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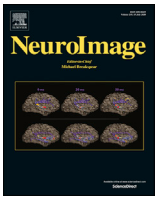

Contextual information resolves uncertainty about ambiguous facial emotions: Behavioral and magnetoencephalographic correlates

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ABSTRACT

Environmental conditions bias our perception of other peoples' facial emotions. This becomes quite relevant in potentially threatening situations, when a fellow's facial expression might indicate potential danger. The present study tested the prediction that a threatening environment biases the recognition of facial emotions. To this end, low- and medium-expressive happy and fearful faces (morphed to 10%, 20%, 30%, or 40% emotional) were presented within a context of instructed threat-of-shock or safety. Self-reported data revealed that instructed threat led to a biased recognition of fearful, but not happy facial expressions. Magnetoencephalographic correlates revealed spatio-temporal clusters of neural network activity associated with emotion recognition and contextual threat/safety in early to mid-latency time intervals in the left parietal cortex, bilateral prefrontal cortex, and the left temporal pole regions. Early parietal activity revealed a double dissociation of face–context information as a function of the expressive level of facial emotions: When facial expressions were difficult to recognize (low-expressive), contextual threat enhanced fear processing and contextual safety enhanced processing of subtle happy faces. However, for rather easily recognizable faces (medium-expressive) the left hemisphere (parietal cortex, PFC, and temporal pole) showed enhanced activity to happy faces during contextual threat and fearful faces during safety. Thus, contextual settings reduce the salience threshold and boost early face processing of low-expressive congruent facial emotions, whereas face-context incongruity or mismatch effects drive neural activity of easier recognizable facial emotions. These results elucidate how environmental settings help recognize facial emotions, and the brain mechanisms underlying the recognition of subtle nuances of fear.

1. Introduction

Recognizing facial emotions is an important function to act adequately in social situations. As facial expressions inform about other people's emotions and intentions, prioritized neural processing and behavioral responding is beneficial to avoid harm or gain profits (Adolphs, 2002; Calder and Young, 2005; Haxby and Gobbini, 2011). Yet, most research on emotional face perception has used highly intense facial emotions, as these are considered most powerful to trigger emotions in the observer. However, subtle nuances of emotion displays are more frequent in everyday life and correctly recognizing them may be particularly helpful in ambiguous situations. This becomes specifically relevant in potentially threatening environments, when subtle fearful or smiling expressions of a fellow might provide additional information signaling danger or safety. Here, the present study focused on facial emotion recognition and its neural network activity during times of perceived threat or safety.

As a powerful mean of non-verbal communication, emotional facial expressions mediate information within a split second. For example, viewing an angry person – directly addressing the observer – has been associated with facilitated electrocortical processing as early as 150 ms after picture onset (compared to neutral faces; e.g., Bublatzky et al., 2017a; Klinkenberg et al., 2016; Schupp et al., 2004). This processing advantage involves enhanced BOLD responses in the amygdala, visual and insular cortices, especially pronounced when viewing fearful facial expressions (Etkin et al., 2004; Lin et al., 2016). This presumably sets the stage for appropriate behaviors such as fight or flight. Corresponding response programs comprise the activation of the autonomous nervous

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system (e.g., Lang and Bradley, 2010), priming of defensive motor reflexes (e.g., enhanced startle reflex; e.g., Anokhin et al., 2010; Bublatzky et al., 2017b, 2018, 2019), and ultimately organize complex behaviors such as avoidant decision-making (Bechara et al., 2000; Bublatzky et al., 2017c). Thus, selective attention to expressions of threat is highly adaptive to find direct or unknown threats in the environment (e.g., anger and fearful faces; Pourtois et al., 2004). However, similar selective attention processes are active when viewing a smile or a loved familiar face, suggesting a more general mechanism of prioritized emotion processing compared to neutral or less salient facial information (Bublatzky et al., 2017a; Guerra et al., 2012; Sander et al., 2003; Schupp et al., 2004).

