500, 95% CI for Rank-Biserial Correlation [.168, .730].

To analyse the effect of sexually dimorphic transform in each sex face we performed two Wilcoxon signed ranks tests, using a Bonferroni corrected alpha of .025. Feminised female faces were considered as attractive more frequently than masculinised female faces, $Z = -3.95$, $p < .001$, VS-MPR = 476.93, Rank-Biserial Correlation = .508, 95% CI for Rank-Biserial Correlation [.178, .735]. No difference was found for male faces.

Although both sex participants considered female faces to be attractive more frequently than male faces, Mann-Whitney tests with Bonferroni corrected alpha of .025 showed that male participants gave a higher percentage of attractive evaluations to female faces than did female participants, $U = 85.00$, $z = -2.25$, $p = .025$, VS-MPR = 3.775, Rank-Biserial Correlation = .441, 95% CI for Rank-Biserial Correlation [.085, .697], while not showing differences in male faces (see Fig. 3). Similar comparisons for feminised and masculinised stimuli showed no differences between groups (all $p > .483$). Also, regarding the effect of sex of participant in each four individual type of stimuli (female feminised, female masculinised, male feminised, male masculinised), Mann-Whitney tests with Bonferroni corrected alpha of .013 showed no further significant comparisons (all $p > .022$). However, not considering the Bonferroni correction, both feminised ($p = .022$) and masculinised ($p = .038$) female faces were considered more attractive by male than female participants.

3.1.1.2. Reaction times. The overall mean reaction time for male faces and female faces was calculated, such as the overall mean reaction time for masculinised faces and feminised faces. Wilcoxon signed ranks tests revealed that participants responded faster when judging overall masculinised faces than overall feminised faces, $Z = -2.60$, $p = .009$, VS-MPR = 9.308, Rank-Biserial Correlation = .505, 95% CI for Rank-Biserial Correlation [.174, .733] (see Fig. 4). This difference was mainly due to participants responding faster when judging masculinised male

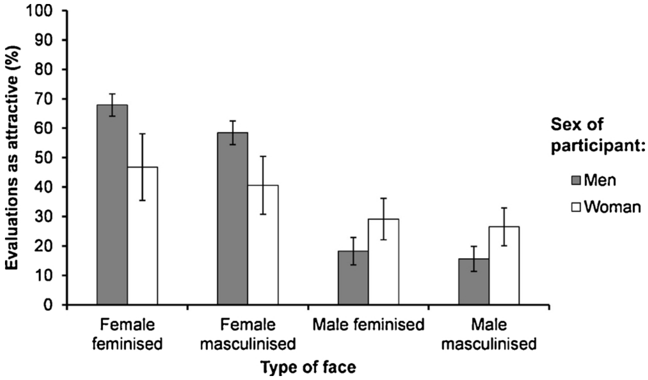

Fig. 3. Percentage of faces evaluated as attractive in the attractiveness task. Error bars show standard errors of the mean.

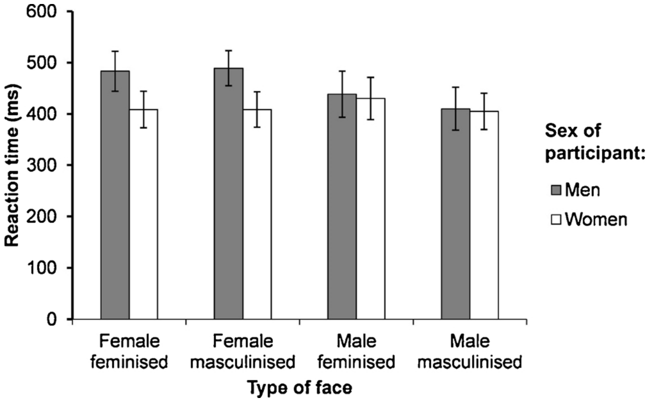

Fig. 4. Reaction times on the attractiveness task. Error bars show standard errors of the mean.

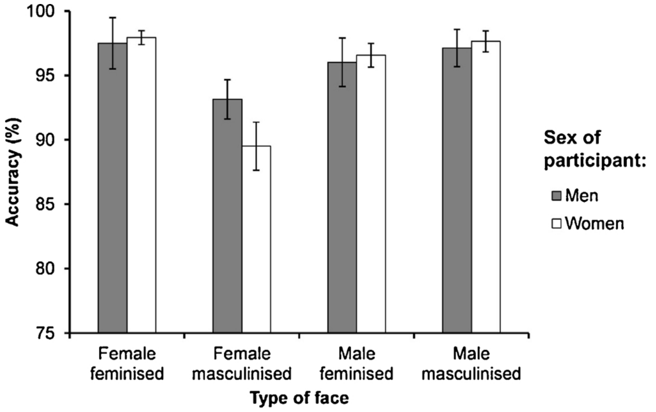

Fig. 5. Accuracy on the sex discrimination task. Error bars show standard errors of the mean.

faces compared to feminised male faces, Wilcoxon signed ranks test with Bonferroni corrected alpha of .025, $Z = -4.16$, $p < .001$, VS-MPR = 4851.34, Rank-Biserial Correlation = .806, 95% CI for Rank-Biserial Correlation [.627, .904], as there was no statistically significant difference between feminised and masculinised female faces. No differences were found depending on participants' sex (all $p > .08$).

