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Increased N250 elicited by facial familiarity: An ERP study including the face inversion effect and facial emotion processing

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ABSTRACT

The present study aims to explore how familiarity modulates the neural processing of faces under different conditions: upright or inverted, neutral or emotional. To this purpose, 32 participants (25 female; age: $M = 27.7$ years, $SD = 9.3$) performed two face/emotion identification tasks during EEG recording. In the first task, to study facial processing, three different categories of facial stimuli were presented during a target detection task: famous familiar faces, faces of loved ones, and unfamiliar faces. To explore the face inversion effect according to each level of familiarity, these facial stimuli were also presented upside down. In the second task, to study emotional face processing, an emotional identification task on personally familiar and unfamiliar faces was conducted. The behavioural results showed an improved performance in the identification of facial expressions of emotion with the increase of facial familiarity, consistent with the previous literature. Regarding electrophysiological results, we found increased amplitudes of the P100, N170, and N250 for inverted compared to upright faces, independently of their degree of familiarity. Moreover, we did not find familiarity effects at the P100 and N170 time-windows, but we found that N250 amplitude was larger for personally familiar compared to unfamiliar faces. This result supports the reasoning that the facial familiarity increases the neural activity during the N250 time-window, which may be explained by the processing of additional information prompted by the viewing of our loved ones faces, in contrast to what happens with unfamiliar individuals.

1. Introduction

Faces are among the most pertinent social stimuli, and this holds true from birth. Through them, humans can extract a variety of information important to guide their behaviour (e.g., related to identity, emotions, intentions; George, 2013). In order to function, both socially and independently, humans have to be able to recognize others by their faces (Schweinberger and Neumann, 2016), differentiating familiar from non-familiar people, as well as to interpret and respond to facial features and movements of both known individuals and strangers. Through facial expressions, the human face becomes a major nonverbal communication channel for emotions, informing about other people's needs and intentions (e.g., escape from something, fight, have a friendly approach; George, 2013). Considering their social relevance, much work has been done to investigate our abilities of coding, learning, and recognizing faces.

Although traditional models of face recognition have largely focused on cognitive processes, current models have included affective aspects into this matter, assuming that the cognitive and affective aspects fit into two distinct routes, as proposed by Bruce and Young (1986). According to their model, the initial stage of face processing corresponds to the structural encoding of the face, subsequently processed by several systems in charge of perceiving personal identity, expressions, and mouth movements related to speech. Following the establishment of the identity of the face, later systems act in the recovery of the name and personal information linked to the stimulus (Haxby et al., 2000). In the

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continuity of this model, Haxby and colleagues (2000) claimed that the human neural system for face perception can be divided into a core system concerning the visual analysis of faces, and an extended system responsible for extracting the meaning behind faces by exploring the direction of attention, speech processing, personal knowledge, and emotional content. Thereby, the extended system would involve regions linked to the neural systems of other cognitive functions, such as the spatial attention system including regions of the intraparietal sulcus and frontal eye fields; the auditory-verbal comprehension systems correspondent to the superior temporal gyrus; systems related to biographical semantic knowledge enrolled in the retrieving of the information related to the face, which include the anterior temporal lobe; and systems for processing emotional content of expression, embracing regions in the amygdala and insula (Haxby et al., 2000). Although the original model has postulated that only the occipital face area, fusiform face area, and the posterior superior temporal sulcus made part of the core system (Haxby et al., 2000), further research has included other face areas of the anterior temporal and right inferior frontal cortices (Ramon and Gobbini, 2018).

Indeed, the models of Bruce and Young (1986) and Haxby and colleagues (2000) support the claim by Rossion (2014) that "the human face is a complex multidimensional visual pattern with which everyone is familiar" (p. 310). A face conveys a large amount of information about an individual (e.g., age, identity, familiarity; Herzmann et al., 2004) and about that individual's current state (e.g., emotional mood, wakefulness) that humans may extract without explicit training. Moreover, humans may detect a face soon after a hundred milliseconds, categorizing it as familiar with only one or two gaze fixations (Bayer et al., 2021; Rossion, 2014). It has been previously observed, across behavioural and neuroimaging findings, that facial processing is optimized for personally familiar faces. This improvement can be perceived through several aspects: recognition throughout a range of image variations (i.e., changes in viewpoints, viewing distances, resolution, or natural changes such as lighting, angle, and expression), efficient retrieval of personal knowledge and emotional responses. Humans are experts in the detection and determination of the familiarity of a face, and this efficiency persists even if the stimuli are presented after substantial time periods (Ramon and Gobbini, 2018). In a study by Bruck et al. (1991), participants identified and provided correct names of 87% of their former classmates from yearbook images 24–26 years after graduate. Also, when asked to match these images with photographs taken 25 years later, participants gave 78% of correct responses for the category of the most familiar classmates, corresponding to the highest results.

Previous research has established that, as personally familiar faces are more regularly encountered throughout the experience of each human being and learned in more diverse and natural conditions, they can inevitably lead to more "robust" neural representations of a variety of semantic and affective traits (Ambrus et al., 2019, 2021). These representations facilitate their detection, the recognition of their identity, and the activation of their personal knowledge. As simple as this process may seem, to be able to recognize a face as familiar it is necessary to separate it from unfamiliar faces at the individual level and access past experience representations (Caharel and Rossion, 2021). Furthermore, when comparing these representations between different individuals, they should be sensitive to structural and textural differences but, in the same person, they should be tolerant to changes in appearance to which the person may be subjected to (Andrews et al., 2017). The optimization of human face processing to relevant persons is highly improved by the experiences with these individuals and has the purpose to enhance social interactions. The viability of these interactions is under the precondition of the retrieval of personal knowledge about familiar individuals (e.g., biographical information, shared memories) determining our approach to each person (Ramon and Gobbini, 2018). To unravel the time-course of the processing of faces according to their familiarity, one prominent approach is to use electroencephalography (EEG) measures of brain activity during the visualization of different facial stimuli, given the excellent temporal resolution of this technique (Luck, 2014).

EEG consists of recordings of electrical activity at the scalp, that are generated by synaptic activity in populations of synchronized cortical pyramidal neurons. From the EEG, it is possible to extract event-related potentials (ERP), which are defined as waveforms of small voltages generated by the firing of cortical cells in response to a particular sensory, motor, or cognitive event (Amodio et al., 2014). The sequence of ERP waves directly represents the flow of information as sensory inputs are processed, and the voltage represents the neural activity that occurs in the brain in that exact moment (Luck, 2014). To address how face familiarity is processed, we will focus on three ERP components that have been proposed as neural correlates of facial processing (P100, N170, and N250), we will investigate the role of familiarity on an effect that typically disrupts facial identification: the Face inversion effect (FIE); and in the behavioural identification of Facial expressions of emotion (FEE).

Regarding the neural correlates of facial processing, the P100 is usually the first major visual component, with a peak latency at around 100 ms witnessed over posterior electrode sites (Luck, 2014). Previous studies, using mathematical modeling procedures, have suggested that the early part of this component originates from the extrastriate visual cortex, with the later portion arising from the fusiform gyrus (Di Russo et al., 2002). The P100 is well known for its high sensitivity to several low-level characteristics of visual stimuli (e.g., contrast; Rossion and Jacques, 2008). Evidence suggests that it may also be influenced by emotional content, increasing for emotion-relevant stimuli (Luck, 2014).

The N170 component corresponds to a negative deflection of large amplitude on the ERP, peaking approximately 170 ms following facial stimulus onset (Bentin et al., 1996). This response appears predominantly on the occipito-temporal region of the scalp, showing a right lateralization. With an interindividual variability ranging between 130 and 200 ms, it has been argued that, when induced by faces, the N170 reflects the recognition of a stimulus as a face, as shown by face-sensitivity effects emerging at the onset of this time window (i.e., 120–130 ms, see Rossion and Jacques, 2008), and the recognition of the face familiarity as an individual, sustained by positive face familiarity effects observed at the peak of this component. There is evidence that these two functions regularly overlap in time. Therefore, it is not yet determined if the familiarity effect of this component is associated with the perceptual awareness of a familiar face (Caharel and Rossion, 2021).

When evoked by faces in comparison to nonface familiar object shapes, N170 shows a more consistent lateralization, a larger amplitude, and earlier peak (Rossion, 2014). A considerable number of studies using personally familiar faces report larger N170 to these stimuli compared to unfamiliar faces. It should also be reinforced that this familiarity effect is usually discovered more frequently in personally familiar than famous faces or experimentally familiarized faces. This may be due to the greater robustness of the neural representations of personally familiar faces, but also to the discrepancy of knowledge of celebrities among the participants of each investigation (Caharel and Rossion, 2021).