Prioritized emotion processing is particularly pronounced when being confronted with intense emotions (Bradley et al., 2001; Schupp et al., 2007; Lin et al., 2016). In real life, however, facial emotions are often rather subtle and more ambiguous (Guo, 2012). Correctly recognizing emotional nuances may thus be particularly beneficial as it provides a better base of information regarding the contextual setting. In fact, some studies showed that inter-individual differences in facial emotion recognition occur especially for subtle, more ambiguous expressions. For instance, depressed patients showed impaired recognition of mildly happy faces (Surguladze et al., 2004), and increased amygdala activation to expressions of sadness (Surguladze et al., 2005). Moreover, higher levels of trait anxiety have been suggested to improve perceptual sensitivity and response times within a threatening context (Doty et al., 2013; Sussman et al., 2016a,b). Thus, impaired interpersonal functioning in depressed and/or anxious participants may at least in part rely on the inability to identify nuances of emotion displays in social situations.

Contextual settings – such as information about social situations, preceding events, and environmental conditions – critically modulate the perception and recognition of facial emotions (Wieser and Brosch, 2012). For instance, face processing varies with affective background scenes (e.g. Aviezer et al., 2008; Righart and de Gelder, 2008), the surrounding people's facial expressions (e.g. Bublatzky et al., 2017a; Masuda et al., 2008), body posture and hand movements of the expresser (e.g. Meeren et al., 2005; Hietanen and Leppänen, 2008). Moreover, temporally preceding information mediated by other faces, scenes or stories, lead to affective priming effects that accelerate responding to a subsequently encountered target faces (e.g. Diéguez-Risco et al., 2013, 2015; Hietanen and Astikainen, 2013; Werheid et al., 2005). Here, the affective congruence between facial and contextual information typically leads to faster and more accurate recognition of facial emotions. On the electrocortical level, however, findings are mixed and show enhanced processing for either congruent or incongruent face–context compounds as indicated by P1, N170, or LPP components (e.g. Hietanen and Astikainen, 2013 Krombholz et al., 2007; Meeren et al., 2005; Werheid et al., 2005). All these studies, however, used fully intense emotion displays and contextual settings may exert particular impact on the perception of low-expressive faces.

Focusing on the recognition of subtle nuances of facial emotions within a threatening environment, in a recent study we used contextual background colors that were instructed as signals for threat of electric shocks or safety (Kavcıoğlu et al., 2019). Within this backdrop, neutral as well as varying expressive happy, angry and fearful facial expressions were presented (i.e. ranging from 20% to 80% expressive level). Intriguingly, threat-of-shock enhanced the categorization accuracy for low-expressive 20% fearful faces and interfered with recognizing 20% happy faces. Thus, the affective congruency between contextual and facial information improved recognition performance especially for low-expressive faces. In addition, more trait anxious individuals more frequently erroneously categorized neutral faces as fearful. This was observed for neutral faces presented during the safety condition, and even more pronounced within the threat context (Kavcıoğlu et al., 2019).

Building upon these findings, the present study examined the involved neuronal correlates in viewing and recognizing subtle nuances of facial emotions as a function of expressive level and contextual threat. To this end, morphed facial expressions with low and medium emotion displays were presented (10%, 20%, 30% and 40%; cf. Guo, 2012). Additionally, we included 0% emotional faces (i.e. neutral expressions) to increase the difficulty of the recognition task and to enhance the number of false classifications (e.g. recognizing emotional information within a neutral face). These stimuli were presented within sustained contextual background colors that were verbally instructed as a signal for shock threat or safety, respectively. This so-called threat-of-shock paradigm models a situation in which participants anticipate uncontrollable threat of aversive events, which has been shown to reliably trigger aversive apprehensions or even anticipatory anxiety (Grillon et al., 1991; Olsson and Phelps, 2004; Bublatzky et al., 2010).

