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Research Report

Conscious perception of fear in faces: Insights from high-density EEG and perceptual awareness scale with threshold stimuli

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ABSTRACT

Contrary to the extensive research on processing subliminal and/or unattended emotional facial expressions, only a minority of studies have investigated the neural correlates of consciousness (NCCs) of emotions conveyed by faces. In the present high-density electroencephalography (EEG) study, we first employed a staircase procedure to identify each participant's perceptual threshold of the emotion expressed by the face and then compared the EEG signals elicited in trials where the participants were aware with the activity elicited in trials where participants were unaware of the emotions expressed by these, otherwise identical, faces. Drawing on existing knowledge of the neural mechanisms of face processing and NCCs, we hypothesized that activity in frontal electrodes would be modulated in relation to participants' awareness of facial emotional content. More specifically, we hypothesized that the NCC of fear seen on someone else's face could be detected as a modulation of a later and more anterior (i.e., at frontal sites) event-related potential (ERP) than the face-sensitive N170. By adopting a data-driven approach and cluster-based statistics to the analysis of EEG signals, the results were clear-cut in showing that visual awareness of fear was associated with the modulation of a frontal ERP component in a 150

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–300 msec interval. These insights are dissected and contextualized in relation to prevailing theories of visual consciousness and their proposed NCC benchmarks.

1. Introduction

A host of research has shown that emotions conveyed by faces can be successfully detected even when faces are unaware and/or unattended. Subliminal facial expression, for instance, can elicit expression-specific oculomotor actions (Vetter et al., 2019) as well as a range of different psychophysiological responses in neurologically intact individuals, including skin conductance responses (e.g., Esteves et al., 1994), facial muscle activity (Dimberg et al., 2000; Tamietto & de Gelder, 2008), and pupillary dilation (e.g., Jessen et al., 2016). Individuals with dense retinal scotomas or those affected by blindsight following V1 lesions often show a residual ability to recognize facial expressions (de Gelder et al., 1999). Neuroimaging studies have shown that, in humans, the processing of subliminal facial expressions recruit vast cortical and subcortical networks including the amygdala (e.g., de Gelder et al., 1999; Dolan & Vuilleumier, 2003; Morris et al., 1998; Öhman, 2002; Tamietto & De Gelder, 2010; see also Mudrik and Deouell (2022) for a critical perspective on non-conscious emotion processing).

Considerably less research has been carried out on the neurophysiological correlates of the awareness of emotions conveyed by faces. Here, we aimed to isolate the neural activity accompanying the subjective experience of seeing/understanding emotions in other people expressed by their faces.

The methodological approach we employed here is based on the established tradition in the search for the neural correlates of consciousness (NCCs; Crick & Koch, 1998). Content-specific NCCs (Koch et al., 2016) are defined as the minimal neuronal mechanisms jointly sufficient for a specific conscious experience, for instance, of colors, oriented lines, faces, and buildings (e.g., Boly et al., 2017). One way to isolate the NCC is to use the contrastive method (Baars, 2005; see also Dehaene et al., 2014), i.e., by subtracting the neural activity elicited by the stimulus/feature of interest in a condition where the participant lacks awareness (on the basis of their report) from the neural activity elicited by the same stimulus/feature in a condition of awareness (i.e., aware-minus-unaware). The assumption behind this approach is that this subtraction cancels out the neural activity commonly elicited in the two conditions, unveiling the neural activity that is uniquely related to the awareness of the stimulus of interest (but see Aru et al. 2012; Lepauvre & Melloni, 2021; Miller, 2007; de Graaf et al. 2012; Tsuchiya et al. 2015). By using this approach, neuroimaging studies have found that these NCCs are content-dependent, such that, for instance, the phenomenal conscious experience of color is linked to the recruitment of the extrastriate area V4/V8 (Zeki, 1973, 1983), that of places to the parahippocampal place area (Mégevand et al., 2014; e.g., Tong et al., 1998), and that of faces to the fusiform gyrus (e.g., Tong et al., 1998). For what concerns conscious face perception, compatible with fMRI evidence, electrocorticography (ECoG) studies using continuous flash suppression and backward masking as blinding methods have provided evidence that the content-dependent NCC of conscious face perception corresponds to the activity in the ventral and lateral sides of the temporal lobe (Baroni et al., 2017).

With respect to the processing of suprathreshold visible faces, the most empirically supported neural model of face processing considers a distributed network: a “core system” for the visual processing of faces comprising regions in the posterior occipitotemporal cortex (i.e., lateral fusiform gyrus [fusiform face area: FFA], inferior occipital gyrus [occipital face area: OFA], and superior temporal sulcus [pSTS]), and an “extended system” comprising more anterior brain regions for additional processing, including the attribution of emotional meaning to facial expressions (Haxby et al., 2000; Haxby & Gobbini, 2011). The extended network for facial expression processing includes the frontal operculum (FO; inferior frontal gyrus and anterior insula), the premotor cortex, and the somatosensory cortex (Haxby et al., 2000). There is also evidence that the FO contains distributed representations of facial expressions, which can be decoded by means of fMRI (Said et al., 2010).

In the context of EEG studies, few well-characterized event-related potential (ERP) components are sensitive to specific categories or attributes of stimuli. Among these, the best known is the N170, an ERP deflection with negative polarity and latency of about 170 msec enhanced in amplitude for face compared to non-face stimuli (such as objects and buildings; Bentin et al., 1996; Rossion et al., 2000) estimated to stem from activity in the occipitotemporal areas corresponding to the “core system” (Herrmann et al., 2005; Itier & Taylor, 2004; Watanabe et al., 2003). N170 is postulated to reflect the structural encoding of a face, since disrupting the organization of the visual features that make up a face leads to a reduction in its amplitude (e.g., Rossion & Jacques, 2008). Some research suggests that the N170 may be sensitive to the presence of faces, regardless of whether they are consciously perceived or not (e.g., Eimer, 2000). However, other research has found that the N170 is more strongly associated with the conscious perception of faces, particularly when the face is the focus of attention (e.g., Harris et al., 2011; Maffei et al., 2021; Navajas et al., 2013; Rodríguez et al., 2012; Rossion, 2014; Tanskanen et al., 2007).

In support of the distributed face processing network, the processing of suprathreshold visible emotional faces compared to that of neutral faces is associated with modulations of other ERP components in addition to the N170 spanning the scalp (Batty & Taylor, 2003; Blau et al., 2007; Eimer et al., 2003; Eimer & Holmes, 2007). These include the mid-latency N2 and Early Posterior Negativity (EPN) and the late P3 and Late Positive Potential (LPP) (Maffei et al., 2021; Jaspers-Fayer et al., 2022; Schindler & Bublatzky, 2020), advocating for the involvement of the “extended system” for the attribution of emotional meaning.

In terms of the NCC of emotional faces, a few traditional ERP studies have manipulated the visibility of emotional faces. Importantly, the goal of these studies was to isolate the NCCs of a face with an emotional expression rather than explicitly isolating the NCCs for the emotional attribute. The NCC of a face with an emotional expression may reflect the recruitment of the core and/or the extended systems. Meanwhile, the NCC for the emotional attribute would ideally isolate the experience of seeing an emotion coming along with a face. Most previous studies were designed to pursue the former goal, employing backward masking and the contrastive approach. There, the authors contrasted and compared different "physical stimuli" under supraliminal and subliminal conditions (see Table in Supplementary materials) (Balconi, 2006; Balconi & Lucchiari, 2005, 2007; Balconi & Mazza, 2009; De Pascalis et al., 2020; Kiss & Eimer, 2008; Liddell et al., 2004; Pegna et al., 2008; Williams et al., 2004; Zhang et al., 2012). The overall pattern of the results from these studies are inconclusive and inconsistent with respect to response modulations (in terms of amplitude and/or latency) as a function of consciousness: N170 (De Pascalis et al., 2020; Wierzchoń et al., 2016; Zhang et al., 2012), the EPN (Wierzchoń et al., 2016), the N2 (Balconi, 2006; Balconi & Lucchiari, 2005, 2007; Balconi & Mazza, 2009; De Pascalis et al., 2020; Kiss & Eimer, 2008; Pegna et al., 2008), and the P3 (Liddell et al., 2004; Kiss & Eimer, 2008; Wierzchoń et al., 2016; De Pascalis et al., 2020).