Despite all these findings, there is no general agreement concerning the effects of familiarity at the level of this component, and their direction, suggesting that the familiarity effect reported in the N170 is too small and inconsistent throughout the studies to be considered as an electrophysiological marker of face familiarity. Indeed, when balanced across familiarity conditions (i.e., controlling for any potential image-based effects), familiarity effects are observed after 200 ms and therefore after the time window of this component (Wiese et al., 2019b).

Indeed, effects of familiarity have been reported for the N250, a negative deflection observed approximately between 200 and 300 ms across occipto-temporal scalp sites. Displaying a clear sensitivity to facial familiarity, this component is increasingly more negative for familiar faces – including experimentally learned, famous and personally known faces – compared to unfamiliar faces. Studies investigating face repetition support that N250 shows an increased negativity for repeated faces, reflecting the activation of an individual face representation that takes place when new facial identities are being learned (Kaufmann et al., 2009; Tanaka et al., 2006). Moreover, Andrews and collaborators (2017) reported that the N250 can distinguish between familiar and unfamiliar faces even when multiple naturally varying stimuli are being presented. In line with these results, when learned through experience, facial stimuli elicit enhanced negativity of the occipto-temporal N250 when compared to novel faces in the late time window of this component (i.e., 280–400 ms). This enhancement was also shown for famous faces in the earlier time range of N250 (i.e., 180–280 ms; Andrews et al., 2017).

Previous research has focused on the effects of face familiarity during face inversion (Marzi and Viggiano, 2007). Evidence suggests that face inversion leads to a significant delay of the peak latency and an increase of the amplitude at the level of the N170 component. Despite being small (around 10 ms), this delay is highly robust and consistent across studies (Rossion and Gauthier, 2002). A similar effect has been found in P100 (see e.g., Bentin et al., 1996; Itier and Taylor, 2002, 2004; Rossion et al., 2000; Taylor et al., 2001). Rossion and Gauthier (2002) suggest that although these effects are typically measured at the N170 peak, they are likely to originate before 170 ms, initiating between the two components – P100 and N170.

The FIE might reflects the necessity of additional effort to recognize a face. Thus, being true, the effect of familiarity should reduce FIE (i.e., by reducing amplitude and latency of the ERP). The high temporal resolution of the ERP may be an essential tool to unravel the time-course of the processing of upright and inverted faces. Marzi and Viggiano (2007) demonstrated that the N170 component was modulated by familiarity for upright faces but, for inverted faces, the degree of familiarity affected only later components. This is consistent with the need for a longer time course of the familiarity decision task for these types of faces. Moreover, the FIE was more prominent for famous than unknown faces, in other words, with respect to unknown inverted faces, inverted famous faces were discriminated with higher difficulty and greater response speed. These authors justify these results, inconsistent with some previous ERP studies where no interaction between familiarity and the inversion effect was found (Bentin and Deouell, 2000; Eimer, 2000; Schweinberger et al., 2002), by their usage of a task requiring face recognition to the correct mastery of their experiment (Marzi and Viggiano, 2007).

Another area of research on face familiarity concerns how it interacts with facial expressions of emotion. Indeed, to have successful social interactions we have to take into account not only what is known about the other individuals but also their current state, and facial expressions are a fundamental vehicle for such information. Indeed, there is a wealth of research on the processing of facial expressions of emotion (for a comprehensive review see Vuilleumier and Pourtois, 2007, as well as previous work by our group has focused on this topic in early development – Pereira et al., 2019 –, adulthood – Almeida et al., 2016 –, and aging – Gonçalves et al., 2018). It is commonly believed that specialized neural systems in inferotemporal cortex are activated by faces at around 150–200 ms post stimulus onset, which is correspondent to the face selective N170 component. Although a consistent number of studies have found that this face-specific component was not affected by the valence of expressions, meta-analytic evidence supports the emotional modulation of N170 amplitude (Hinojosa et al., 2015). While earlier research hypothesized that the N170 would be mostly sensitive to negative emotions (Vuilleumier and Pourtois, 2007), more recent evidence shows that N170 amplitude seems to be modulated by the arousal of emotional faces regardless of their valence or emotional category (Almeida et al., 2016). Additionally, at around 250 ms after face onset, posterior ERP components are believed to discriminate emotional from neutral expressions. The late ERP responses to emotional faces, posterior to 300 ms, have also been found to be sustained over prolonged periods of time, which may reflect processes triggered by emotional stimuli in addition to the perceptual processing of faces (Vuilleumier and Pourtois, 2007).

With regard to the study of the familiarity effect in the recognition of emotional expressions, Caharel and colleagues (2005) found that the emotional expressions did not interact with the familiarity of faces at both behavioural and electrophysiological levels, supporting the parallel and independent processing of faces defended by the classical models of face processing. However, an accelerated processing speed for faces with more personal importance, as well as an augmented N170 response for faces expressing negative emotions was found. In an evolutionary perspective, both personally familiar and negative faces have a greater association with survival and danger which might explain this result (Caharel et al., 2005). One study by Martens and colleagues (2010) also examined the temporal organization of facial identity and expression and supported the finding that both processes seem to occur in parallel, with facial identity being typically faster analysed than facial expression. However, while some authors assume identity and expression as independent pathways, face perception studies have been challenging this view. Using two distinct experiments, Wild-Wall and colleagues (2008) demonstrated that facial familiarity and expression may not be independent processes: an expression discrimination task showed a faster categorization for personally familiar versus unfamiliar facial stimuli portraying happiness; and a familiarity discrimination task showed an advantage of happiness over disgust for familiar faces.

This study aims to investigate the effect of familiarity in the modulation of the ERPs associated with face processing when a face is inverted and expressing an emotion. Although previous studies have attempted to study the interactions between these processes, there is still a large field to explore in this area considering that, for example: (1) there is a lack of studies with a complete paradigm which would include personally familiar faces to the study of facial inversion effect, in addition to famous and unknown facial stimuli; (2) the grand majority of studies fail to find methodological ways to ensure that the level of familiarity that participants have with personally familiar and famous facial stimuli is equivalent; (3) and the relationship between the neural response of emotional identification and the recognition of a face as familiar is not yet determined (Caharel and Rossion, 2021).

With this purpose, two experimental tasks were developed. Firstly, with the aim to study facial processing, facial stimuli of three different categories of familiarity were presented in a Face Processing Task: (1) personally familiar faces (of family or very close friends), to explore the effect of familiarity and affective proximity; (2) famous familiar faces (of celebrities), to investigate the effect of familiarity without the influence of affective connections; and (3) unfamiliar faces. To this end participants known and unknown to each other were recruited and their photos were identified as "personally familiar" and "unfamiliar", faces of famous individuals were then used to the "famous familiar" category in conformity with the indication of each participant. With the purpose to explore the role of familiarity in the FIE, these stimuli were also presented in inverted form. Secondly, to study the effects of familiarity on emotion identification abilities, an Emotion Identification Task was conducted, composed of these personally familiar and unfamiliar faces displaying facial expressions of happiness, sadness, disgust, fear, anger, surprise, and neutral. Both tasks were performed during EEG recordings to allow the extraction of the neural correlates of face processing presented above.

With respect to the first task, stronger evidence appears to be needed to determine the effects of face inversion at the level of later ERP components. Therefore, with the presentation of inverted faces, amplitude increases and a delay at the level of the components analysed in the present study can be expected (H1). We also expected that the amplitudes of the ERP components will be higher with the increase of familiarity of each face (H2). In other words, higher amplitudes of each ERP component are expected for personally familiar faces than for unfamiliar faces (H2.1), for famous than for unfamiliar faces (H2.2), and for personally familiar faces than famous faces (H2.3). This can be explained by the greater robustness of the neural representations for these stimuli, which may induce extra neural processes to the ones already prompted by facial identification (e.g., affective processes and autobiographical information related to the individual recognized; Caharel and Rossion, 2021; Wiese et al., 2019a).

As far as we know, studies using personally familiar faces during the presentation of upright and inverted faces have been scarce. Thus, we hypothesize a relationship between familiarity and the FIE with the inclusion of this new level of familiarity (H3). However it is uncertain what the direction of this effect may be: (1) it is possible that the FIE can persist through the different levels of familiarity as defended by the previous research advocating the FIE as independent of the familiarity of faces (see e.g., Collishaw and Hole, 2000; Yarmey, 1971); (2) or, in contrast, the FIE can be less expressive as the familiarity of faces increases, given the evidence that familiarity improves the recognition of facial stimuli, even when the face is inverted.