3.1.2. Sex discrimination task

3.1.2.1. Accuracy. The percentage of correct responses in the sex discrimination task was analysed for participants of each sex in each experimental condition. In order to analyse the effect of sex of the face, we calculated the overall mean accuracy for male faces and female faces. Wilcoxon signed ranks tests, $Z = -3.09$, $p = .002$, VS-MPR = 29.35, Rank-Biserial Correlation = .363, 95% CI for Rank-Biserial Correlation [.001, .624], showed that participants were better at discriminating male faces than female faces (see Fig. 5). To analyse the effect of sexually dimorphic transform we calculated overall mean accuracy for masculinised faces and feminised faces. Participants were better at discriminating feminised faces in general, comparing to masculinised ones, $Z = -3.95$, $p < .001$, VS-MPR = 416.9, Rank-Biserial Correlation = −.846, 95% CI for Rank-Biserial Correlation [−.925, −.697].

Regarding the effect of sexually dimorphic transform in each sex face (Bonferroni corrected alpha of .025), participants were more accurate when discriminating feminised female faces than masculinised female faces, $Z = -4.72$, $p < .001$, VS-MPR = 11165.45, Rank-Biserial Correlation = .381, 95% CI for Rank-Biserial Correlation [.021, .653], and slightly better when discriminating masculinised male faces compared to feminised male faces, although this last comparison did not reach statistical significance, $Z = -1.88$, $p = .06$, VS-MPR = 1.986, Rank-Biserial Correlation = −.670, 95% CI for Rank-Biserial Correlation [−.831, −.406] (see Fig. 5). Mann-Whitney tests showed that male and female participants did not differ in the percentage of correct responses for any of the face conditions (all $p > .168$).

3.1.2.2. Reaction times. In order to analyse the effect of sex of the face, we calculated the overall mean reaction time for male faces and female faces. Wilcoxon signed ranks tests showed that participants gave faster responses to male faces than to female faces, $Z = -2.97$, $p = .003$, VS-MPR = 25.75, Rank-Biserial Correlation = .575, 95% CI for Rank-Biserial Correlation [.268, .776] (see Fig. 6). Mean reaction times for overall masculinised and feminised faces were also calculated, however this comparison was not statistically significant.

Regarding the effect of sexually dimorphic transform in each sex face, we performed two Wilcoxon signed ranks tests, using a Bonferroni corrected alpha of .025. Participants gave faster responses to feminised female faces compared to masculinised female faces, $Z = -4.01$, $p < .001$, VS-MPR = 2074, Rank-Biserial Correlation = −.778, 95% CI for Rank-Biserial Correlation [−.890, −.578] and to masculinised male faces compared to feminised male faces, $Z = -4.11$, $p < .001$, VS-MPR = 3623, Rank-Biserial Correlation = .797, 95% CI for Rank-Biserial Correlation [.611, .900]. Mann-Whitney tests showed that male and female participants did not differ in the percentage of correct responses for any of the face conditions (all $p > .287$) (see Fig. 6).

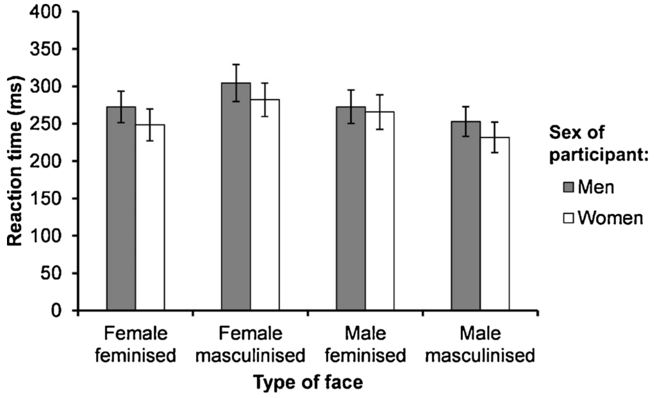

Fig. 6. Reaction times on the sex discrimination task. Error bars show standard errors of the mean.