One of the major limitations of this traditional ERP research, which has been overcome by more contemporary methodologies, is their use of a priori selection of the electrodes and/or ERP components (Liddell et al., 2004; Williams et al., 2004; Balconi & Lucchiari, 2005, 2007; Balconi, 2006; Pegna et al., 2008; Kiss & Eimer, 2008; Balconi & Mazza, 2009; Zhang et al., 2012; Wierzchoń et al., 2016; De Pascalis et al., 2020). This methodological approach is known to result in over-generosity in quantifying statistical effects. Its weakness has been pointed out discerningly by Luck and Gaspelin (2017) and has been criticized since. Such methodological inclinations might explain seemingly contradictory results.

Additionally, it is crucial to distinguish the NCC of a face with an emotional expression from the NCC for the emotional attribute. Drawing upon the seminal model of face processing by Haxby and Gobbini (2011), the act of attributing emotion to a face engages neural territories extending beyond the confines of the core visual cortices, especially venturing into the frontal region.

With these perspectives in mind, our data-driven methodology offers a more refined instrument attuned to the multifaceted nature of face and emotion processing. In particular, our present investigation embraces an unbiased statistical approach, as championed by Luck and Gaspelin (2017). Our intent is not merely to address these methodological quandaries but to further elucidate the intricate interplay underlying conscious emotional processing. Using this methodological and analytical approach, we expected to observe ERP modulations in anterior electrodes as a function of the emotion's awareness (i.e., following the contrastive approach aware-minus-unaware).

In a high-density EEG (hd-EEG; 256 sensors) study, we optimized methodological choices to isolate neural activity linked with awareness of an emotion of fear conveyed by a face. In other words, awareness of "fear" conveyed by a face rather than awareness of "a face expressing fear" was the objective of our contrastive approach. Firstly, we used threshold stimuli calibrated for each participant before the main EEG experimental session using a double staircase procedure. Secondly, since the study of consciousness requires measuring subjective experience, in this investigation, we opted for a variant of the PAS (Overgaard & Sandberg, 2021; Ramsøy & Overgaard, 2004) to obtain introspective participants' reports of their awareness of seeing an emotion of fear conveyed by a face. The trials were divided into unaware and aware conditions of the emotion expressed by the faces (for details, see Methods), and the neural activity was then contrasted between the two conditions: aware fearful versus unaware fearful.

With regard to the use of threshold stimuli, faces were presented with Gaussian noise with varying intensity. The Gaussian noise was adaptively adjusted based on the participant's response to identify stimuli in which emotion awareness occurred in ~50% of the trials. In general, NCCs have often been isolated using similar stimuli but with different physical characteristics (e.g., in terms of duration (Koivisto et al., 2016; Pins & Ffytche, 2003), intensity (Auksztulewicz & Blankenburg, 2013; Wyart & Tallon-Baudry, 2008) or masking (Del Cul et al., 2007)) such that they could produce different experiences, i.e., seen versus unseen. As already mentioned in a previous paragraph, this is also the case for previous EEG/ERP studies investigating the NCCs for emotional faces since almost all of them used subliminal/unconscious and supraliminal/conscious emotional faces that differed in terms of duration within the context of a backward masking paradigm (Balconi, 2006; Balconi & Lucchiari, 2005, 2007; Balconi & Mazza, 2009; De Pascalis et al., 2020; Kiss & Eimer, 2008; Liddell et al., 2004; Pegna et al., 2008; Williams et al., 2004; Zhang et al., 2012). Here, instead, we contrasted neural activity between the conditions of emotion awareness and unawareness by presenting identical physical stimuli that only differed in terms of participants' experience.

For our purpose, we also employed a modified version of the PAS. In its most used version, PAS includes four different levels that map the experience from "No experience" (PAS 1; no impression of the stimulus) to "Clear experience" (PAS 4; non-ambiguous experience of the stimulus; Ramsøy & Overgaard, 2004), where PAS 1 reports are typically regarded as unconscious trials. In the present study, we employed a 5-level PAS to monitor the clarity of the experience of the emotion expressed by the face (see Method). Our choice to use such a tool is based on the view that the study of consciousness should primarily be based on subjective experience reports and that there is a (close) one-to-one relationship between subjective reports and inner states (Overgaard & Sandberg, 2021).

To characterize the space-time distribution of these NCCs, we opted for a data-driven approach, and more specifically for the massive univariate nonparametric permutation approach (Groppe et al., 2011) combined with a cluster-based approach (Bullmore et al., 1999) also in order to appropriately deal with the large number of contrasts that typically arise with high-density EEG recordings.

Finally, we explored if functional connectivity between the core and the extended systems for facial expressions processing would differ as a function of awareness of the emotional expression presented. This latter analysis may help clarify whether content-dependent localized and possibly reverberant activity is sufficient for specific consciousness contents to arise (Lamme, 2006; Lamme & Roelfsema, 2000; Pascual-Leone & Walsh, 2001; e.g., Pins & Ffytche, 2003; Ress et al., 2000; Ress & Heeger, 2003; Supèr et al., 2001; Tong, 2003; Zeki, 2003; Seth & Bayne, 2022; Koch et al., 2016; Mashour et al., 2020), or complex long-range neural dynamics are necessary (Beck et al., 2001; Lumer & Rees, 1999; Marois et al., 2004; e.g., Rees et al., 2002; Tononi, 2004; Vuilleumier et al., 2001).

2. Method

2.1. *Participants*

Forty participants (35 females and 5 males, mean age = 23.4 y, SD = 1.9 y) were recruited to take part in this experiment. Participants were undergraduate students from the University of Padova, with no history of neurological or psychiatric diseases with normal or corrected-to-normal vision. They were paid 10 € for their participation. The study received approval from the University of Padova ethics committee for psychological studies (protocol no 4032). All the procedures were carried out according to the principles expressed in the Declaration of Helsinki for human research. No power analysis ws performed to determine the sample size and no part of the study procedures or analysis plans was preregistered prior to the research being conducted. In the following sections, we report how we determined all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.2. *Experimental task and procedure*

Each participant completed 1) a psychophysical calibration procedure in order to estimate the facial expression detection threshold and 2) the main experimental session with the EEG recordings.

As facial stimuli, we selected 8 identities (4 females and 4 males) from the Karolinska Directed Emotional Faces database (KDEF; Lundqvist et al., 1998) with neutral and fearful facial expressions for a total of 16 faces. Each stimulus was converted to grayscale and cropped using an oval mask.