Regarding the second task, based on previous findings concerning the effects of familiarity on the recognition of social cues (e.g., Caharel and Rossion, 2021), a better performance in the identification of FEE with the increase of facial familiarity can be predicted (H4).

2. Method

2.1. Participants

To obtain facial stimuli of personally familiar individuals, we recruited participants in triads, where the three people within the triad had close relationships to each other (family or close friends), but were unknown to members of other triads. Eleven triads of participants were recruited from the local university and community, composing a total sample of 33 healthy adults. Nonetheless, one participant dropped out the study before the second session, originating a final sample of 32 participants (25 female; age: $M = 27.7$ years, $SD = 9.3$). One participant was excluded in task 2 due to an error in the recording of the EEG signal. The current study was favourably appraised by the local Ethics Committee. All participants provided written informed consent to participate in the study, accordingly with the Declaration of Helsinki.

2.2. Procedures

2.2.1. Session 1

To avoid fatigue effects, participants were tested individually in two different sessions. The first session included the collection of demographic information and information regarding the inclusion/exclusion criteria. We included healthy participants between 20 and 65 years of age, both men and women, with more than four years of formal education. Participants would be excluded if they reported uncorrected visual impairments. The participants who meet the inclusion criteria were invited to the second session of data collection. The photographs of participants displaying FEE were also collected during the first session. For the personally familiar category we included the photographs of the members of each participants triad. For the unfamiliar category, photographs of the members of other triads were included, pseudo-randomly selected to have similar demographic characteristics to the triad of each participant. Moreover, to select the famous faces, each participant was asked to nominate "10 famous persons by order of familiarity" (i.e., beginning with the person with a face that is more familiar). Thus, the famous facial stimuli were retrieved from the internet according to the most known celebrities reported by each participant that had similar demographic characteristics to their loved ones that participated in the study (i.e., age, sex, and ethnicity). Therefore, each participant was presented with facial stimuli of two different individuals of each category of familiarity with the same demographic characteristics between them (two personally familiar faces, two famous faces, and two unknown faces; the famous faces were only used in the Face Processing Task, described below).

2.2.2. Session 2

In the second session, approximately one week after the first, each participant sat inside an EEG chamber and completed two tasks while simultaneously undergoing an EEG recording. Participants were seated with ~115 cm between them and a 17″ screen, where the task was displayed. These tasks were counterbalanced and delivered in E-Prime 2.0 (2011, Psychology Software Tools, Inc., Sharpsburg, PA, USA).

2.2.2.1. Task 1: Face processing task. In this task, neutral expressions of the three categories of familiarity (i.e., personally familiar faces, famous faces, and unfamiliar faces) were presented both in an upright and inverted way. To avoid making this a passive task and to ensure that the participant pays attention to every stimulus, participants were asked to press a button as quickly as possible to pictures of butterflies (these stimuli were randomly selected from an original dataset – Vagnoni et al., 2012 – to be used as targets). The behavioural and EEG data elicited by these stimuli were not analysed.

For the selection of famous stimuli, we used specific criteria to minimize potentially confounding visual characteristics: we chose pictures where the famous person made eye contact with the camera and the photos with less makeup. The stimuli collected during the first session and from the internet were resized in IrfanView Thumbnails (version 4.51; www.irfanview.com) to a resolution of 418 by 600 pixels. Each picture was enclosed within an oval frame using GIMP (version 2.8; www.gimp.org) to eliminate hair and non-facial contours, also ensuring the same number of pixels per stimulus. In a procedure prior to the inclusion of the oval frame, this program also allowed editing the luminance, measured using the "Luminance" tool, and adjusting each image by visual comparison through the "Colors – Brightness-Contrast" menu. In both tasks, each stimulus was presented at a visual angle of $6.89^\circ \times 9.86^\circ$. To assure that both celebrities presented to each participant were actually recognized, after the experiment, participants were asked to select the degree of familiarity with each of the famous stimuli, in a scale from 1 to 7.

This task was composed by 210 experimental trials: 180 neutral faces (60 photographs of loved ones, 60 famous faces, and 60 unfamiliar faces) and 30 butterflies. As each category of familiarity was composed by facial stimuli of two different individuals, each face was repeated 15 times. The task was organized in a practice block (8 practice trials: 4 butterflies and 4 faces randomly selected), and three experimental blocks (with 70 trials each) divided by unlimited pauses. The structure of four trials is depicted in Fig. 1. Participants were instructed to pay attention to every stimulus and press a key to a response box when a butterfly appeared. This task had an approximate duration of 8 min.

2.2.2.2. Task 2: Emotion identification task. This task aimed to assess identification and neural processing of FEE from personally familiar (loved ones) and unfamiliar faces. Thereby, stimuli included different facial expressions (i.e., neutral, happiness, sadness, disgust, fear, anger, and surprise) taken in the first experimental session. Once again, for the personally familiar category of stimuli, each participant saw photographs of the members of their triad. For the unfamiliar category, participants were presented with photographs of the members of other triads pseudo-randomly selected to have similar demographic characteristics to the triad of each participant.

This task was composed by 420 experimental trials: 30 photographs of loved ones and 30 photographs of unfamiliar faces, displaying the seven emotional expressions. The organization of the task consisted in a practice block (3 trials), and three experimental blocks (with 140 trials each) divided by an unlimited pause. Participants were asked to categorise the emotions displayed by the facial stimuli on a response slide displaying labels of the seven emotions (1. Neutral, 2. Happiness, 3. Sadness, 4. Disgust, 5. Fear, 6. Anger, and 7. Surprise). Each participant was instructed to respond in the response slide, to ensure that artifacts of preparatory response potentials during the facial stimuli were avoided.

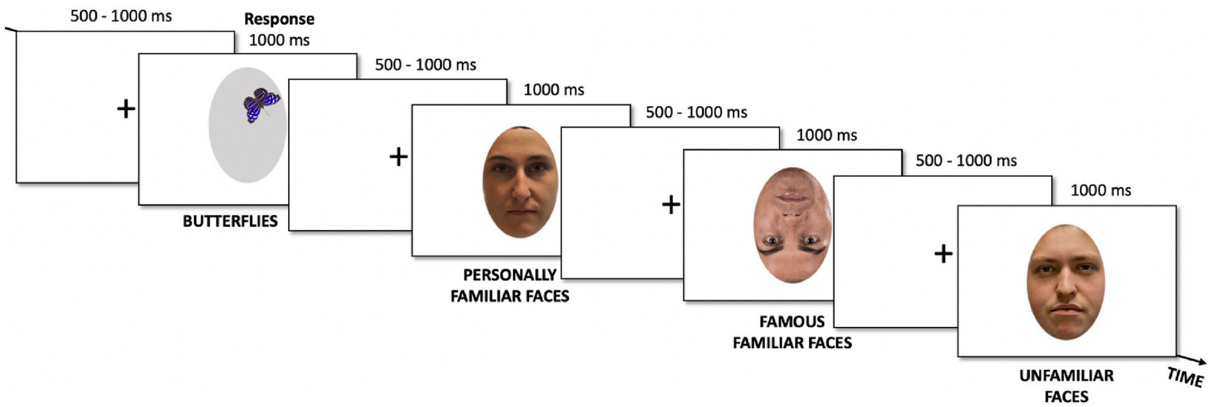

Fig. 1. Schematic representation of the Face Processing Task (Task 1)
Note. The facial stimuli depicted in the figure are not the actual stimuli used (not shown to safeguard the privacy of the participants) and are part of an open-access set of facial stimuli (Conley et al., 2018) used here only for illustrative purposes.

This task had a duration of approximately 21 min. Fig. 2 presents a scheme of two trials of this task.

2.2.3. EEG recording and signal processing

The electroencephalographic (EEG) data recorded from both tasks was recorded through the NetStation V4.5.2 software (2008, Electrical Geodesics Inc., Eugene, OR, USA – EGI), using a 128-electrode HydroCel Geodesic Sensor Net connected to a Net Amps 300 amplifier (EGI). Impedances were kept below 50 kOhm for all electrodes (as this is a high impedance system). Data was recorded with a sampling rate of 500 Hz and the electrodes were referenced to the vertex (Cz). The pre-processing of the raw data was conducted through EEGLAB (version 2021.0; Delorme and Makeig, 2004) a toolbox of MATLAB (version 2017b, The Mathworks Inc., Natick, MA, USA). Firstly, the EEG signal was downsampled to 250 Hz, bandpass filtered (0.1–30 Hz), and bad channels were removed (maximum of 10% of the electrodes). Then, data was decomposed in Independent Components Analysis (ICA) and artifacts (i.e., eye blinks, saccades, and heart rate) were corrected through the subtraction of the respective activity of these components from the data. Channels previously removed were subsequently interpolated, the signal was re-referenced offline to the average of all electrodes and segmented into epochs ranging from −200 to 800 ms time-locked to faces onset. Every segment was then visually inspected, and the remaining artifacts were manually rejected. All epochs were baseline corrected (200 ms pre-stimulus) and averaged by condition.