3.2. ERP data

ERP data were analysed through mixed-design ANOVAs (between-subjects factor: sex of participant; within-subjects factors: task, sex of the face, sexually dimorphic transform and electrode). Peak amplitude was analysed for P1, N170, and P2 and mean amplitude was considered for EPN and LPP potentials. The Greenhouse-Geisser correction was used for violations of sphericity and corrected degrees of freedom are reported. Bonferroni corrections were used in pairwise comparisons to explore significant effects. Supplementary Table 1, in the supplementary materials, shows results of all analyses performed for all components. Figs. 7 and 10 represent the grand-average waveforms for the attractiveness (Fig. 7) and sex discrimination (Fig. 10) tasks for female and male participants at electrodes CP1, PO4, PO8 and O2.

3.2.1. P1 (90–140 ms; electrodes O1, OZ, and O2)

For the P1 component, there was a significant interaction between task and sex of the face, $F(1, 33) = 5.18$, $p = .03$, $\eta_p^2 = 0.136$. In particular, for the sex discrimination task, P1 amplitude was more positive for male faces ($M = 8.11\,\mu V$, $SE = 1.07$) than female faces ($M = 7.35\,\mu V$, $SE = 0.97$). No significant differences were found in the attractiveness task. The interaction effect between sex of the face and electrode was marginally significant, $F(2, 66) = 3.05$, $p = .054$, $\eta_p^2 = .085$. Although no significant pairwise comparisons were found, this marginal interaction is due to a more pronounced difference between male and female faces in O1 and O2, when compared to OZ. Lastly, an interaction between sex of participant, task, sex of the face, sexually dimorphic transform and electrode, $F(1.62, 53.47) = 4.23$, $p = .027$, $\eta_p^2 = 0.114$, demonstrated that for women, when judging female feminised faces, in the attractiveness task, P1 amplitude was more positive in OZ compared to O2.

3.2.2. N170 (140–200 ms; electrodes P7, P8, PO7, PO8, O1, OZ, and O2).

The N170 potential revealed enhanced amplitudes over right parietal electrodes (P8 and PO8), compared to other locations, $F(2.55, 84.08) = 21.81$, $p < .001$, $\eta_p^2 = 0.398$. Peak amplitudes were larger for female faces ($M = -10.72\,\mu V$, $SE = 0.93$) than for male faces ($M = -9.50\,\mu V$, $SE = 0.96$), $F(1, 33) = 27.01$, $p < .001$, $\eta_p^2 = 0.450$. A significant interaction effect between sex of the face and electrode, F