For the psychophysical calibration, we used a 1-up–1-down staircase (Levitt, 1971) varying the amount of Gaussian visual noise added to the face stimulus in order to manipulate the visibility. The Gaussian noise was added to each pixel with a varying level of the variance (with fixed the mean to be zero). The larger the variance, the stronger the masking effects to reduce the visibility of the underlying face. For this calibration, we used the Palamedes toolbox (Kingdom & Prins, 2016) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in MATLAB. The trial started with a fixation cross for 1000 msec. Then the face stimulus (with superimposed Gaussian stimuli) appeared for 50 msec and was immediately followed by a mask stimulus for 500 msec. The mask was created by randomly scrambling the face stimulus using a custom MATLAB function which, first randomly creates a new image by dividing the original image into $n = 100$ squares, and then randomizes the position of each square. Then participants were required to report the face visibility using a modified version of the PAS, which included the following alternatives: PAS 0 = no experience of a face nor of its expression; PAS 1 = experience of a face but not of its expression; PAS 2 = experience of a face and a brief glimpse of its expression; PAS 3 = experience of a face and almost clear experience of its expression; PAS 4 = experience of a face and clear experience of its expression. Labels for PAS 1 to 4 were derived by translating in Italian the original 4 PAS labels (Sandberg & Overgaard, 2015), stressing the focus of the awareness question on the emotional expression conveyed by the face. The additional level was defined by using the lower edge of the traditional PAS (No experience), but asking the participants about both the face and its expression. Before starting the experiment, the participants were familiarized with the different alternatives of the PAS so that they learned to map their subjective experiences using this tool. This consisted in reading a series of written instructions where the meaning of each PAS level according to Ramsøy and Overgaard (2004), was explained, and practiced its use in 10 practice trials. The Gaussian noise was decreased after a PAS 1 response, while it was increased after a PAS 2, 3, or 4 response. Finally, for trials in which participants reported facial expression awareness (i.e., PAS 2, 3, and 4), they were also asked if they saw a neutral or fearful face. The intertrial interval was a blank screen presented for 1500 msec. The decreasing step size was .04, and the increasing step size was .04 multiplied by .871, corresponding to the optimal factor for a 1-up–1-down staircase (García-Pérez, 2001). The final threshold was estimated by averaging all reversals, excluding the first two. Each face was presented 5 times, and we also included 16 catch trials (where the face was replaced by the mask) for a total of 96 trials.

The experimental EEG session consisted of the presentation of the face stimuli, convolved with the amount of Gaussian noise estimated individually for each participant in the calibration phase, followed by the PAS (and emotion discrimination in a subset of trials, see above). The trial was structured in the same way as the calibration session. The only difference was the intertrial interval, where the duration was randomly set between 1400 and 1700 msec.

Trials for which participants' response on the PAS was 0 or 1 were considered Unaware trials with regards to emotional expression. Trials for which participants' response was 2, 3 or 4 were considered Aware trials with regard to emotional expression. Additionally, for Aware trials only, participants were probed with a second question in which they were asked to report which expression they saw. Only trials in which participants correctly recognized the expressions were considered for the subsequent analysis. An example of the trial structure with the possible response alternatives is presented in Fig. 1B.

The experiment consisted of 800 trials, grouped in 4 blocks to minimize participants' fatigue. For each block, 80 trials consisted of fearful expressions (320 in total), 80 trials

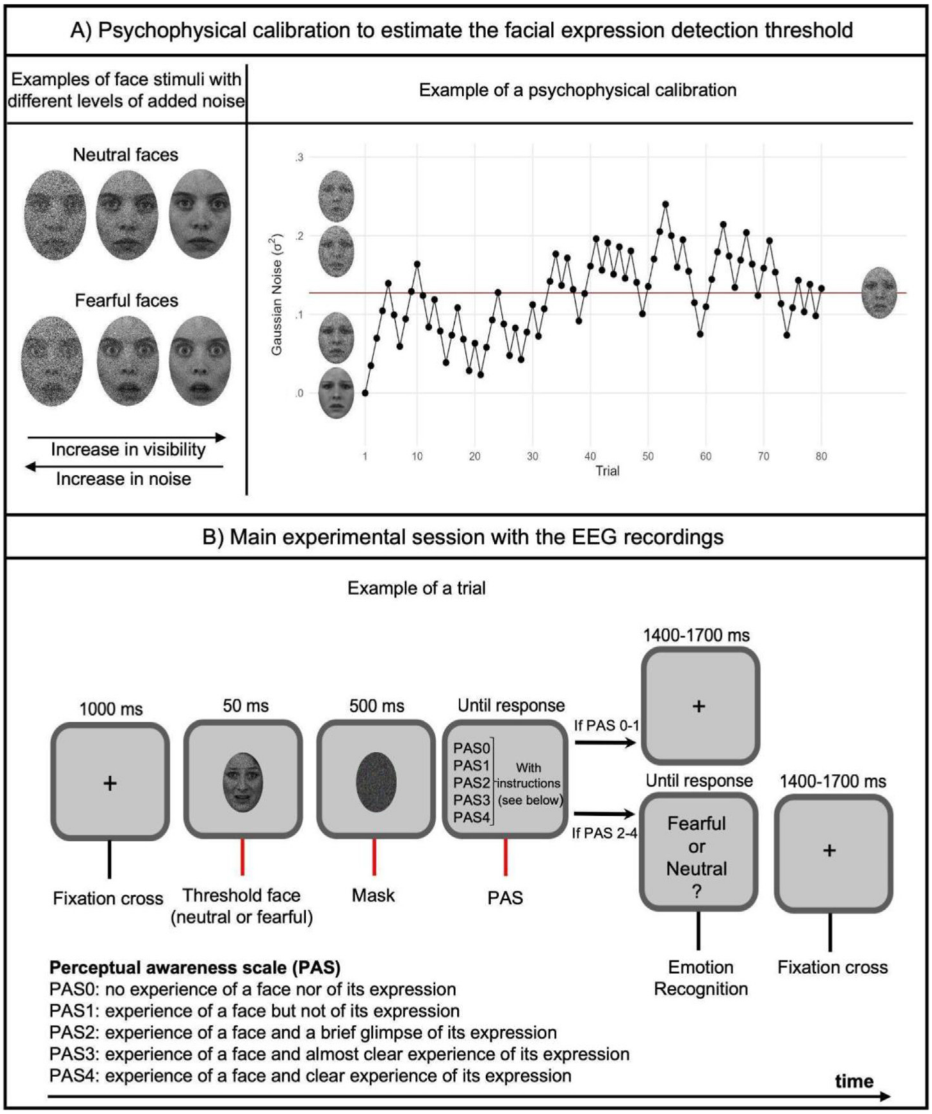

Fig. 1 – Panel A shows examples of face stimuli (with neutral and fearful expressions) with added levels of Gaussian noise (on the left) and an example from one participant of the structure of the psychophysical calibration procedure (1-up–1-down) used to identify the perceptual threshold for the emotional expression (on the right). Panel B shows an example of a trial structure. When the participant responded with PAS0 and PAS1, the trial was considered Unaware; when the participant responded with PAS2, PAS3, and PAS4 the trial was considered Aware.

consisted of neutral expressions (320 in total), and the remaining 40 were catch trials (160 in total). Stimuli were presented on a 21.5″ LCD monitor with 60 Hz refresh rate. The whole procedure lasted around 90 min.

2.3. *EEG recording and preprocessing*

EEG activity was collected continuously using a 256-channel HydroCel Geodesic Sensor Net connected to an EGI NetAmp 400 amplifier with a sampling rate of 256 Hz. The vertex channel was used as the online reference, and all channels' impedance was kept below 50 kΩ.