Piloting tests confirmed that the emotional expression of morphed facial expressions were quite difficult to recognize, and a better recognition performance was predicted for more expressive (e.g. 30% and 40%) relative to less expressive facial expressions (e.g. 10% and 20%; cf. Hoffmann et al., 2010). Regarding the safety context, we assumed that recognition of happy faces is more precise compared to other facial expressions. This recognition advantage for happy faces has been suggested to be based on the diagnostic value of visually salient facial features (e.g., the mouth region; for a review see Nummenmaa and Calvo, 2015). For the threat condition, however, we predicted that specifically the recognition of fearful faces might be boosted by congruent contextual threat (Kavcioglu et al., 2019). For instance, prestimulus brain activity which was driven by threatening context information, led to improved perceptual decision-making (Koizumi et al., 2016; Sussman et al., 2016a, b).

On the neuronal level, we predicted a dissociation between facial emotions and their expressive level as a function of threat/safety contexts. As observed on the behavioral level (Kavcioglu et al., 2019), enhanced neural activity was hypothesized for congruent face–context compounds (i.e. fearful faces during threat, and happy faces during safety). We searched for this interaction effect in three time intervals of the visual processing stream. First, around the P1 peak of the event-related potential (i.e. 80-130 ms), which has been associated with enhanced vigilance in potentially dangerous situations (e.g. Bublatzky and Schupp, 2012; Steinberg et al., 2012) and processing of threatening faces (e.g. fear or anger; Cornwell et al., 2011; Pourtois et al., 2004). Moreover, indicators of selective face and emotion processing have been consistently observed at mid-latency (e.g., N170, EPN; Hinojosa et al., 2014; Junghöfer et al., 2016; Schupp et al., 2004, 2006; Wieser and Keil, 2014), and late-latency processing stages (LPP; Bublatzky and Schupp, 2012; Olofsson et al., 2008; Schupp et al., 2004, Schupp et al., 2006). For instance, Sprengelmeyer and Jentzsch (2006) reported elevated N170 amplitudes that increased with more expressive emotion displays. For all three time windows (e.g. around P1, N170, LPP; Aguado et al., 2019; Hietanen and Astikainen, 2013), the affective congruency of face–context compounds has been shown as a relevant factor for face processing. Finally, of central interest were processing differences for expressive levels at which emotion recognition is below or above chance level (10%–20% versus 30%–40%), as these provide insights into the temporal dynamics of recognition biases. Similarly, false classifications of the most ambiguous expressions (i.e. misidentifying neutral faces as fearful; Kavcioglu et al., 2019) were hypothesized to vary with neural activity.

2. Methods

2.1. Participants

Thirty healthy students were recruited from the University of Münster. Participants age was between 21 and 36 years ($M = 25.1$, $SD = 3.9$) and scores on depression (BDI-2, $M = 3.6$, $SD = 4.7$; Hautzinger et al., 2006), general anxiety (STAI-state, $M = 33.7$, $SD = 8.7$; STAI-trait, $M = 31.9$, $SD = 6.4$; Spielberger et al., 1983), and social anxiety (SPIN, $M = 9.5$, $SD = 7.0$; Connor et al., 2000), were within regular norms. All participants gave informed consent to the protocol approved by the ethic committee. Participants received monetary compensation (25 €) for their participation. Due to poor data quality, one participant was excluded from the MEG-analyses.

2.2. Materials and design

A total set of 20 face actors[1] (10 females), each displaying happy, neutral, and fearful facial expressions, was selected from the Karolinska Directed Emotional Faces (KDEF; Lundqvist et al., 1998). Emotional facial expressions were morphed to reduce the displayed expressive level of an emotion (cf., Guo, 2012), thus enhancing the difficulty to correctly recognize emotions. To this end, 40%, 30%, 20%, or 10% of an emotional expression was superimposed on the neutral expression of the same face actor using Morpheus Photo Morpher software.[2] Please note, since the recognition bias of fearful versus happy faces was our of-interest comparison, we chose an objective criterion for our face morphs (e.g. superimposing 10% emotional expression on a neutral face). Thus, a fixed ratio of emotional–neutral face compounds were compared (e.g. 10% happy face was compared with a 10% fearful expression).