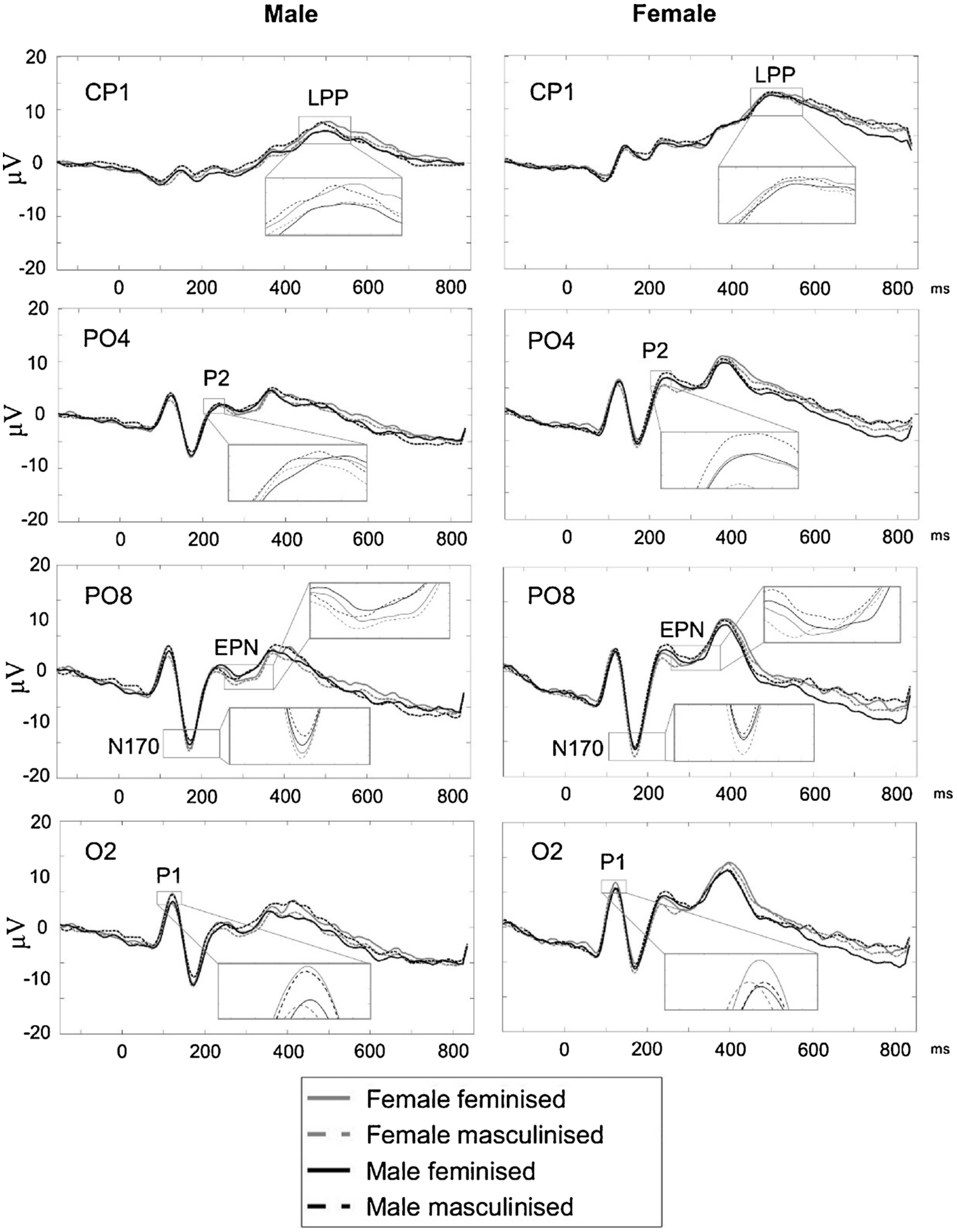

Fig. 7. Grand-average waveforms in the attractiveness task, for male (left panel) and female participants (right panel) over centro-parietal (CP1), parieto-occipital (PO4, PO8) and occipital (O2) sites.

(2.78, 91.70) = 4.45, $p = .007$, $\eta_p^2 = 0.119$, with significant differences in all seven locations, showed increased negativities for female faces that were more pronounced in right parietal electrodes, P8 ($\eta_p^2 = 0.571$) and PO8 ($\eta_p^2 = 0.443$). The effect of sex of the face was also more evident for female participants (significant interaction effect between sex of the face and sex of participant, F (1, 33) = 5.99, $p = .020$, $\eta_p^2 = 0.154$). There was an interaction effect between task, sex of the face and sexually dimorphic transform, F (1, 33) = 7.04, $p = .012$, $\eta_p^2 = 0.176$, showing that in the attractiveness task, the N170 was increased for masculinised female faces compared to masculinised male faces, and that in the sex discrimination task, more negative amplitudes were associated with feminised female faces comparing to feminised male faces. There was a significant interaction between sex of participant and electrode, F (2.55, 84.08) = 3.43, $p = .027$, $\eta_p^2 = 0.094$. Although there were no significant differences between the sexes in any of the locations, the interaction is due to larger and more frequent differences between electrode sites in women than in men.

3.2.3. P2 (200–260 ms; electrodes PO3 and PO4)

Regarding P2 amplitude, there was a significant effect of sex of participant, F (1, 33) = 8.79, $p = .006$, $\eta_p^2 = 0.210$, wherein more positive amplitudes were observed for female participants ($M = 9.66$ μV, $SE = 1.39$) compared to male participants ($M = 3.89$ μV, $SE = 1.36$). Male faces elicited larger amplitudes ($M = 7.32$ μV, $SE = 1.03$) than female faces ($M = 6.23$ μV, $SE = 0.94$), F (1, 33) = 9.83, $p = .004$, $\eta_p^2 = 0.229$, mainly in the sex discrimination task (significant interaction effect between sex of the face and task, F (1, 33) = 6.83, $p = .013$, $\eta_p^2 = 0.172$) and in female participants (marginally significant interaction effect between sex of the face and sex of participant, F (1, 33) = 3.96, $p = .055$, $\eta_p^2 = 0.229$). There was a significant interaction effect between sex of the face and sexually dimorphic transform, F (1, 33) = 5.54, $p = .025$, $\eta_p^2 = 0.144$, and a significant interaction effect between sex of participant, sex of the face and

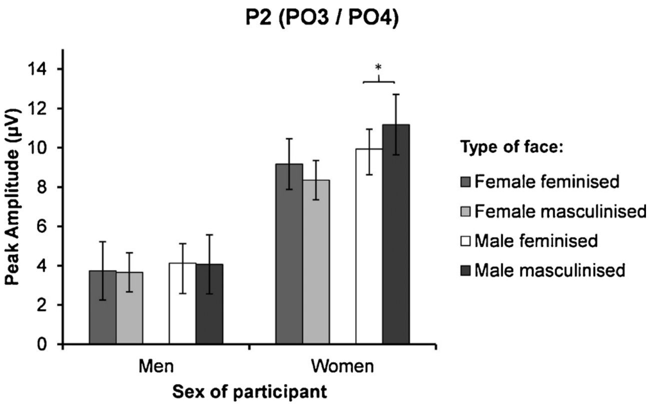

Fig. 8. P2 peak amplitudes for masculinised and feminised faces of both sexes, for male and female participants. Error bars show standard errors of the mean. * $p < .05$.