Data preprocessing consisted of 1) high-pass filtering at .5 Hz, with a Kaiser windowed FIR filter; 2) automatic detection of bad channels using the *clean_rawdata* routine (v. 2.5) implemented in EEGLab marking a channel as bad according to any of the following parameters: a) 5 s or more of flatline recording; b) less than .8 correlation with nearby channels; c) 4 standard deviations of more of line noise relative to signal; the average number of bad channels detected was 26.28 (SD = 15.96) 3) segmentation of the continuous recording into epochs starting at −1000 msec and ending 1000 msec around stimulus onset. According to participants' responses to the PAS, epochs have been assigned to one of the following conditions: Neutral Aware, Neutral Unaware, Fear Aware, Fear Unaware; 4) application of ICA to reduce the data to 40 independent components; 5) semi-automatic rejection of artifactual components using the ICLabel plugin (v.1.3) implemented in EEGLab (Pion-Tonachini et al., 2019). The average number of discarded ICs was 16.5; 6) reconstruction of activity from artifact-free ICs, interpolation of missing channels, and re-referencing to the average of all channels; 7) reduction of epoch length to −200 msec–600 msec around stimulus onset and baseline correction; 8) automatic rejection of epochs with a peak-to-peak amplitude exceeding ±100 μV in any channel using a moving window procedure (window size = 200 msec, step size = 200 msec) in order to discard epochs contaminated by residual artifacts; 9) averaging the activity of artifact-clean epochs. The average number of epochs for each condition was: Fear Aware = 198.9, Fear Unaware = 118.5, Neutral Aware = 189.5, Neutral Unaware = 128; 10). Finally, we performed a low-pass filtering of the averaged waveforms at 30 Hz using a 2nd-order Butterworth filter.

Due to excessive noise in the recordings (less than 60% of artifact-free trials), data from 8 participants were discarded during preprocessing. The final sample for statistical analyses included 32 participants. EEG/ERP data quality assessment is provided in the Supplementary Materials.

In order to have a fine-grained assessment of information flow within the face processing network, we computed the routing efficiency, a graph theoretical metric suited to capture the integration of information within a network, which has been successfully used in the investigation of the network dynamics subtending emotional face processing. Following the approach described in Maffei and Sessa (2021) we first projected EEG activity in the source space using a three-layer boundary element method (BEM) as the forward model and the weighted Minimum Norm Estimation (wMNE) as the inverse solution. Then, we downsampled the source activity to the cortical parcels included in the Destrieux atlas (Destrieux et al., 2010), and computed the pairwise connectivity in the alpha (8–12 Hz) frequency range using the corrected imaginary part of the phase-locking value (ciPLV). Finally, we computed the maximum routing efficiency between a node belonging to the Core System (CS) and a node belonging to the Extended System (ES) of the face processing network.

Preprocessing was performed in MATLAB (v. 2019a) employing functions from EEGLab (v. 2019, Delorme & Makeig, 2004), ERPLab (v. 8.3, Lopez-Calderon & Luck, 2014), Brainstorm (Tadel et al., 2011) and the Brain Connectivity Toolbox (Rubinov & Sporns, 2010).

2.4. Statistical analysis

Statistical modeling of event-related activity was performed within a massive univariate nonparametric permutation framework (Groppe et al., 2011). This approach consists in performing a statistical test (like a t-test or ANOVA) for every point in the electrode by time plane, then iteratively permuting the within-subject condition assignments (i.e., conditions labels) and performing the test a sufficient number of times to have an empirical null-distribution of the test statistic under the null hypothesis of no difference between conditions. This empirical null distribution is then used to derive the exact probability of the observed difference and thus perform the statistical inference. This statistical framework, combined with a cluster-based approach to handle the problem of multiple comparisons (Bullmore et al., 1999), represents the gold standard for EEG/ERP analysis (Maris & Oostenveld, 2007), allowing for relaxing the rarely satisfied assumptions of parametric models and exploiting the full multidimensional structure of EEG/ERP data.

In the present research, we contrasted the activity elicited by fearful faces in the Aware condition with the activity elicited by fearful faces in the Unaware condition and contrasted the activity elicited by neutral faces in the Aware condition with the activity elicited by neutral faces in the Unaware condition. In order to test our hypotheses regarding both the timing and the spatial distribution of conscious access to emotional expressions, we performed these contrasts separately for a subset of anterior and posterior sensors and in an *early* time interval comprising time points between 150 msec and 300 msec (to monitor for ERP components such as the N170, the EPN, the visual awareness negativity (Förster et al., 2020), and the anterior N2) and a *late* time interval between 300 msec and 500 msec (to monitor for the P3b and the LPP ERP components). The two electrode subsets were created by splitting the scalp into two regions, one anterior and one posterior, according to the central line (Fig. 2; the complete list of sensors included in the two subsets is provided in the Supplementary Materials). Our approach resulted in four sets

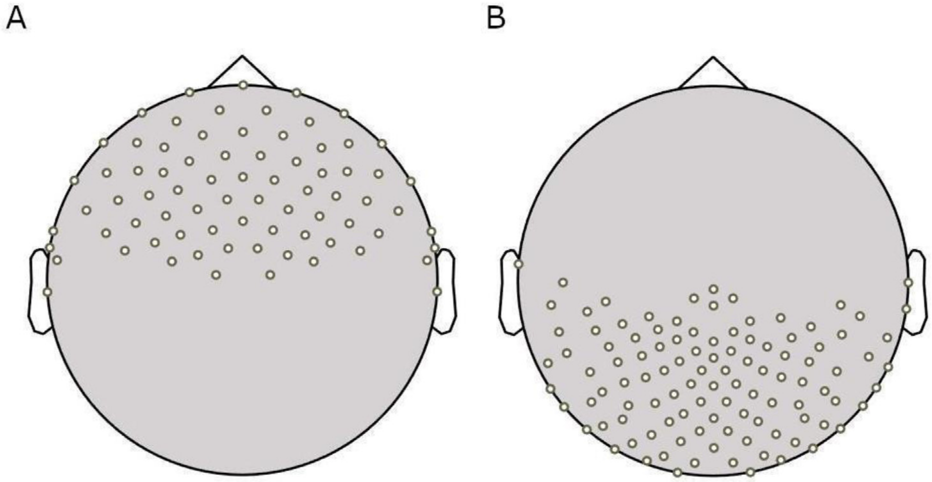

Fig. 2 – Panel A shows the sensors in the anterior cluster considered for the statistical analysis. Panel B shows the sensors in the posterior cluster considered for the statistical analysis.

of contrasts, one for each combination of clusters (Anterior and Posterior) and time-window (early and late). For each test, statistical significance was assessed using $\alpha = .05$, the number of permutations employed was 5000, and the alpha level used as the cluster-forming threshold was set at .05. In the results section, we report the sum of the t-values comprising a significant cluster as a test statistic and the extent of this cluster as the number of adjacent points in the spatiotemporal plane. Statistical analysis was performed using Fieltrip's *ft_timelockstatistic* function accessed from Brainstorm.

3. Results

3.1. *Behavior*

Fig. 3A shows the percentage of PAS responses for catch trials and valid trials, split by emotion category of the valid stimulus. The distribution of responses across the different PAS levels demonstrates that the calibration phase was successful. The proportion of PAS 0 responses for catch trials is substantially higher than the proportion of PAS 0 responses for valid trials, as shown by a multilevel logistic regression modeling the proportion of unaware trials as a function of trial type (log OR = 4.122, SE = .393, z = 10.487, p < .001). Furthermore, for the latter, the responses tend to be distributed over all the PAS levels, with a clustering of responses for the PAS 1 and PAS 2 levels as expected from using threshold face stimuli.