Pictures were presented rapidly (100 ms; with an ITI of 1–2 s showing a black frame) in blocks of 60 pictures (each actor was presented three times in a pseudo-random order). Each block displayed only face pictures depicting the same emotion and expressive level combination (e.g., only 10% happy faces during Block 1; see Fig. 1). All emotion/expressive level combinations (10%, 20%, 30% and 40% expressive fearful and happy faces) were presented twice amounting to 16 blocks. In addition, four blocks displaying only neutral facial expressions (i.e., 0% emotion) were included in the block sequence to make the recognition task more difficult and to enhance the number of false classifications. Every participant had an individual block order that was pseudorandom with the restriction of maximal two blocks in a row displaying the same expression, and no immediate repetition of the same emotion/expressive level combination.

The participants' task was to watch all pictures presented on the screen and to complete a facial expression recognition task and confidence ratings at the end of each experimental block. For the recognition task, which also has been referred to as categorization or identification task in the literature (see e.g. Adolphs, 2002; Calder et al., 1996), participants indicated by button press whether the preceding block had been a block of happy, neutral or fearful faces. To this end, three response options – predefined as "happy", "neutral" and "fearful" – were displayed on the screen; choices could be done without time limit. Moreover, confidence ratings were scored using a visual analog scale ranging from *not all* to *very confident* (0–10 confidence). Participants also rated the perceived intensity of facial expressions. However, in the present study these ratings are skewed by recognition performance (i.e. intensity ratings rely on correctly identified expressions) and should be therefore interpreted with caution (see supplementary materials).

Half of the experimental blocks were presented within a context of instructed threat-of-shock, and the other half was presented within an instructed safety context. Context conditions were indicated by a green and blue background frames (1024 × 768 pixels; RGB-values: 0,255,0 and 0,0,255) alternating across the experiment. Participants were verbally instructed that one color (e.g., green) indicated that they may receive unpleasant electric shocks (threat condition), whereas the other color (e.g., blue) indicated that no shocks would be delivered (safety condition; cf. Bublatzky et al., 2010, 2014). Color assignment to context and order of context (first threat or first safety) was counterbalanced across participants. Each block was preceded by a colored instruction slide (5 s) reminding "Shock possible" or "No shock".

Pictures were projected onto a translucent screen via a mirror system. The screen was placed at a distance of about 90 cm from the participant's head, and the pictures extended over a visual angle of 16.1° vertically and 12.4° horizontally. Electrical pulses for the shock work-up (maximum 10 mA, 100 ms) were generated by a dual-channel square-pulse stimulator (Grass Instrument Division, Astro-Med Inc., West Warwick, RI, USA), and administered at the left medial forearm. Procedures were controlled by Presentation software (Neurobehavioral Systems, Inc., Albany, CA, USA).

2.3. Procedure

After questionnaires on depression, general and social anxiety were completed, participants' head shape was measured using a 3Space Fastrak System (Polhemus). Then participants were seated in a dimly lit, sound attenuated and magnetically shielded MEG chamber. To track the participants' head position and head movements in the MEG scanner, before and during each recording session, location of landmark coils in each ear and on the nasion were continuously registered. Overall, head movements of any participant during MEG scans did not exceed 5 mm.