sexually dimorphic transform, $F\ (1, 33) = 5.36$, $p = .027$, $\eta_p^2 = 0.140$. The latter effect showed that masculinised male faces ($M = 11.17\,\mu V$, $SE = 1.54$) elicited more positive P2 amplitudes than feminised male faces ($M = 9.93\,\mu V$, $SE = 1.46$) in female participants (see Fig. 8). No differences were found for female faces or male participants (all $p > .124$).

3.2.4. EPN (260–340 ms; electrodes P7, P8, PO7 and PO8)

The EPN mean amplitude was more negative in the attractiveness task ($M = -.15\,\mu V$, $SE = 0.84$) than in the sex discrimination task ($M = .88\,\mu V$, $SE = 0.68$), $F\ (1, 33) = 4.58$, $p = .040$, $\eta_p^2 = 0.122$. Also, more negative amplitudes emerged for female faces ($M = -.19\,\mu V$, $SE = 0.79$) than for male faces ($M = .92\,\mu V$, $SE = 0.67$), $F\ (1, 33) = 13.50$, $p = .001$, $\eta_p^2 = 0.290$, mainly in the sex discrimination task, $F\ (1, 33) = 6.05$, $p = .019$, $\eta_p^2 = 0.155$, and over all four locations, $F\ (1.99, 65.53) = 6.93$, $p = .002$, $\eta_p^2 = 0.174$, but with increased effect size over PO8 ($\eta_p^2 = 0.376$). An interaction effect between task, sex of the face and electrode confirms such results, $F\ (1.69, 55.62) = 4.71$, $p = .017$, $\eta_p^2 = 0.125$. Higher amplitudes for female faces in the sex discrimination task were also mainly attributed to female participants, $F\ (1, 33) = 4.87$, $p = .034$, $\eta_p^2 = 0.129$. An interaction effect between sex of participant, sex of the face and sexually dimorphic transform, $F\ (1, 33) = 4.38$, $p = .044$, $\eta_p^2 = 0.117$, showed that only women had a larger EPN response when judging feminised male faces ($M = 2.00\,\mu V$, $SE = 1.03$) than when judging masculinised male faces ($M = 3.45\,\mu V$, $SE = 1.04$) (see Fig. 9), with no differences found for female faces and male participants (all other $p > .467$). Amplitudes were, in general, more negative over parietal locations (P7 and P8), $F\ (2.00, 66.06) = 9.26$, $p < .001$, $\eta_p^2 = 0.219$, and also more negative for male participants ($M = -1.23\,\mu V$, $SE = 1.01$) compared to female participants ($M = 1.96\,\mu V$, $SE = 1.04$), $F\ (1, 33) = 4.83$, $p = .035$, $\eta_p^2 = 0.128$.

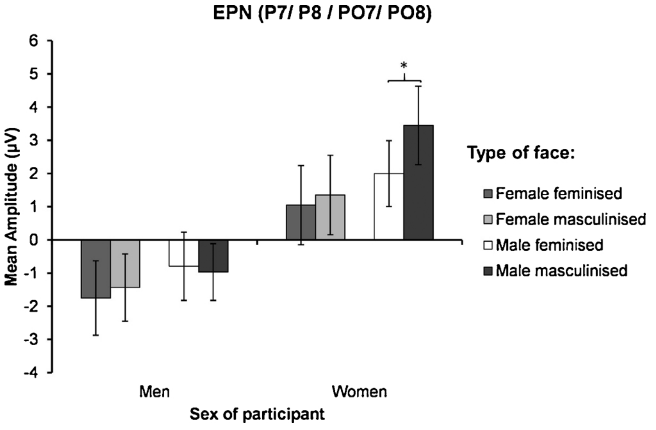

Fig. 9. Mean EPN amplitudes for masculinised and feminised faces of both sexes, for male and female participants. Error bars show standard errors of the mean. * $p < .05$.

3.2.5. LPP (330–430 ms, 430–530 ms, 530–630 ms, 630–730 ms; electrodes CP1, CPZ, CP2)

LPP mean amplitudes were consistently larger for female participants compared to male participants (see Table 1). In the first three time windows, the sex discrimination task elicited larger amplitudes than the attractiveness task. However, female participants exhibited larger amplitudes for the attractiveness task between 630 and 730 ms. During the first two time periods, masculinised male faces elicited larger amplitudes compared to feminised male faces. Between 530 and 630 ms, male faces were associated with larger amplitudes than female faces exclusively in the sex discrimination task. Despite the fact that, in the first time window, LPP amplitudes were larger over CP1, in the following three time windows, LPP amplitudes were more positive over CPZ.