Fig. 3B shows the percentages of emotion categorization for fearful and neutral faces, at each PAS level corresponding to awareness of the emotional feature of the face (PAS2-4). The results from a multilevel logistic regression predicting the accuracy in the emotion categorization indicate that at the PAS 2 participants already show above-chance discrimination of fearful (ACC = .634, SE = .040, 95% CI = [.553, .708], z = 3.202, p = .001) and neutral expressions (ACC = .837, SE = .024, 95% CI = [.785, .878], z = 9.443, p < .001).

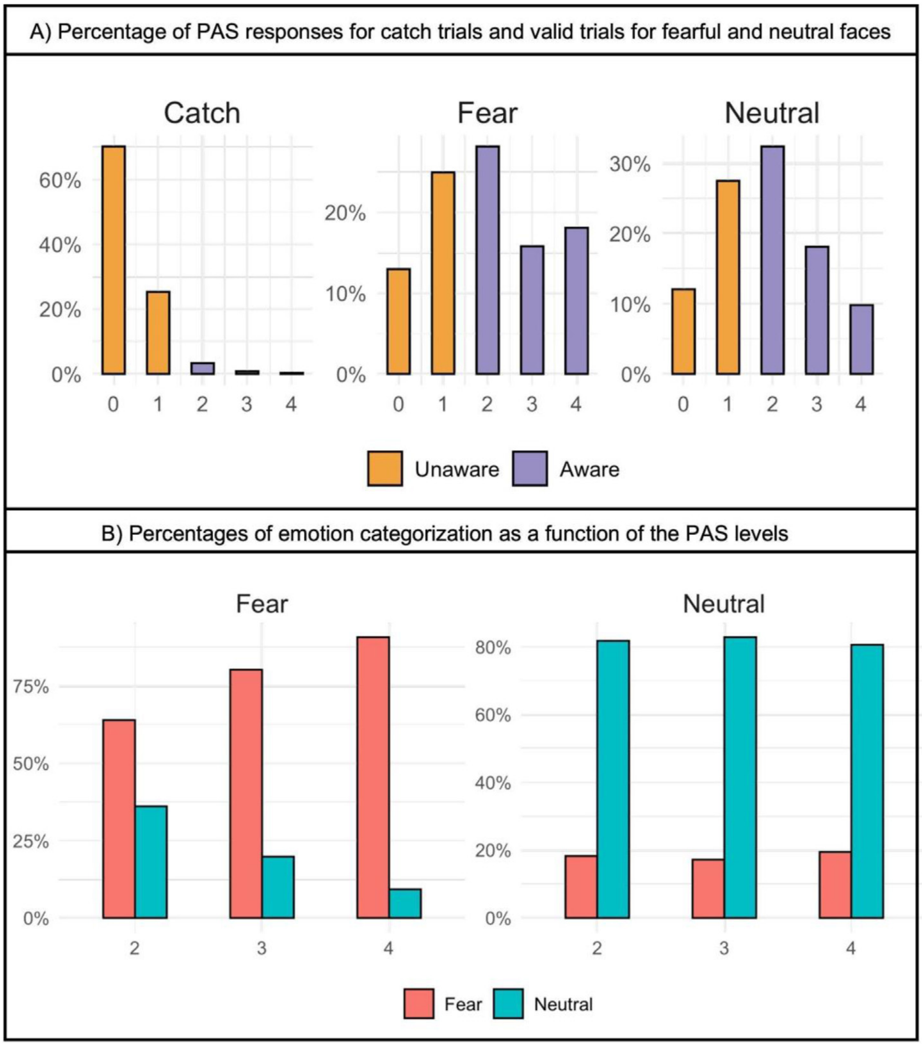

Fig. 3 – Panel A shows the percentage of PAS responses for catch trials and valid trials, split by emotion category of the valid stimulus, for the whole sample. Panel B shows the percentages of emotion categorization for fearful and neutral faces, at each PAS level corresponding to awareness of the emotional feature of the face (PAS2–4).

3.2. *Event-related activity*

The analysis of the event-related activity as a function of participants' awareness and separately for fearful and neutral faces revealed a significant difference in the cortical activity elicited by fearful faces. The contrast between ERP response to fearful expressions subjectively perceived by participants with ERP responses to fearful expressions not consciously perceived yielded a significant result in the test considering the *early* time window and the anterior scalp sites ($t_{sum} = 1299$, cluster size = 517, $p = .02$).

Fig. 4 shows the grand average waveforms of the anterior electrodes cluster for the Aware and Unaware trials, separately for Fearful faces (on the left) and Neutral faces (on the right), while Fig. 5 shows on scalp maps the significant effect found.

The other statistical tests performed (reported in Table 1) did not reveal significant results.

The only notable exception was the contrast between Fear Aware versus Fear Unaware in the *late* time window, for which the probability to reject the null hypothesis was $p = .052$.

In light of our findings and the existing literature, we identified intervals of interest for our ERP effects. However, during our analysis, we also noted intriguing patterns in the 200–400 msec window (also visible in Fig. 3 for the fear condition). To ensure the robustness of our findings and address concerns of potential double-dipping (Kriegeskorte et al., 2009), we present our detailed exploratory analysis of this interval in the Supplementary Materials. Readers interested in a comprehensive understanding of the observed effects in this window are encouraged to refer to this supplementary section. The primary manuscript focuses on the main findings (about the confirmatory analysis of the a-priori determined time interval of 150–300 and 300–500 msec), ensuring alignment with the established literature and maintaining clarity.

The analysis of the information flow between the two portions of the face processing system with the routing efficiency did not reveal any difference ($t = .78$, $p = .44$, $BF_{01} = 3.93$) in the levels of integration between the core and the extended systems during processing of fearful expressions as a function of awareness (Fig. 6). Analogous result was observed for the neutral expressions ($t = .04$, $p = .97$, $BF_{01} = 5.29$).

Finally, in Fig. 7, we outline the average ERP amplitude for each distinct PAS level. PAS 0 denotes an absence of visual experience—neither recognizing the face nor its expression. PAS 1 represents the conscious recognition of a face without its expression. PAS 2 through 4 sequentially chart the varying degrees of consciousness associated with identifying a facial expression of fear.

The variation in ERP across PAS levels offers an interesting perspective on the nature of consciousness. Drawing upon Windey and Cleeremans (2015), the neural representations between PAS 0 and PAS 1 suggest a graded consciousness consistent with low-level stimuli/features. In contrast, the transition from simply recognizing a face to interpreting its emotional expression (from PAS 1 to subsequent levels) seems to reflect high-level processing, where a more all-or-none nature of consciousness becomes evident. This interpretation, while thought-provoking, aligns with the gradations proposed by Windey and Cleeremans.

However, it is crucial to underline that our experimental design was not specifically tailored to delve deeply into the subtle differences of neural activity evoked by various PAS levels. Our study lacks the statistical power for definitive conclusions in this realm. Thus, while this data offers qualitative insights and could inspire subsequent research trajectories, we abstain from delving deeper into these findings in the Discussion section, treating them primarily as preliminary observations.