For peak scoring, two regions where peaks were most prominent (maximum positive/negative voltage) and consistent with the previous literature were chosen through the inspection of the topographical maps. The P100 was measured at O1/O2 cluster (O1: electrodes 65, 66, 70, 71; O2: 76, 83, 84, 90), while the N170 and N250 were measured at P7/P8 cluster (P7: 50, 57, 58, 63, 64; P8: 95, 96, 99, 100, 101). The peak amplitudes and latencies were measured in the time window of 100–200 ms after stimulus onset for the P100, 150–255 ms for the N170, and 250–360 ms for the N250 (see Figs. 3 and 4).

2.3. Statistical analysis

2.3.1. Behavioural Results

For the Face Processing Task (Task 1) the percentage of accuracy and reaction times were analysed. For Task 2 (Emotion Identification Task), accuracy rates were computed for each participant, emotional condition (neutral, happiness, sadness, disgust, fear, and anger), and familiarity (personally familiar and unfamiliar faces). The results of Task 2 were analysed through repeated measures ANOVAs (rmANOVAs), with *familiarity* and *emotion* as within-participants factors.

2.3.2. Electrophysiological results

For Task 1, rmANOVAs were computed to analyse the effects of *familiarity* (personally familiar faces, famous faces, unfamiliar faces), *orientation* (inverted, upright) and *hemisphere* (left, right) – all within-participants factors – on the amplitude and latency of the P100, N170, and N250. For Task 2, rmANOVAs were computed to analyse the effects of *familiarity* (personally familiar faces, famous faces, unfamiliar faces), *emotion* (neutral, happiness, sadness, disgust, fear, anger, and surprise) and *hemisphere* (left, right) – within-participants factors – on the amplitude and latency of the P100, N170, and N250.

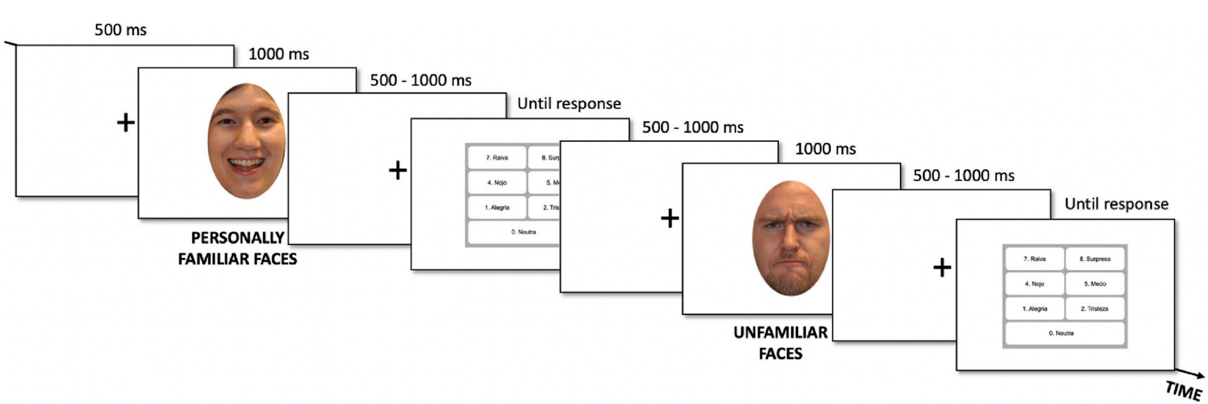

Fig. 2. Schematic representation of the Emotion Identification Task (Task 2)
Note. The facial stimuli depicted in the figure are not the actual stimuli used (not shown to safeguard the privacy of the participants) and are part of an open-access set of facial stimuli (Conley et al., 2018) used here only for illustrative purposes.

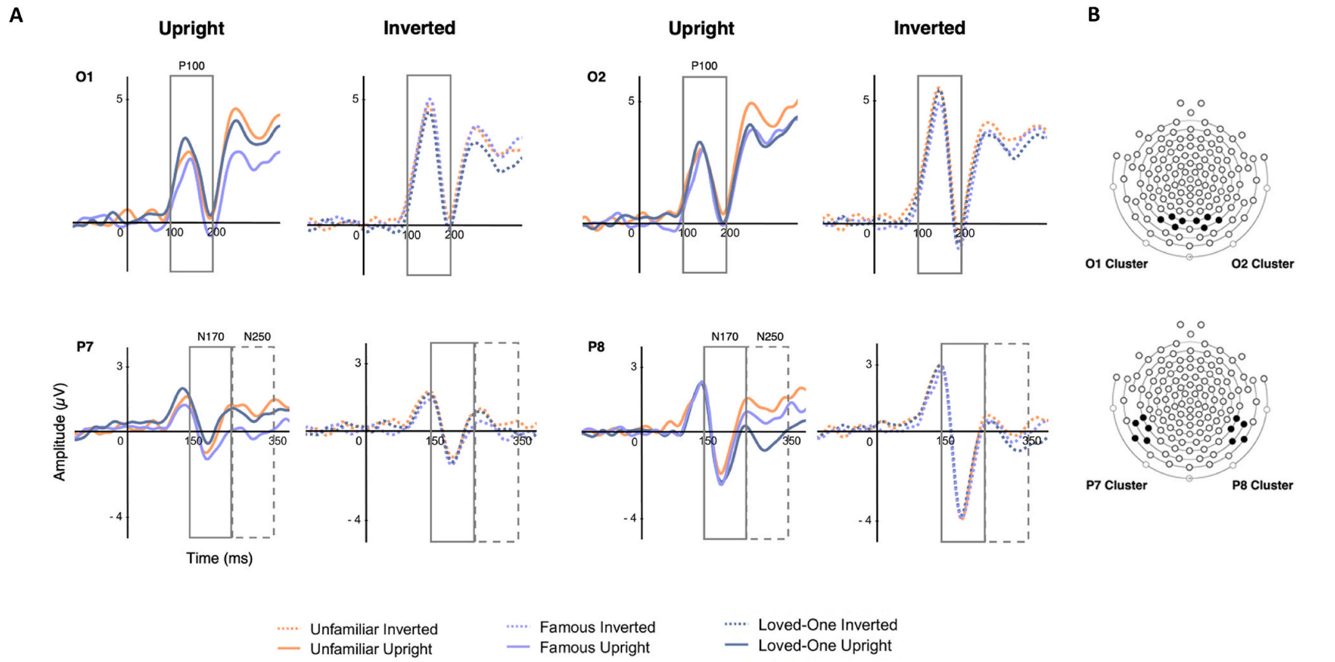

Fig. 3. A: Grand averages of P100, N170, and N250 peak amplitudes when faces of the three categories of familiarity were presented (personally familiar, famous, unfamiliar) in an upright and inverted orientation (results from Task 1). B: Electrode locations of O1/O2 and P7/P8 Clusters in the 128-channel HydroCel.