4. Discussion

This study aimed to understand the effect of sexually dimorphic facial traits on sex discrimination and attractiveness judgments, analysing both behavioural and electrophysiological measures. The analyses of attractiveness judgments showed that, regardless of the sex of participant, a higher number of attractive evaluations was attributed to female faces when compared to male faces. Feminised faces of both sexes were also considered to be attractive more frequently than masculinised faces, by both male and female participants. Apparently, the attractiveness of female and male faces seems to be assessed somewhat similarly by men and women. Additionally, masculinised stimuli, in general, were associated with faster reaction times, possibly demonstrating that both male and female participants are more engaged by feminised faces overall, thus taking longer to subsequently respond after viewing these faces. Since feminisation is associated with increased attractiveness, longer response times may reflect the intrinsic reward of attractiveness (Aharon et al., 2001; Leder, Tinio, Fuchs, & Bohrn, 2010) to both male and female participants. In fact, similar findings, with no behavioural differences dependent on participant's sex, when assessing the attractiveness of both sex faces, have been reported in previous research (Levy et al., 2008), namely in studies using eye-tracking (Alexander & Charles, 2008) and fMRI (Bray & O'Doherty, 2007; Kranz & Ishai, 2006).

The effect of sexual dimorphism on attractiveness judgments was mainly visible for female faces, with femininity clearly increasing attractiveness in those faces as predicted by previous studies (Rhodes, 2006). The non-significant effect of sexually dimorphic transform in male faces possibly represents the absence of consensus among female participants who show different preferences towards masculinity according to own condition and environmental influences (Gangestad & Simpson, 2000). A tendency to prefer masculinity traits in male faces is usually found in women who consider themselves attractive (Little, Burt, Penton-Voak, & Perrett, 2001), who are seen as attractive by others (Penton-Voak et al., 2003), who are ovulating (Gildersleeve, Haselton, & Fales, 2014), when considering short-term relationships (Penton-Voak & Perrett, 2000) and when partnered (Little, Jones, Penton-Voak, Burt, & Perrett, 2002). Women in opposite situations tend to prefer more feminine males who are perceived as more cooperative, warm and honest (Perrett et al., 1998). Such diversified preferences between women, in addition to men's general dislike of male faces, caring little if they were feminised or masculinised, possibly prevented sexual dimorphism influencing attractiveness judgments in a specific direction.