4. Discussion

In the present investigation, we used high-density EEG and an optimized experimental paradigm to isolate the NCCs for an emotion conveyed by a face. We employed threshold stimuli so that the neural activity contrasted to identify the NCCs was

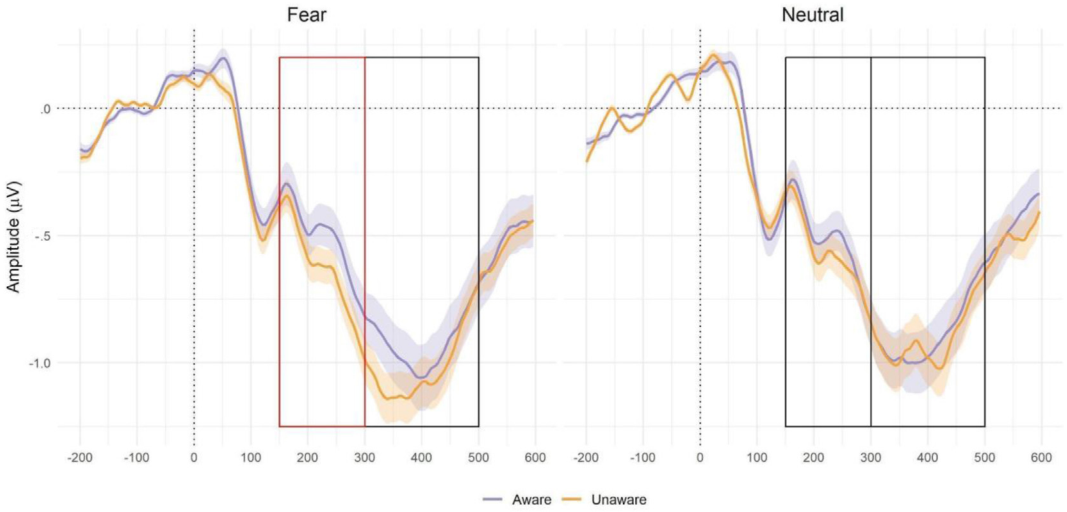

Fig. 4 – Grand average waveforms displaying average activity within the significant anterior electrode cluster. The left panel shows the activity for Fearful faces as a function of participants' awareness. The right panel shows the activity for Neutral faces as a function of participants' awareness. The red borders mark the time window for which the difference was significant.

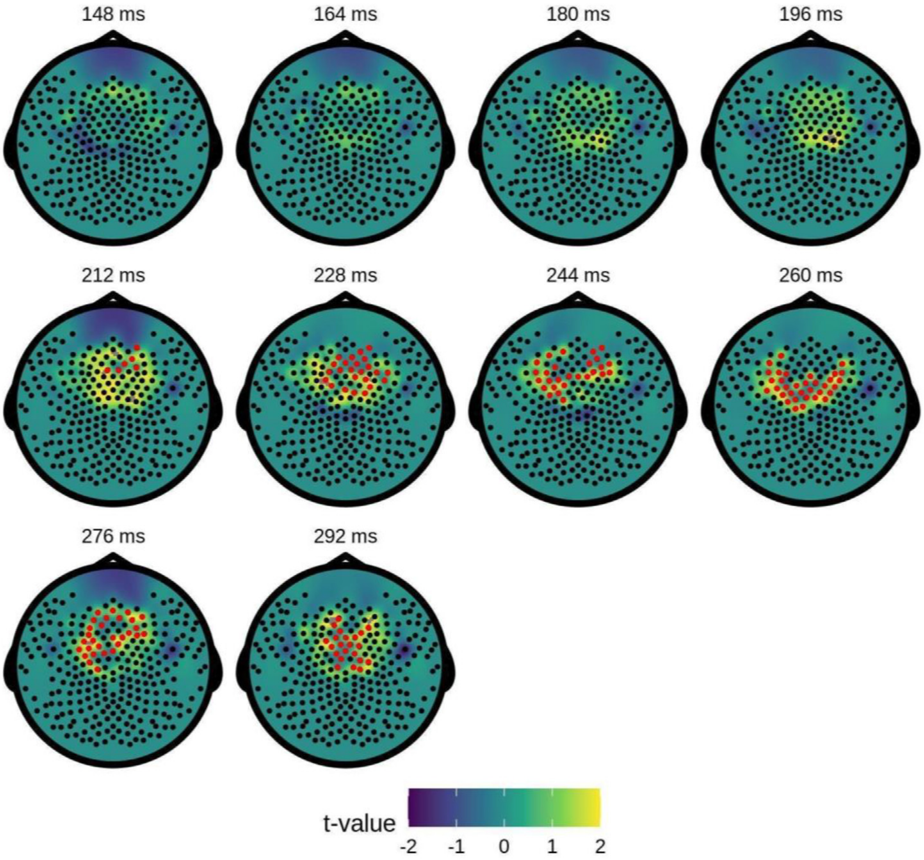

Fig. 5 – Scalp maps show the significant statistical effect for the contrast between Fearful Face Aware (PAS 2–4) and Fearful Face Unaware (PAS 0–1) in the early time window (150–300 msec). Electrodes comprising the significant cluster are marked in red.

Table 1 – Results of the statistics performed according to our *a-priori* hypothesis.

Contrast	Window	Statistic	*p*-value
Fear Aware versus Fear Unaware	150–300 msec	$t_{sum} = 1299$	$p = .02$
Fear Aware versus Fear Unaware	300–500 msec	$t_{sum} = 1364$	$p = .052$
Neutral Aware versus Neutral Unaware	150–300 msec	$t_{sum} = 4$	$p = .99$
Neutral Aware versus Neutral Unaware	300–500 msec	$t_{sum} = 190$	$p = .44$

elicited by stimuli with identical physical properties. This strategy should strongly limit the possibility that activity elicited posteriorly by higher visible stimuli in the supraliminal condition (*vs* the subliminal condition) could improperly lead to the conclusion that activity of the core system for face processing is (part of) the NCC of emotion seen on others' faces. Furthermore, we used the perceptual awareness scale to assign trials into aware and unaware conditions (rather than requiring a dichotomous response, i.e., aware/seen *vs* unaware/unseen). This procedure minimizes the risk of categorizing "experience of a face with a brief glimpse of expression" as unaware. If participants were to be asked to categorize trials as either visible or invisible, they might do so based on the visibility of the face per se or the expression. Our explicit instruction and 5 levels of PAS reduces such ambiguity. Specifically, according to our PAS system, we regarded that participants were unaware of expression, even if they saw a face (PAS = 1) and they were aware of expression if PAS ≥ 2 as long as expression was experienced even as a brief glimpse. Fig. 2B shows that at the PAS = 2 participants already show significant discrimination of fearful and neutral expressions.

In a recent perspective discussing visual consciousness, Lamme suggested that the experience of emotions associated with facial expressions might rely on recurrent interactions between neurons representing various facial features and specialized neurons signaling emotional content. These specialized neurons are believed to be located in subcortical structures such as the amygdala or in ventromedial prefrontal cortices (Lamme, 2020; p. 7). The results of our investigation conceptually confirmed this prediction because, focusing on the component of "fearfulness" conveyed by the face, we observed a pattern of activity on the scalp compatible with the recruitment of frontal regions for the processing of emotions (specifically, fear). More specifically, our results corroborate the hypothesis - grounded on the knowledge of face processing - that the NCC of fear (on someone else's face) entails