The experiment began with three practice blocks (excluded from analyses) familiarizing the participants with the picture presentation and recognition task. As the threat-of-shock manipulation was used to trigger aversive anticipations but not experiences, no electric shocks were applied throughout the experiment (e.g., Bradley et al., 2005; Bublatzky et al., 2014a; Costa et al., 2015). However, similar to previous research, a brief shock work-up procedure was carried out to ensure credibility of the threat-of-shock instruction. To this end, participants received up to eight electric shocks to decide upon a stimulus intensity – rated as maximal unpleasant but not yet painful – to be used during the experiment (see Bublatzky et al., 2010; Riemer et al., 2015). Then, participants were verbally instructed about the following threat and safety contingencies. Specifically, one background color (e.g., green) indicated that they might receive up to three electric shocks (threat context), whereas the other color (e.g., blue) indicated that no shocks would be administered (safety context). After each experimental block, participants were asked to indicate by button press which facial emotion had been presented during this block (recognition task) and how confident they were about their decision (confidence rating). Emotion intensity ratings were also assessed, however, not reported because these were overly skewed by the poor emotion-recognition performance in the low-expressive (10%–20%) emotional faces. A brief break separated first and second half of the experiment. Finally, overall perceived arousal, valence and threat during the threat-of-shock and safety blocks were rated by the Self-Assessment Manikin (SAM; Bradley and Lang, 1994; arousal and valence) and with a visual analog scale ranging from *not at all* to *very much threatening* (0–10; threat).

2.4. Data recording and reduction

Recognition performance was measured in terms of hit rates (i.e. correctly identified emotional facial expressions; HR = [number of hits + 0.5]/[number of targets + 1]) and false alarm rates (i.e. recognizing a neutral face as an emotional; FAR = [number of false alarms + 0.5]/

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[1] KDEF identifiers for the experimental stimuli were: 01f, 02f, 03f, 04f, 06f, 07f, 08f, 09f, 10f, 11f, 14m, 16m, 17m, 18m, 20m, 21m, 23m, 25m, 26m, and 27m. The practice run used different stimuli: 05f, 13f, 15m, and 22m.

[2] The final picture set was pretested in a piloting study (N = 10). To this end, we presented a larger set of face actors with 10, 20, 30 and 40% happy and fearful expressions. Participants' task was to indicate by button press which facial expression they have seen (i.e. happy, neutral or fearful). Building upon this pilot data, we selected and excluded face actors who were the easiest and the most difficult to recognize. Thus, the face actors used in the present experiment were comparable regarding the overall emotion recognizability, but not the facial expressions per se.