Regarding the sex discrimination task, there were no differences

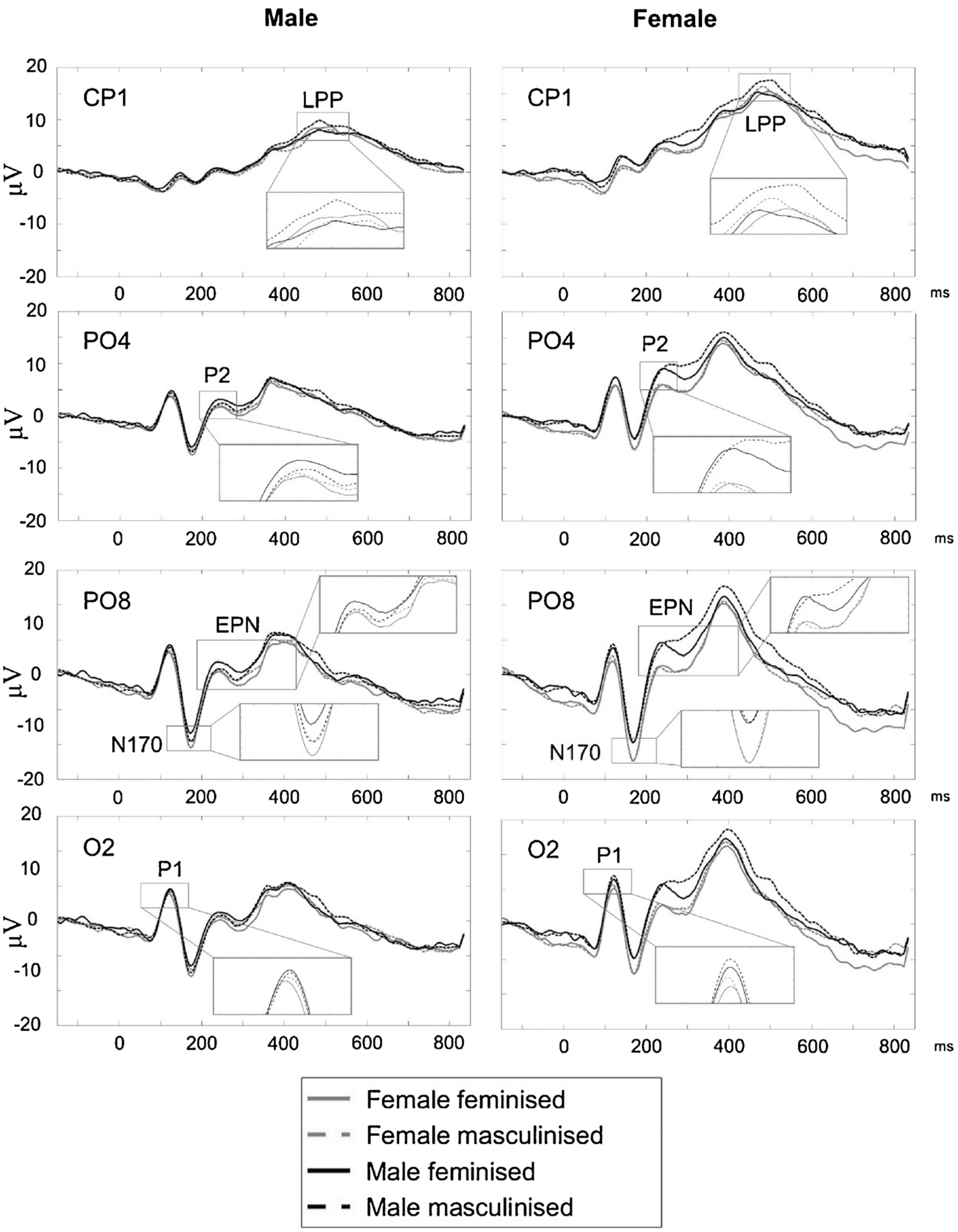

Fig. 10. Grand-average waveforms for the sex discrimination task, for male (left panel) and female participants (right panel) over centro-parietal (CP1), parieto-occipital (PO4, PO8) and occipital (O2) sites.

between the sexes in the percentage of correct responses, as found in previous research (O'Toole et al., 1998), which shows that both men and women are extremely good at discriminating the sex of faces. Also, as expected, congruent stimuli (mainly feminised female faces) were associated with the highest levels of correct responses and fastest reaction times, as previously found (e.g. Freeman et al., 2010), suggesting a possible beneficial effect of congruent sexual dimorphism on this categorisation decision. Higher levels of accuracy and faster responses were associated with male compared to female faces, as reported in other studies (Dzhelyova et al., 2012; O'Toole et al., 1998).

In contrast with this similarity in men and women's behaviour in attractiveness judgments and sex discrimination, ERP measures did reveal sex differences. In fact, compared to male participants, women exhibited more differentiated responses in N170, P2, EPN and LPP amplitudes, when viewing female and male faces. Also, as in previous research (e.g. Sun et al., 2010), the N170 component was modulated by the sex of the face, with larger N170 amplitudes for female compared to male faces, especially for women. The fact that such differences were especially evident for female participants is in line with previous claims of women responding more strongly to social stimuli than men (Proverbio, Zani, & Adorni, 2008).

Similarly to the N170, both P2 and EPN components were different in amplitude depending on the sex of faces, particularly in the sex discrimination task and for female participants (although the interaction effect between the sex of faces and sex of participant was marginally significant for P2), which again supports the idea that women are more sensitive to cues that indicate different social categories (Sun et al., 2010). As both P2 and EPN components are thought to be linked to attentional processes (Carretié et al., 2001; Schacht, Werheid, & Sommer, 2008) we can conclude that, although men and women did not perform differently in the sex discrimination task, ERP data suggest that there are differences in the way women attend to information about the sex of faces compared to men. Both P2 and EPN components were also influenced by face shape sexual dimorphism, which means that such shape information starts to be resolved in the brain around 200 ms after stimulus onset. Importantly, significant interactions

Table 1
Significant effects found in the results of the ANOVAs, analysing the mean amplitudes of the LPP (late positive potentials) in the considered time windows.