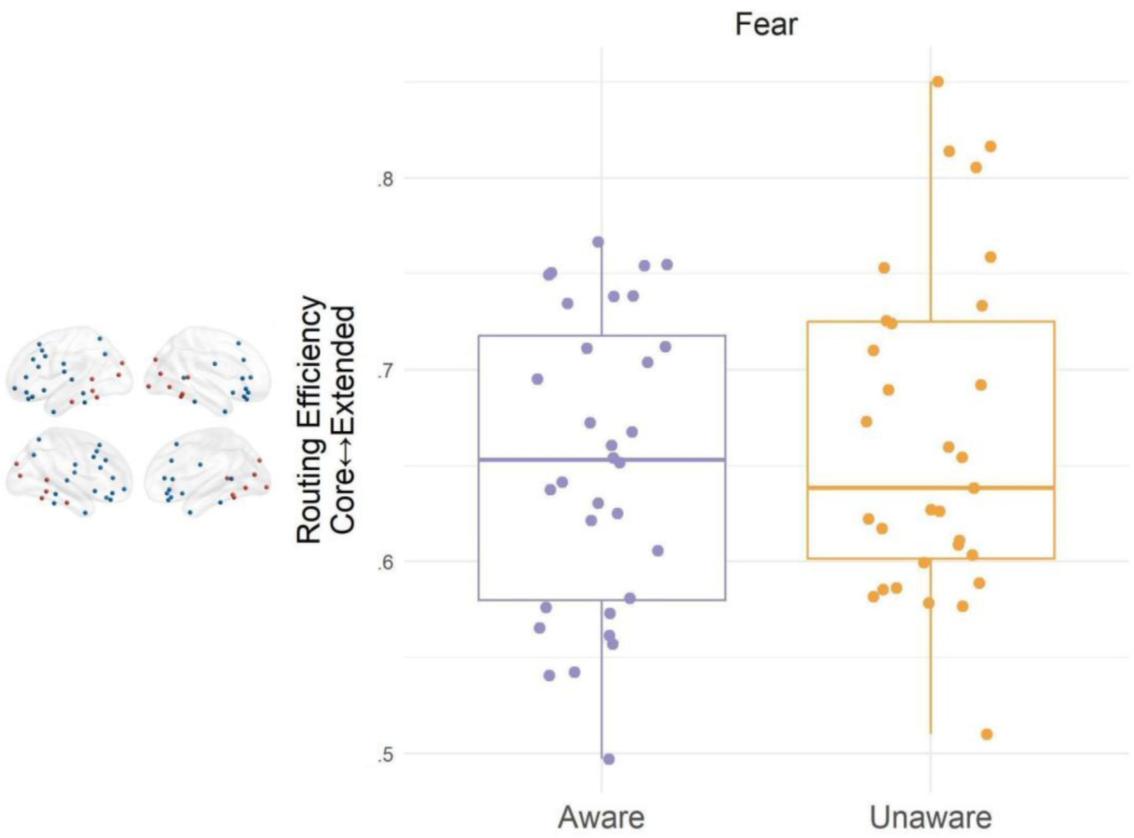

Fig. 6 – Boxplots showing the levels of the routing efficiency between the Core (red nodes) and the Extended (blue nodes) system of the Face Processing Network, as a function of awareness of fearful expressions.

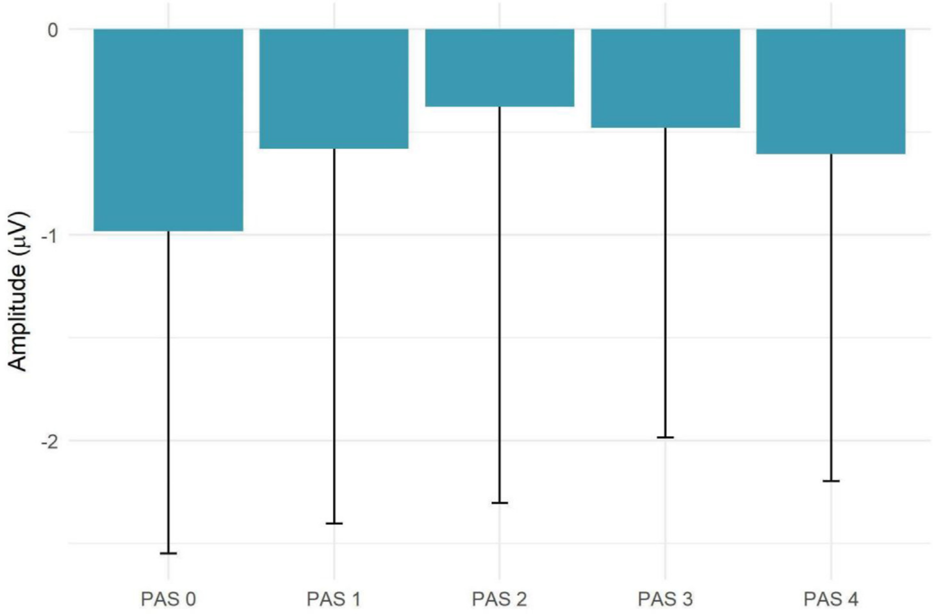

Fig. 7 – Mean amplitude and standard error of the anterior cluster ERP activity in the *early* time window (150–300 msec), split for the levels of participants' awareness during the presentation of fearful faces.

neural activity following, in time, the N170 ERP component and elicited in anterior sensors.

Although in line with the body of evidence and predictions discussed in the introductory section, these results must also be discussed in the context of the ongoing debate about electrophysiological markers of consciousness. Indeed, two main ERP markers of consciousness have been so far suggested, each with a unique spatiotemporal signature: 1) an earlier ERP with a scalp distribution dependent on the stimulus' sensory modality, which arises 120–200 msec following the stimulus and is likely generated within the underlying sensory cortices, i.e., the perceptual awareness negativity (Dembski et al., 2021), and 2) a later ERP with an onset latency of around 300 msec and a parietal distribution, i.e., the P3b/Late Positivity (LP; Dehaene et al., 2014; Dehaene & Changeux, 2011; Del Cul et al., 2007; Naccache et al., 2016; Sergent et al., 2005; Sergent & Naccache, 2012). The discussion on which of the two ERP responses is the "true marker" of consciousness fuels the controversy on the early/late onset of consciousness (see Förster et al., 2020 for a critical review on this topic), with the perceptual awareness negativity supporting an early onset versus the P3b/LP supporting a late onset. These two ERP markers are also compatible with different localization of the brain regions critical for consciousness, thus feeding the intricacy of the overall scenario. These two viewpoints may not be necessarily mutually exclusive, as the two ERPs responses could be neural indexes of two different kinds of consciousness, namely sensory consciousness (i.e., indexed by the perceptual awareness negativity) and reflective/access consciousness (i.e., indexed by P3b/LP).

Nonetheless, our results do not fit with either one or the other ERP marker of consciousness (sensory and access). In fact, our findings do not align with neither the perceptual awareness negativity nor the P3b/LP as markers of consciousness in terms of scalp distribution, polarity, and timing. Indeed, the isolated neural activity as the NCC for fear seen on another's face has negative polarity, frontal distribution and emerges in an intermediate time window (between 150 and 400 msec) between the perceptual awareness negativity and the P3b.

How can we reconcile the present results with this previous literature?

The starting point is a suggestion provided by Northoff and Lamme (2020), who argued how the phenomena that the diverse theories try to explain (i.e., "explananda") are fundamentally different from each other. As a consequence, the different kinds of phenomenal experiences under scrutiny lead to different predictions regarding NCC. On the one hand, the theories that hypothesize a central role of the posterior regions of the brain in the generation of consciousness (e.g., Recurrent Processing Theory; RPT; Lamme, 2006, 2010; Lamme & Roelfsema, 2000) and consider relatively early neural responses as potential markers of consciousness (i.e., perceptual awareness negativity) aim to explain consciousness of (visual) sensory contents (see, e.g., Boly et al., 2017; Tsuchiya et al., 2015). On the other hand, theories that regard frontal/prefrontal regions as crucial (Global Neuronal Workspace Theory; GNWT; Dehaene et al., 1998, 2014; Dehaene & Changeux, 2011; Dehaene & Naccache, 2001; and the Higher-Order Thought Theory; HOT; Brown et al., 2019; Gennaro, 2018; Lau & Rosenthal, 2011), along with the associated late neural responses (i.e., P3b/LP), tag a different aspect of consciousness related to higher-level cognitive processing such as context updating (Donchin, 1981).