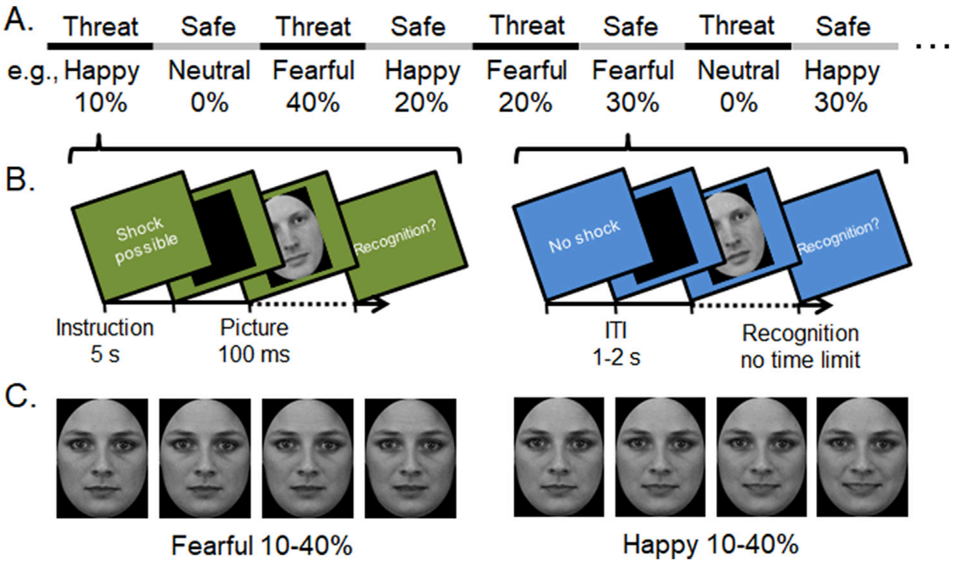

Fig. 1. Schematic illustration of the experimental procedure. (A) Alternating threat-of-shock and safety blocks (indicated by background colors) displayed either happy, neutral, or fearful facial expressions (10%, 20%, 30%, or 40% emotional). (B) In each block, 60 pictures of one facial emotion and expressive level (e.g., 10% happy during threat) were presented for 100 ms each with varying intertrial intervals (ITI, 1–2 s). After each block, a recognition task and confidence rating were completed without time limit. Blocks were preceded by instruction slides (5 s) announcing the condition (threat or safety). No shocks were applied throughout the experiment. (C) Examples of the morphed fearful and happy facial expressions varying from 10% to 40% expressive level. Example pictures are taken from the KDEF (numbers: af01, am10).

[number of distractors + 1]).[3] These parameters were converted into discrimination accuracy (Pr) and response bias (Br) scores based on the two-high threshold (2-HT) model (Corwin, 1994). This model accounts for uncertainty that arise when categorizing subtle emotion displays which are likely to be confused with neutral expressions (Pollak et al., 2000; Surguladze et al., 2004). The general logic is that recognition uncertainty might lead to increased false alarm rates (Snodgrass and Corwin, 1988), and hit rates (HR) alone include the uncertainty due to ambiguity of morphed faces. Accounting for this uncertainty, Pr scores (Pr = HR-FAR) were proposed as the more sensitive measure. Building upon this, a response bias (Br = FAR/(1-Pr)) – defined as the participants' readiness to label an ambiguous stimulus as the target – was calculated and ranges between conservative and liberal responding (0–1). Thus, for the recognition of neutral faces, two separate FAR scores ($FAR^{fearful}$ and FAR^{happy}) were calculated indicating the false categorization of neutral faces as either fearful or as happy (i.e. recognizing an emotional expression where there actually is no facial emotion).

Magnetoencephalographic data was recorded using a 275-channel whole-head sensor system (Omega 275, CTF, VSM Medtech Ltd., Coquitlam, British Columbia, Canada) with first-order axial gradiometers. MEG data was recorded continuously with a sampling rate of 600 Hz and a hardware lowpass filter of 150 Hz to guarantee anti-aliasing. Afterwards, data was sampled down to 300 Hz, high-pass filtered using a zero-phase Butterworth second-order filter of 0.1 Hz and low-pass filtered applying a fourth-order 48 Hz cutoff. Single epochs were extracted from 200 ms before to 600 ms after stimulus onset and were averaged across conditions. MEG data were baseline-adjusted based on a pre-stimulus interval of 150 ms before stimulus onset. Artifact detection and rejection was performed with an established method for the statistical control of artifacts in high-density electro- and magnetoencephalography data (Junghöfer et al., 2000). This procedure (1) detects individual sensor artifacts, (2) detects global artifacts, (3) replaces artifact-contaminated sensors by spherical spline interpolation statistically weighted on the basis of all remaining sensors, and (4) computes the variance of the signal across trials to document the stability of the averaged waveform. The rejection of artifact-contaminated trials and the interpolation of artifact-contaminated sensors relies on the calculation of statistical parameters for the absolute measured magnetic field amplitudes over time, their standard deviation over time, as well as on the determination of boundaries for each parameter based on their distribution across trials.