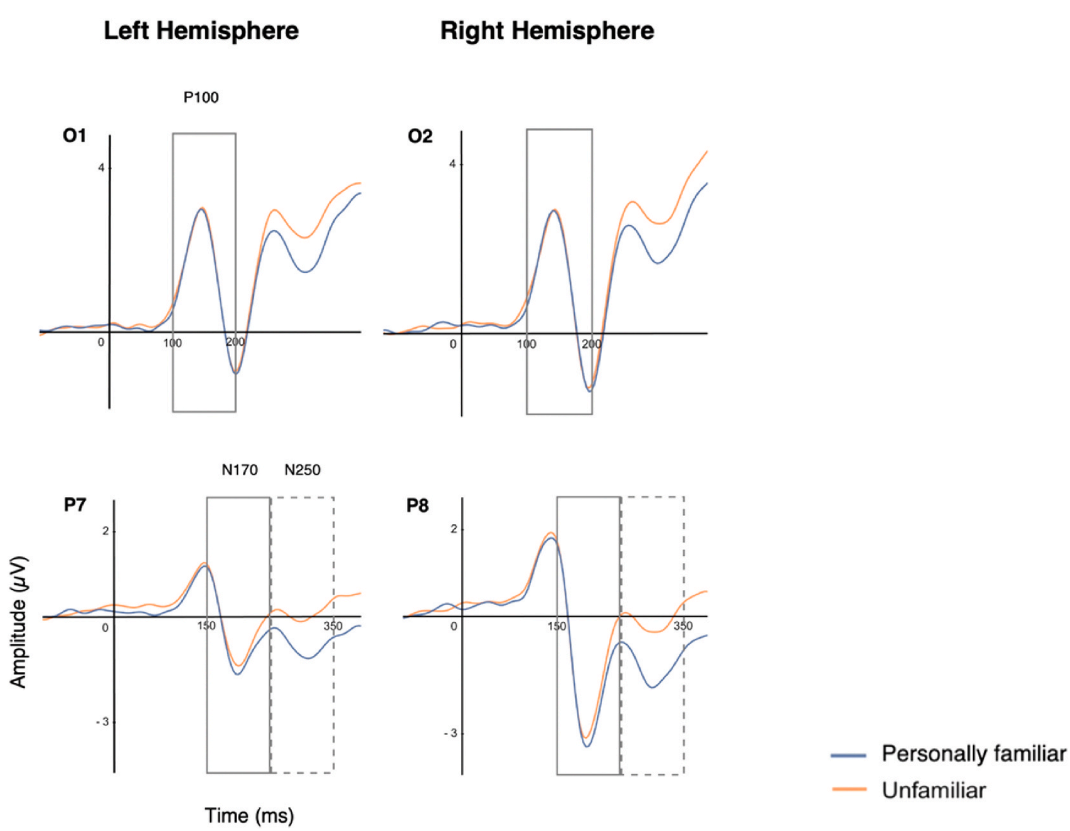

Fig. 4. Grand averages of P100, N170, and N250 peak amplitudes when personally familiar versus unfamiliar faces were presented (results from Task 2) Note. As no significant differences were found according to emotion, the results for personally familiar faces and unfamiliar faces were concatenated.

The threshold for statistical significance was set at $\alpha = 0.05$ for all analyses. In case of a violation of sphericity, Greenhouse-Geisser corrected results were reported. Post-hoc pairwise comparisons were corrected to multiple comparisons using the Bonferroni correction. All statistical analyses were carried out using SPSS software, version 27 (IBM Corp., Armonk, NY, USA).

3. Results

Descriptive statistics of the demographic information and self-report measures can be found in the Supplementary Material (Table 1), along with the descriptive statistics of ERP amplitudes obtained for both experimental tasks (Tables 2 and 3, respectively).

3.1. Behavioural results

3.1.1. Face processing task (Task 1)

For the manipulation check conducted we found that the participants were attentive during this task as we obtained an average of 99.7% for accuracy rates ($SD = 0.4$) and of 427.6 ms for reaction time ($SD = 47.32$).

3.1.2. Emotion identification task (Task 2)

A main effect of *familiarity* was found $F(1, 30) = 4.88$, $p = .035$, $\eta_p^2 = .140$, revealing higher accuracy rates for familiar ($M = 79.9$, $SD = 2.1$) compared to unfamiliar faces ($M = 76.0$, $SD = 1.8$). A main effect of *emotion* was also found, $F(6, 180) = 43.94$, $p < .001$, $\eta_p^2 = .594$, $\varepsilon = 0.598$, showing that happiness ($M = 98.1$, $SD = 0.9$) and neutral expressions ($M = 95.0$, $SD = 1.5$) were more accurately identified compared with the others (all $ps < .001$). The identification of fear ($M = 41.7$, $SD = 3.7$) was significantly less accurate than the other emotions (Anger: $M = 81.3$, $SD = 3.5$; Disgust: $M = 76.3$, $SD = 3.7$; Sadness: $M = 77.8$, $SD = 3.7$; Surprise: $M = 75.6$, $SD = 3.5$; all $ps < .001$). The familiarity*emotion interaction was also significant, $F(6, 180) = 3.40$, $p = .011$, $\eta_p^2 = .102$, $\varepsilon = 0.685$, revealing that fear (Familiar: $M = 47.5$, $SD = 4.6$; Unfamiliar: $M = 35.8$, $SD = 4.5$; $p = .034$) and neutral expressions (Familiar: $M = 97.5$, $SD = 1.2$; Unfamiliar: $M = 92.5$, $SD = 2.3$; $p = .030$) were better recognized when expressed by familiar faces. However, the emotion of surprise was better recognized in unfamiliar faces (Familiar: $M = 69.2$, $SD = 4.3$; Unfamiliar: $M = 81.9$, $SD = 69.2$; $p = .002$).

3.2. Electrophysiological results

3.2.1. Face processing task (Task 1)

3.2.1.1. P100. For the P100 peak amplitude, we did not find a main effect of *familiarity,* $F(2, 62) = 2.26$, $p = .113$, $\eta_p^2 = .068$, but we found a main effect of *orientation,* $F(1, 31) = 48.35$, $p < .001$, $\eta_p^2 = .609$, showing that inverted faces ($M = 6.0$, $SD = 0.7$) elicited higher amplitudes than upright faces ($M = 4.4$, $SD = 0.6$). The familiarity*orientation interaction was non-significant $F(2, 62) = 1.47$, $p = .238$, $\eta_p^2 = .045$. Regarding latencies, no main effects of *familiarity* were found, $F(2, 62) = 1.21$, $p = .307$, $\eta_p^2 = .037$. However, a main effect of *orientation* was found, $F(1, 31) = 13.68$, $p < .001$, $\eta_p^2 = .306$, revealing that inverted faces ($M = 153.5$, $SD = 2.0$) elicited higher latencies than upright faces ($M = 149.0$, $SD = 2.5$). The remaining main effects and interactions were non-significant for the P100 peak amplitude and latency (all $ps > .113$).

3.2.1.2. N170. For the N170 peak amplitude, we did not find a main effect of *familiarity,* $F(2, 62) = 0.79$, $p = .438$, $\eta_p^2 = .025$. However, we found a main effect of *orientation,* $F(1, 31) = 23.20$, $p < .001$, $\eta_p^2 = .428$, showing that inverted faces ($M = -3.7$, $SD = 0.6$) elicited higher N170 peak amplitudes than upright faces ($M = -2.6$, $SD = 0.5$). A main effect of *hemisphere,* $F(1, 31) = 28.60$, $p < .001$, $\eta_p^2 = .480$, was also found, revealing significantly higher amplitudes in the right hemisphere ($M = -4.3$, $SD = 0.4$) compared to the left hemisphere ($M = -2.1$, $SD = 0.7$). We did not find a significant familiarity*orientation interaction, $F(2, 62) = 0.80$, $p = .456$, $\eta_p^2 = .025$. However, the orientation*hemisphere interaction was significant, $F(1, 31) = 12.25$, $p < .001$, $\eta_p^2 = .283$, showing that, in the right hemisphere, the N170 peak amplitude was significantly higher for inverted ($M = -5.1$, $SD = 0.8$) than upright faces ($M = -3.4$, $SD = 0.6$). No other significant main effects or interactions emerged (all $ps > .289$).

Regarding latencies, we also did not find a significant effect of *familiarity*, $F(2, 62) = 0.920$, $p = .404$, $\eta_p^2 = .029$. We also did not find a significant orientation*familiarity interaction $F(2, 62) = 2.42$, $p = .097$, $\eta_p^2 = .072$, the familiarity*orientation*hemisphere interaction was significant, $F(2, 62) = 4.77$, $p = .023$, $\eta_p^2 = .133$, $\varepsilon = 0.712$, showing that, in the left hemisphere, the upright unfamiliar faces ($M = 197.6$, $SD = 2.8$) elicited lower latencies than upright famous faces ($M = 206.4$, $SD = 2.9$), and higher latencies than the upright personally familiar faces ($M = 196.9$, $SD = 2.7$). The remaining main effects and interactions were non-significant (all $ps > .404$).