This acknowledgment is pivotal to tailoring hypotheses and systematizing knowledge. Furthermore, upon closer reading, the Integrated Information Theory (IIT; Tononi, 2004) offers a theory-based solution since it posits that every conscious experience is associated with a specific pattern of integrated information, that is, a complex structure that describes how parts of the system causes and effects specifically to the whole of the system in a specific way (see IIT 4.0, Albantakis et al., 2022 for more details; for computation of a proxy of the integrated information structure from empirical neural recordings, see Haun et al., 2017; Leung et al. 2021), i.e., consciousness arises from the particular patterns of integrated information generated by an experience-related network. From this follows that the physical substrate of consciousness (PSC) is not fixed and not necessarily located posteriorly (the so-called posterior "hot zone"). In fact, the authors predict that the "PSC can shrink, expand or move during normal wakefulness" (Tononi et al., 2016; p. 455), for example, as a function of functional connectivity.

Moving carefully within this very contrastive debate, we suggest that there is no evidence that a single ERP marker of an aspect of consciousness must exist, even though the scientific debate has long stalled between the advocates of perceptual awareness negativity and those of the P3b/LPP (Förster et al., 2020). Rather we suggest that the ERP marker of consciousness, in terms of distribution and timing, might critically depend on the subjective experience studied and experimentally isolated. With the spatial resolution offered by the EEG/ERP technique, the hypothesis of multiple, content-dependent, NCCs may be hard to test under certain circumstances, also when considering perceptual awareness only. For instance, when investigating the subjective experience of seeing simple visual stimuli, such as oriented lines and colors, neural responses elicited on the scalp tend to overlap (although the underlying cortical source might partially differ), leading to the possibly incorrect conclusion that they share the same NCC in terms of ERP (e.g., the perceptual awareness negativity, and in particular, the visual component).

An additional point we want to raise regards the debate around the localizationist/anti-localizationist positions. Our findings align with the view that content-dependent localized and possibly reverberant activity is sufficient for specific consciousness contents to arise, and, more specifically, in the context of this investigation, this type of localized and perchance reverberating activity measured on frontal sensors is a correlate of the awareness of an emotion of fear conveyed by a face. However, caution is necessary, as we cannot exclude that the spatial resolution of the high-density EEG might not be adequate to detect complex long-range neural dynamics. Furthermore, high-density EEG is unsuitable for detecting subcortical structures' activation, likely involved in the conscious processing of facial emotion (see Pessoa et al., 2006 for clear-cut evidence that amygdala responses vary as a function of fearful faces visibility).

While in our study we endeavored to implement various methodological enhancements, it did not eliminate all potential confounds in identifying the "true" NCC for fear perception. In particular, our experimental design requested participants to report on facial stimuli (both neutral and fearful) in all trials. This task-relevance has been pointed out as a potential confound for identifying the NCC (Aru et al., 2012; de Graaf et al., 2012; Miller, 2007; Tsuchiya et al., 2015).

Indeed, recent EEG and MEG studies that adopt "no-report" paradigms or related designs tend to find that late positivity (LP) as a neural correlate of post-perceptual processes tied to reporting rather than actual consciousness (Förster et al., 2020). In these studies, actual conscious seeing of stimuli in the no-report condition is either inferred from obviously visible stimuli (e.g., long exposure, no mask etc.) or confirmed in separated blocks. When recording EEG in the no-report condition, neural activity such as LP prominently reduces, implying LP is reflecting the report process. Meanwhile, other components, especially the perceptual awareness negativity (in particular the visual component, i.e., visual awareness negativity/VAN) seem to remain intact under the no-report conditions (Dellert et al., 2021; Kronemer et al., 2022; Pitts et al., 2012, 2014; Shafto & Pitts, 2015).

With respect to the experiences of faces, a standout effort in teasing apart genuine NCCs comes from Kronemer et al. (2022). Their approach blended EEG, thalamic depth recordings, and fMRI to examine conscious visual perception, adeptly bypassing issues related to overt reporting. Their findings spotlighted ERPs, notably the VAN, as a credible, report-independent visual consciousness indicator. Yet, it is important to underscore that their approach, while enlightening, centered on face stimuli with neutral expression.

Emotional aspects of face were investigated by Sun et al. (2023), who employed the three-stage inattentional blindness paradigm (Pitts et al., 2012, 2014; Shafto & Pitts, 2015) to make face stimuli, including fearful ones, task-irrelevant. Their findings with neutral faces were largely consistent with previous experiments with faces (Dellert et al., 2021; Shafto & Pitts, 2015). With happy and fearful faces, however, they found both VAN and LP to be correlated with the conscious processing of emotional faces, after removing confounds of task-relevance (as seen in their Fig. 2, panels A and B). Although their methodological and analytical approaches differ substantially from ours—including the use of schematic faces and a traditional ERP electrode selection—their ERP patterns are consistent with our observations, particularly concerning the late modulation associated with awareness of fearful faces. Remarkably, in both our study and Sun et al.'s work, aware fearful faces elicited a more pronounced positive activity on fronto-central electrodes within a similar temporal window, compared to faces not consciously perceived (further details can be found in the Additional Materials). A key divergence between the two studies lies in the experimental design of choice: their 3-stage inattentional blindness to tease apart task-relevance from the NCC versus our trial-by-trial detailed probing of awareness in the masking paradigm. It would be an interesting future paradigm to combine our paradigm with the no-report condition as done by Cohen et al. (2020) or Sergent et al. (2021).

Despite the limitations inherent in our study, particularly concerning manipulation of the task-relevance of the face stimuli, it remains encouraging to see our results in alignment with the investigation that explored the conscious perception of happy and fearful faces deemed task-irrelevant.

To conclude, our study sheds light on a significant association between conscious processing of facial emotions, notably fear, and distinctive modulations in frontal ERP components. We have precisely localized neural activity to the anterior region of the scalp within a 150–300 msec timeframe, crucially during the discernment of fear in another's facial expression. Given the wide-ranging spectrum encompassed by consciousness research, our findings underscore the necessity for methodological precision. Our study serves as an initial exploration, prompting more exhaustive future inquiries into these neural correlates, also integrating various neuroimaging techniques, and considering an expansive array of neurological and clinical profiles. Furthermore, our research has centered predominantly on the emotion of fear, leaving a fertile ground for subsequent studies to investigate the manifestation of neural correlates of awareness for other facial emotions and their potential variations across distinct individuals and conditions. In relation to clinical implications, our identified neural signatures hold substantial promise, particularly for addressing challenges in face and emotional processing found in conditions like prosopagnosia, autism, and alexithymia. Deciphering the intricacies of these neural markers might open the door to the development of targeted therapeutic interventions for conditions impinging on facial and emotional recognition. Questions remain, such as whether modulating these frontal ERP components (e.g., by means of transcranial magnetic stimulation) could facilitate the recognition of facial emotions for individuals with prosopagnosia, or aid those with autism in emotion processing.

Data availability

The dataset and analyses reported in this manuscript are available at the Open Science Framework repository: https://osf.io/EV38Q/

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Open practices

The study in this article has earned Open Data and Open Material Badges for transparent practices. The data and material used in this study are available at: https://osf.io/EV38Q.

CRediT authorship contribution statement

Antonio Maffei: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Filippo Gambarota:** Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – original draft. **Mario Liotti:** Writing – review & editing. **Roberto Dell'Acqua:** Writing – review & editing. **Naotsugu Tsuchiya:** Conceptualization, Methodology, Writing – original draft. **Paola Sessa:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Visualization, Writing – original draft.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2024.02.010.

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