		LPP			
		330–430 ms	430–530 ms	530–630 ms	630–730 ms
Sex of participant	*F* (1, 33)	10.64**	17.62***	20.84***	20.21***
	p	.003	< .001	< .001	< .001
	η_p^2	0.244	0.348	0.387	0.380
Sex of the face x Sexually dimorphic transform	*F* (1, 33)	6.36*	10.32**	0.82	0.26
	p	.017	.003	.372	.611
	η_p^2	0.161	0.238	0.024	0.008
Task	*F* (1, 33)	21.26***	15.72***	4.21*	0.04
	p	< .001	< .001	.048	.851
	η_p^2	0.392	0.323	0.113	0.001
Task x Sex of participant	*F* (1, 33)	2.20	1.15	3.47	7.55**
	p	.148	.292	.072	.010
	η_p^2	0.062	0.034	0.095	0.186
Task x Sex of the face	*F* (1, 33)	1.06	1.38	4.39*	3.47
	p	.311	.248	.044	.071
	η_p^2	0.031	0.040	0.118	0.095
Electrode	*F* (2, 66)	4.10*	19.26***	24.80***	29.20***
	p	.021	< .001	< .001	< .001
	η_p^2	0.111	0.369	0.429	0.469

Note: * $p < .05$; ** $p < .01$; *** $p < .001$.

between sex of participant, sex of the face and the sexually dimorphic transform in those components (EPN and P2), with pairwise comparisons only significant for opposite-sex faces, may indicate a specific effect of sexual dimorphism on the perception of faces of possible mates. The absence of significant differences for same-sex faces implies that masculinity assumes special relevance when participants visualise individuals that could constitute partners. Such an effect was only visible for female participants, which means that, although they do not overtly discriminate male face attractiveness based on masculinity, they are attending to masculinity when processing male faces.

The EPN and LPP were modulated by the type of task that the participant was performing. These task effects might represent top-down influences, with participants focusing visual attention and expectations conditionally on the task announced (Clark, Fan, & Hillyard, 1994; Shulman et al., 1997). Masculinised male faces were associated with larger LPP amplitudes compared to feminised male faces between 330 and 530 ms. Given that facial threat also elicits augmented LPP (Schupp, Öhman et al., 2004), this result might be due to increased attention to apparently threatening males because of the positive relation between masculinity and perceived anger (Hess, Adams, Grammer, & Kleck, 2009) and reduced trustworthiness (Oosterhof & Todorov, 2008).

At first sight, our results seem contradictory to the findings of Cellerino et al. (2007) and Freeman et al. (2010), as we did not find a modulation of the N170 component by the sexually dimorphic transform within each face sex. However, we believe that Cellerino et al.'s (2007, p. 516) "correlates for the perception of sexual dimorphism" do correspond to our correlates of the sex discrimination process. As they used gender-ambiguous stimuli, and participants were asked to judge faces as female or male, their N170 effect probably corresponds to the identification or attribution of a sex category to faces. Thus, as we also found a significant difference in N170 amplitude contingent on the sex of the face, we believe that our results do coincide. Regarding Freeman et al.' (2010) work, their manipulation of "face typicality" does resemble our sexually dimorphic manipulation within each sex category of faces. The differences between our findings and theirs may be due to methodological divergences in the manipulation of masculinity/femininity of faces, although we cannot confirm such an assumption as the authors did not address how this transform was carried out by the software used. Also, the fact that we used composites of real faces while they used computer-generated faces could also be the cause of the differentiated findings. According to the uncanny valley theory (Mori, 1970), humanoids avatars or computer generated faces may cause an "eerie feeling" in the perceiver. Despite the lack of agreement regarding the perceptual mechanisms underlying this effect, recent studies have shown that indeed computerized faces generate differentiated EEG responses when compared with real faces, namely in components such as the N170 and LPP (Schindler, Zell, Botsch, Kissler, 2017).

5. Conclusions

This study aimed to shed some light over the time course of the neurophysiological processes underlying the perception of sexually dimorphic traits in faces. Expected preferences for femininity in female faces were found. Also as expected, we found evidence for the advantage of congruency between sex of the face and sexually dimorphic traits in a sex discrimination task, mainly visible on reactions times. ERP results showed that sexual dimorphism modulates P2, EPN and LPP responses. Moreover, P2 and EPN amplitudes were modulated by masculinity, specifically when female participants visualised opposite-sex faces. Such effects may indicate that the perception of masculine traits in faces may hold a special relevance in faces of potential mates. This difference was not apparent in male participants.

Since this study focused exclusively on face shape and recent studies have shown that human faces are also sexually dimorphic in terms of reflectance (Said & Todorov, 2011), future research could try to repeat this study using faces with more masculinised/feminised colouration. Also, it would be of interest to investigate if individual differences in women, as in self-attractiveness level, relationship status, menstrual cycle phase or relationship goal, do influence electrophysiological correlates as they have been proven to influence behavioural responses (Little et al., 2011).

In summary, the evidence found suggests that masculine/feminine facial features seem to contribute to decisions regarding sex discrimination as well as to attractiveness judgments. Although the relationship between attractiveness and sexual dimorphism is evident given the numerous behavioural findings in previous studies, its relation with sex categorisation and the neurophysiological correlates of these processes have seldom been investigated. This study helps to understand the first stages of face perception that ultimately precede mating decisions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.biopsycho.2018.06.002.

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