3.2.1.3. N250. For the N250 peak amplitudes, we found a main effect of *familiarity,* $F(2, 62) = 3.70$, $p = .040$, $\eta_p^2 = .107$, $\varepsilon = 0.784$, revealing significantly higher N250 peak amplitudes for famous faces ($M = -1.0$, $SD = 0.4$) in comparison to unfamiliar faces ($M = -0.4$, $SD = 0.4$). However, the difference between personally familiar and unfamiliar or famous faces were non-significant (both $ps > .076$). We also found a main effect of *orientation,* $F(1, 31) = 6.91$, $p = .013$, $\eta_p^2 = .182$, showing that inverted faces ($M = -1.1$, $SD = 0.4$) elicited higher amplitudes than upright faces ($M = -0.6$, $SD = 0.4$). No significant orientation*familiarity interaction was found, $F(2, 62) = 1.38$, $p = .257$, $\eta_p^2 = .043$. However, we found a significant familiarity*hemisphere interaction, $F(2, 62) = 4.71$, $p = .012$, $\eta_p^2 = .132$, showing that, in the left hemisphere, the amplitudes were significantly higher for famous faces ($M = -1.1$, $SD = 0.5$) than unfamiliar faces ($M = -0.3$, $SD = 0.5$). In the right hemisphere, the personally familiar faces ($M = -1.8$, $SD = 0.6$) elicited significantly higher amplitudes than unfamiliar faces ($M = -0.6$, $SD = 0.4$). Regarding latencies, we did not find a main effect of *familiarity,* $F(2, 62) = 1.98$, $p = .147$, $\eta_p^2 = .060$. However, we found a main effect of *orientation,* $F(1, 31) = 5.78$, $p = .022$, $\eta_p^2 = .157$, revealing higher latencies for inverted ($M = 311.4$, $SD = 1.9$) in comparison to upright faces ($M = 307.4$, $SD = 1.7$). The remaining main effects and interactions were non-significant (all $ps > .130$).

3.2.2. Emotion identification Task (Task 2)

3.2.2.1. P100. We did not find a main effect of *familiarity* $F(1, 30) = 0.32$, $p = .578$, $\eta_p^2 = .010$ for the P100 peak amplitude. We found a main effect of *emotion,* $F(6, 180) = 2.81$, $p = .012$, $\eta_p^2 = .086$. However, after correcting for multiple comparisons, the post-hoc tests did not reveal significant contrasts between emotional categories. No other significant main effects or interactions emerged for the P100 peak amplitude and latency (all $ps > .203$).

3.2.2.2. N170. For the N170 peak amplitude, we did not find a main effect of *familiarity,* $F(1, 30) = 2.15$, $p = .153$, $\eta_p^2 = .067$, but we found a main effect of *hemisphere,* $F(1, 30) = 18.55$, $p < .001$, $\eta_p^2 = .382$, showing that the right hemisphere ($M = -4.3$, $SD = 0.6$) had higher amplitudes compared to the left hemisphere ($M = -2.2$, $SD = 0.4$). We did not find a significant emotion*familiarity interaction, however a significant familiarity*emotion*hemisphere interaction was found, $F(6, 180) = 2.45$, $p = .026$, $\eta_p^2 = .076$. According to this interaction, on the right hemisphere, anger familiar faces elicited significantly higher N170 peak amplitude ($M = -5.0$, $SD = 0.7$) than unfamiliar faces ($M = -3.8$, $SD = 0.7$). Regarding N170 latency, the main effect of *familiarity* was also not found, $F(1, 30) = 1.21$, $p = .281$, $\eta_p^2 = .039$. All the remaining main effects and interactions were non-significant (all $ps > .147$).

3.2.2.3. N250. A main effect of *familiarity* was found for the N250 peak amplitude, $F(1, 30) = 14.32$, $p < .001$, $\eta_p^2 = .323$, revealing higher amplitudes for personally familiar ($M = -2.3$, $SD = 0.5$) than for unfamiliar faces ($M = -1.3$, $SD = 0.4$). Additionally, a main effect of *emotion* was also obtained, $F(6, 180) = 3.02$, $p = .022$, $\eta_p^2 = .091$, $\varepsilon = 0.641$, but the post-hoc tests did not reveal significant contrasts between emotional categories. Regarding latencies, it was discovered a main effect of *familiarity,* $F(1, 30) = 7.45$, $p = .010$, $\eta_p^2 = .199$, showing higher latencies for personally familiar faces ($M = 308.0$; $SD = 1.7$) than unfamiliar faces ($M = 305.3$; $SD = 1.7$). No other main effects and interactions were found (all $ps > .101$).

4. Discussion

A strong relationship between familiarity and face processing has been reported in the literature advocating that this process is optimized in familiar faces – specially personally familiar faces (e.g., Bruck et al., 1991; Caharel and Rossion, 2021; Ramon and Gobbini, 2018; Rossion, 2014). The present study aimed to explore this improvement by analysing the neural processes elicited by inverted and emotional faces with different levels of familiarity. Concerning the first task, we hypothesized increased amplitudes and latencies of the ERP components for inverted than upright faces (H1), but we also explored if the familiarity of the face maintained or attenuated the face inversion effect. Similarly, it was hypothesized that, with the increase of the facial familiarity, the ERP amplitudes would be higher (H2) and, in relation to the second task, the participants would have a better performance in the identification of FEE (H3).

4.1. Face Processing Task

At a behavioural level, our manipulation check reveals a ceiling effect of the responses which shows us that the participants were attentive during the task. At a neural level, there were no main effects of familiarity on the amplitudes and latencies of the first two components (P100 and N170), partially refuting our second hypothesis. Regarding the N170, in the right hemisphere, upright personally familiar faces elicited larger peak amplitude than upright unfamiliar faces. In line with these findings, in the left hemisphere, upright famous faces elicited larger N170 latency than upright unfamiliar faces.

Our hypothesis was based on evidence suggesting greater robustness of the neural representations for more familiar stimuli, which might induce extra neural processes (e.g., related to affective processes and autobiographical information from the individual recognized; Caharel and Rossion, 2021; Wiese et al., 2019a; Caharel and Rossion, 2021). However, as we did not find a main effect of familiarity for the P100 and N170 amplitudes and latencies, our results do not support this hypothesis for the temporal windows of these components. However, the significant familiarity*orientation*hemisphere interactions found for these components further suggests punctual increased amplitudes and latencies for familiar faces compared to unfamiliar faces, as well as for famous faces compared to unfamiliar faces.

In contrast, for the N250 component, the results concerning familiarity are partially consistent with our expectations. We found a higher N250 peak amplitude for famous than for unfamiliar faces, despite the difference between personally familiar and famous or unfamiliar faces being non-significant. Additionally, we obtained a significantly larger N250 peak amplitude for famous than for unfamiliar faces in the left hemisphere, as well as for personally familiar than unfamiliar faces in the right hemisphere. Higher neural responses following increased familiarity are supported in the literature and appear to occur as a result of the robustness of the neural representations prompted by familiar faces. These faces not only induce neural processes regarding facial identification, but also affective processes related to memories and autobiographical information (Caharel and Rossion, 2021).

It is interesting to note that the P100 component, as the major visual component (Luck, 2014), seems to translate a basic visual processing of information. The results for the N170 component, in turn, appear to be explained by the detection of information related to the face in the visual field (i.e., processing of different components of the face) that allows the distinction of the face from any other object. Our results suggest that both processes may be similar for both familiar and unfamiliar faces. Since the N250 component may translate the comparison of sensorial inputs with the ones already stored in memory, its increased amplitude for famous and personally familiar faces, in comparison with unfamiliar faces, may be explained by the increased amount of information stored in memory for the former categories of stimuli. This finding is consistent with the variety of studies that have been associating the N250 component to the familiarity of faces as a robust neural index of facial familiarity (Sommer et al., 2021; Tanaka et al., 2006; Wiese et al., 2019b). Recent evidence suggests that this ERP component embodies robust visual representations that are successively refined with the increasing exposure to a specific face, which is the case of famous and personally familiar faces (Wiese et al., 2021).

We obtained larger peak amplitudes of the P100, N170, and N250 for inverted faces in comparison to upright faces. This is in agreement with our first hypothesis and the literature concerning the Face Inversion Effect (see e.g., Bentin et al., 1996; Itier and Taylor, 2002, 2004; Jacques and Rossion, 2007; Rossion et al., 2000; Rossion and Gauthier, 2002; Taylor et al., 2001). A delayed latency was found at the level of the P100 and N250. Surprisingly, in the time window of the N170 the differences were not significant. This component is typically delayed in face inversion, an event that also happens when face features are displaced, removed, or masked, or even when isolated features are presented. This demonstrates that the inversion of a face causes a disruption of our expert use of local relational information between parts of the faces (Rossion and Gauthier, 2002). This latency effect can reflect a delayed activation of face representations or a slower enrolment of neural activity when the faces are displayed in these unusual views (Jacques and Rossion, 2007). A particularly striking aspect of this lack of latency results is that, as speculated by Jacques and Rossion (2007), the phenomenon that may explain the amplitude effect expected for inverted faces may be the same for the latency effect.

The absence of a significant orientation*familiarity interaction at this level is worth mentioning. This result is inconsistent with the Marzi and Viggiano (2007) findings where the later components (e.g., P250) were actually found to be modulated by the degree of familiarity in inverted faces. However, our results are supported by previous studies suggesting that the FIE is independent of the degree of face familiarity, persisting through the different levels of familiarity (see e.g., Collishaw and Hole, 2000; Yarmey, 1971). This is inconsistent with the familiarity effect, as it should enhance the recognition of faces and therefore could make the FIE less expressive with the increase of familiarity. However, possible explanations for these results may be: (1) the nature of the task, as defended by Marzi and Viggiano (2007), their finding of a significant interaction between orientation and familiarity may have been due to the use of a task that required face recognition to be correctly executed; (2) and the lack of statistical power to turn possible the observation of the familiarity effect in this task. This later limitation can also explain the lack of ambiguity regarding the second hypothesis, through the results of this first task, more specifically from the N170 component outcomes.

4.2. Emotion identification task

At a behavioural level, we found that the participants had better results in the identification of emotions displayed in personally familiar than unfamiliar faces. This result supports our third hypothesis and previous findings systematically advocating that there is an optimization in terms of performance as the familiarity of faces increases (e.g., Caharel and Rossion, 2021; Ramon and Gobbini, 2018). There is no doubt of the crucial social purpose of this improvement: to enrich social interactions with relevant persons (Ramon and Gobbini, 2018). However, previous evidence also suggests otherwise as Caharel and colleagues (2005) support a parallel and independent facial processing at the level of familiarity and emotional expressions consistent with their finding that familiarity did not interact with emotional expression at both behavioural and electrophysiological levels. This inconsistency can be due to the discrepancy between the personally familiar stimuli used in our study and "faces with personal importance" used in this study (i.e., the subject's own face and the face of the subject's mother). In contrast with this paradigm, in the personally familiar category of stimuli our study included faces of individuals that each participant chose to bring as loved-ones, a method that attempted to "standardise" the degree of proximity between each participant and their loved ones.

We also found that fearful and the neutral expressions were better recognized when displayed in personally familiar than unfamiliar faces, but the same did not happen with the expression of surprise, better recognized when expressed by unfamiliar faces. A possible explanation for this inconsistency may be related to the well-known trade-off between the control of the stimuli and ecological validity (Ferreira-Santos, 2015). In favour of the ecological validity of the study, the photographs were taken without asking participants to remove any visible accessories (e.g., glasses), and kept in the original colors. Nevertheless, multiple steps to ensure the control of the stimuli were also taken (i.e., the effort to take all the photographs in the same conditions, the preparation of standard instructions for the training of each FEE with the participants, the edition of changes in luminance/contrast, and the inclusion of an oval mask). The effort to reduce the variability of the stimuli is a plausible factor of the lack of consistency and effects throughout the different emotions. For example, the usage of standard instructions may possibly have led the participants to fake their expression of the emotions, while a more "open" instruction, (e.g., example of a situation that would elicit the intended facial expression) could have elicited more genuine expressions that would facilitate their detection by their loved ones.

At a neural level, the results of this task were consistent with the results of our Face Processing Task. In the P100 and N170 time-windows, there were no main effects found for amplitudes and latencies, but personally familiar anger faces elicited higher N170 amplitudes than unfamiliar anger faces in the right hemisphere. Regarding the N250 component, we found a larger amplitude and latency for personally familiar than unfamiliar faces, allowing a more robust confirmation of our hypothesis for the neural processing of familiar faces occurring on this time-window. As this task has more trials per familiar conditions than the previous one, it has increased statistical power. Moreover, the lack of significant emotion*familiarity interaction, may suggest that the effect of familiarity on this ERP component is related to the identification of the identity of the face, independently of the emotion expressed.

Although the higher number of trials per condition for this task can be seen as an advantage to find more robust results, it can also be seen as a limitation. The necessity of repeating stimuli comes from the denoising method used in ERP analysis, namely averaging evoked activity over trials to attenuate noise while maintaining the signal present. However, it is recognizable that this factor corresponds to a major limitation of this study as it may raise issues due to the lack of variability of the stimuli. As has been demonstrated in previous research, the absence of familiarity effects (i.e., differences between conditions) can be related to image repetition (Wiese et al., 2019b, 2022). This limitation has important implications for future research: it is strongly advisable that future studies make greater efforts to collect and create stimuli with greater variability of identities and angles of the same faces to diminish the effects of stimuli repetition.

5. Conclusion

The present study has revealed a general enhanced response of the P100, N170, and N250 for inverted faces in comparison to upright faces. However, the facial familiarity does not seem to reduce the face inversion effect, as suggested by the lack of a significant interaction between face inversion and familiarity. Additionally, we found a higher N250 response for personally familiar faces in comparison to unfamiliar ones. This result supports the reasoning that the facial familiarity increases the neural activity during the N250 time-window, which may be explained by the processing of additional information prompted by the viewing of our loved ones faces, in contrast to what happens with unfamiliar individuals. The absence of familiarity results concerning the P100 and N170 reflects the immediate nature of these components in facial processing, previous to the awareness of the identity of the face, giving us insights about the timing of facial familiarity recognition. Lastly, one of the most obvious findings to emerge from this study is that facial familiarity improves the identification of facial expressions of emotion, as systematically reported across the literature (e.g., Caharel and Rossion, 2021).

Our findings provide a new understanding of familiarity effects on facial processing, as we examined the facial inversion effect on personally familiar faces, along with famous and unknown ones. Our approach also included an efficient method to ensure equivalent proximity levels between each participant with both personally familiar and famous faces. Altogether, these findings contribute to the ongoing exploration of facial familiarity and its relation to face inversion effect and facial emotion processing.

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Credit author statement

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Declaration of competing interest

The authors have no conflicts of interest to disclose.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108623.

References

Ambrus, G.G., Eick, C.M., Kaiser, D., Kovács, G., 2021. Getting to know you: emerging neural representations during face familiarization. J. Neurosci. 41 (26), 5687–5698. https://doi.org/10.1523/JNEUROSCI.2466-20.2021.

Ambrus, G.G., Kaiser, D., Cichy, R.M., Kovács, G., 2019. The neural dynamics of familiar face recognition. Cerebr. Cortex 29 (11), 4775–4784. https://doi.org/10.1093/cercor/bhz010.

Almeida, P.R., Ferreira-Santos, F., Chaves, P.L., Paiva, T.O., Barbosa, F., Marques-Teixeira, J., 2016. Perceived arousal of facial expressions of emotion modulates the N170, regardless of emotional category: time domain and time–frequency dynamics. Int. J. Psychophysiol. 99, 48–56. https://doi.org/10.1016/J.IJPSYCHO.2015.11.017.

Amodio, D.M., Bartholow, B.D., Ito, T.A., 2014. Tracking the dynamics of the social brain: ERP approaches for social cognitive and affective neuroscience. Soc. Cognit. Affect Neurosci. 9 (3), 385–393. https://doi.org/10.1093/scan/nst177.

Andrews, S., Burton, A.M., Schweinberger, S.R., Wiese, H., 2017. Event-related potentials reveal the development of stable face representations from natural variability. Q. J. Exp. Psychol. 70 (8), 1620–1632. https://doi.org/10.1080/17470218.2016.1195851.

Bayer, M., Berhe, O., Dziobek, I., Johnstone, T., 2021. Rapid neural representations of personally relevant faces. Cerebr. Cortex 31 (10), 4699–4708. https://doi.org/10.1093/cercor/bhab116.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cognit. Neurosci. 8 (6), 551–565. https://doi.org/10.1162/jocn.1996.8.6.551.

Bentin, S., Deouell, L.Y., 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. Cogn. Neuropsychol. 17 (1), 35–55. https://doi.org/10.1080/026432900380472.

Bruck, M., Cavanagh, P., Ceci, S.J., 1991. Fortysomething: recognizing faces at one's 25th reunion. Mem. Cognit. 19 (3), 221–228. https://doi.org/10.3758/BF03211146, 1991 19:3.

Bruce, V., Young, A., 1986. Understanding face recognition. Br. J. Psychol. 77, 305–327.

Caharel, S., Courtay, N., Bernard, C., Lalonde, R., Rebaï, M., 2005. Familiarity and emotional expression influence an early stage of face processing: an electrophysiological study. Brain Cognit. 59 (1), 96–100. https://doi.org/10.1016/j.bandc.2005.05.005.

Caharel, S., Rossion, B., 2021. The N170 is sensitive to long-term (personal) familiarity of a face identity. Neuroscience 458, 244–255. https://doi.org/10.1016/j.neuroscience.2020.12.036. Elsevier Ltd.

Collishaw, S.M., Hole, G.J., 2000. Featural and configurational processes in the recognition of faces of different familiarity. Perception 29 (8), 893–909. https://doi.org/10.1068/p2949.

Conley, M.I., Dellarco, D.V., Rubien-Thomas, E., Cohen, A.O., Cervera, A., Tottenham, N., Casey, B.J., 2018. The racially diverse affective expression (RADIATE) face stimulus set. Psychiatr. Res. 270, 1059–1067. https://doi.org/10.1016/j.psychres.2018.04.066.

Delorme, A., Makeig, S., 2004. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134 (1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009.

Di Russo, F., Martínez, A., Sereno, M.I., Pitzalis, S., Hillyard, S.A., 2002. Cortical sources of the early components of the visual evoked potential. Hum. Brain Mapp. 15 (2), 95–111. https://doi.org/10.1002/hbm.10010.

Eimer, M., 2000. Event-related brain potentials distinguish processing stages involved in face perception and recognition. Clin. Neurophysiol. 111 (4), 694–705. https://doi.org/10.1016/s1388-2457(99)00285-0.

Ferreira-Santos, F., 2015. Facial emotion processing in the laboratory (and elsewhere): tradeoffs between stimulus control and ecological validity. AIMS Neurosci. 2 (4), 236–239. https://doi.org/10.3934/Neuroscience.2015.4.236.

George, N., 2013. In: Armony, J., Vuilleumier, P. (Eds.), The facial expression of emotions, The Cambridge Handbook of Human Affective Neuroscience, vol. 39, pp. 171–197. https://doi.org/10.1176/pn.39.2.0031b. Issue 2.

Gonçalves, A.R., Fernandes, C., Pasion, R., Ferreira-Santos, F., Barbosa, F., Marques-Teixeira, J., 2018. Effects of age on the identification of emotions in facial expressions: a metaanalysis. PeerJ 2018 (7), 1–19. https://doi.org/10.7717/peerj.5278.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. In: The distributed human neural system for face perception. Trends in Cognitive Sciences, vol. 4. Trends Cogn Sci, pp. 223–233. https://doi.org/10.1016/S1364-6613(00)01482-0. Issue 6.

Herzmann, G., Schweinberger, S.R., Sommer, W., Jentzsch, I., 2004. What's special about personally familiar faces? A multimodal approach. Psychophysiology 41 (5), 688–701. https://doi.org/10.1111/j.1469-8986.2004.00196.x.

Hinojosa, J.A., Mercado, F., Carretié, L., 2015. N170 sensitivity to facial expression: a meta-analysis. Neurosci. Biobehav. Rev. 55, 498–509. https://doi.org/10.1016/j.neubiorev.2015.06.002.

Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. Neuroimage 15 (2), 353–372. https://doi.org/10.1006/nimg.2001.0982.

Itier, R.J., Taylor, M.J., 2004. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cerebr. Cortex 14 (2), 132–142. https://doi.org/10.1093/cercor/bhg111.

Jacques, C., Rossion, B., 2007. Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. Neuroimage 36 (3), 863–876. https://doi.org/10.1016/j.neuroimage.2007.04.016.

Kaufmann, J.M., Schweinberger, S.R., Burton, A.M., 2009. N250 ERP Correlates of the acquisition of face representations across different images. J. Cognit. Neurosci. 21 (4), 625–641. https://doi.org/10.1162/jocn.2009.21080.

Luck, S.J., 2014. An Introduction to the Event-Related Potential Technique. MIT Press, London, England.

Martens, U., Leuthold, H., Schweinberger, S.R., 2010. On the temporal organization of facial identity and expression analysis: inferences from event-related brain potentials. Cognit. Affect Behav. Neurosci. 10 (4), 505–522. https://doi.org/10.3758/CABN.10.4.505.

Marzi, T., Viggiano, M.P., 2007. Interplay between familiarity and orientation in face processing: an ERP study. Int. J. Psychophysiol. 65 (3), 182–192. https://doi.org/10.1016/j.ijpsycho.2007.04.003.

Pereira, M.R., Barbosa, F., de Haan, M., Ferreira-Santos, F., 2019. Understanding the development of face and emotion processing under a predictive processing framework. Dev. Psychol. 55 (9), 1868–1881. https://doi.org/10.1037/dev0000706.

Ramon, M., Gobbini, M.I., 2018. Familiarity matters: a review on prioritized processing of personally familiar faces. Vis. Cognit. 26 (3), 179–195. https://doi.org/10.1080/13506285.2017.1405134.

Rossion, B., Gauthier, I., Tarr, M.J., Despland, P., Bruyer, R., Linotte, S., Crommelinck, M., 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport 11 (1), 69–74. https://doi.org/10.1097/00001756-200001170-00014.

Rossion, B., 2014. Understanding face perception by means of human electrophysiology. Trends Cognit. Sci. 18 (6), 310–318. https://doi.org/10.1016/j.tics.2014.02.013.

Rossion, B., Gauthier, I., 2002. How does the brain process upright and inverted faces? Behav. Cognit. Neurosci. Rev. 1 (1), 63–75. https://doi.org/10.1177/1534582302001001004.

Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. Neuroimage 39 (4), 1959–1979. https://doi.org/10.1016/j.neuroimage.2007.10.011.

Schweinberger, S.R., Neumann, M.F., 2016. Repetition effects in human ERPs to faces. Cortex 80, 141–153. https://doi.org/10.1016/j.cortex.2015.11.001.

Schweinberger, S.R., Pickering, E.C., Jentzsch, I., Burton, A.M., Kaufmann, J.M., 2002. Event-related potential evidence for a response of inferior temporal cortex to familiar face repetitions. Cognit. Brain Res. 14, 398–409. https://doi.org/10.1016/S0926-6410(02)00142-8.

Sommer, W., Stapor, K., Kończak, G., Kotowski, K., Fabian, P., Ochab, J., Bereś, A., Ślusarczyk, G., 2021. The N250 event-related potential as an index of face familiarity: a replication study. R. Soc. Open Sci. 8 (6), 202356 https://doi.org/10.1098/rsos.202356.

Tanaka, J.W., Curran, T., Porterfield, A.L., Collins, D., 2006. Activation of preexisting and acquired face representations: the N250 event-related potential as an index of face familiarity. J. Cognit. Neurosci. 18 (9), 1488–1497. https://doi.org/10.1162/jocn.2006.18.9.1488.

Taylor, M.J., Edmonds, G.E., McCarthy, G., Allison, T., 2001. Eyes first! Eye processing develops before face processing in children. Neuroreport 12 (8), 1671–1676. https://doi.org/10.1097/00001756-200106130-00031.

Vagnoni, E., Lourenco, S.F., Longo, M.R., 2012. Threat modulates perception of looming visual stimuli. Curr. Biol. 22 (19), R826–R827. https://doi.org/10.1016/J.CUB.2012.07.053.

Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. Neuropsychologia 45 (1), 174–194. https://doi.org/10.1016/j.neuropsychologia.2006.06.003.

Wiese, H., Anderson, D., Beierholm, U., Tüttenberg, S.C., Young, A.W., Burton, A.M., 2022. Detecting a viewer's familiarity with a face: evidence from event-related brain potentials and classifier analyses. Psychophysiology 59 (1), e13950. https://doi.org/10.1111/psyp.13950.

Wiese, H., Hobden, G., Siilbek, E., Martignac, V., Flack, T.R., Ritchie, K.L., Young, A.W., Burton, A.M., 2021. Familiarity is familiarity is familiarity: event-related brain potentials reveal qualitatively similar representations of personally familiar and famous faces. J. Exp. Psychol. Learn. Mem. Cognit. https://doi.org/10.1037/xlm0001063.

Wiese, H., Ingram, B.T., Elley, M.L., Tüttenberg, S.C., Burton, A.M., Young, A.W., 2019a. Later but not early stages of familiar face recognition depend strongly on attentional resources: evidence from event-related brain potentials. Cortex 120, 147–158. https://doi.org/10.1016/j.cortex.2019.06.004.

Wiese, H., Tüttenberg, S.C., Ingram, B.T., Chan, C.Y.X., Gurbuz, Z., Burton, A.M., Young, A.W., 2019b. A robust neural index of high face familiarity. Psychol. Sci. 30 (2), 261–272. https://doi.org/10.1177/0956797618813572.

Wild-Wall, N., Dimigen, O., Sommer, W., 2008. Interaction of facial expressions and familiarity: ERP evidence. Biol. Psychol. 77 (2), 138–149. https://doi.org/10.1016/j.biopsycho.2007.10.001.

Yarmey, A.D., 1971. Recognition memory for familiar "public" faces: effects of orientation and delay. Psychonomic Sci. 24 (6), 286–288. https://doi.org/10.3758/BF03329007.