L2-Minimum-Norm-Estimation (L2-MNE; Hämäläinen and Ilmoniemi, 1994) with Tikhonov regularization (Tikhonov, 1963) was used to examine the underlying cortical sources. This method allows estimating distributed neural network activity without a priori assumptions regarding the location and/or number of current sources (Hauk, 2004). A spherical shell with evenly distributed dipoles in azimuthal and polar direction at 350 positions was used as source model. A spherical shell is a reasonable approximation of the cortical surface and circumvents the necessity for the regularization of quasi-radial sources in more realistic MEG head modelling. A source shell radius of 87% of the individually fitted head radius was chosen, roughly corresponding to gray matter depth. Across all participants and conditions, a Tikhonov regularization parameter k of 0.1 was applied. Topographies of source-direction-independent neural activities – the vector length of the estimated source activities at each position – were calculated for each individual participant, condition and time point. For visualization purposes, L2-MNE results were finally projected onto a 3d model brain. Pre-processing and analysis of MEG data was conducted using the MATLAB-based software EMEGS (Peyk et al., 2011).

2.5. Data analysis

Self-reported threat, valence, and arousal were compared between threat and safety context. Behavioral performance, as indicated by discrimination accuracy (Pr) and response bias (Br), was analyzed based on repeated measures ANOVAs with the within-subject factors Context (threat vs. safety), Facial Expression (fearful vs. happy), and Expressive Level (10% vs. 20% vs. 30% vs. 40% emotion display). For the categorization of neutral facial expressions, false alarm rates (FAR) were tested with Context (threat vs. safety) and Facial Expression (fearful vs. happy).

Across all participants, mean hit rates (ranging between 0.25 and 0.75) for recognizing 10% and 20% expressive faces were low to moderate (HR = 0.33 and 0.55), and for the 30% and 40% expressive facial expressions very good (HR = 0.68 and 0.74). In order to enhance statistical power for the MEG analyses we merged low (10%, 20%) and medium (30%, 40%) Expressive Levels (see Supplements 2 for separate analyses of expressive levels). Repeated measures ANOVAs with the

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[3] Because participants underwent each experimental condition exactly once (i.e. one block of happy 10% during threat, one block of happy 10% during safety, and so on), the number of targets was 1, and responses were either correct or wrong (HR = 0.75 or 0.25).

within-subject factors Context (threat vs. safety), Facial Expression (fearful vs. happy), and Expressive Level (low vs. medium) were calculated for each estimated neural source and each time point. We searched for spatio-temporal clusters showing a significant three-way interaction of all factors. A non-parametric testing procedure similar to the cluster mass-test used for analyses of fMRI data was applied for the statistical analyses of the MEG data including a priori defined of-interest time intervals and correction for multiple comparisons (Maris and Oostenveld, 2007). To this end, F-values of the parametric three-way interaction of spatially neighboring and temporally consecutive dipoles below a critical alpha level of $p = .05$ (sensor-level criterion), were summed up to so-called cluster masses. Based on previous research, we a priori defined three time windows, which were consistently observed to be sensitive to the processing of emotional facial expressions and instructed threat. Associated with rapid vigilance effects, an early time window of interest ranged from 80 to 130 ms post-stimulus (e.g., P1 effects; Carretié et al., 2004; Steinberg et al., 2012; Pourtois et al., 2004). Moreover, indicators of selective face and emotion processing have been reported at two time windows. A mid-latency time interval ranging from 100 to 300 ms (e.g., N170 and EPN; Hinojosa et al., 2014; Liu et al., 2002; Pegna et al., 2011; Schupp et al., 2006, 2007), and the so-called Late Positive Potential (LPP) between 300 and 600 ms (Bublatzky and Schupp, 2012; Olofsson et al., 2008; Schupp et al., 2004, Schupp et al., 2006).

Thus, cluster masses for the of-interest three-way interaction were identified separately for these three time intervals (early: 80–130 ms; mid-latency: 100–300 ms; late: 300–600 ms) against a random cluster-based permutation alpha level of $p = .05$. Permutations were conducted using Monte Carlo simulations of identical analyses based on 1000 permuted drawings of the experimental labels of conditions. For each permutation, the biggest cluster mass identified at any region of the source space and any time within the respective time window of interest was considered. When the cluster mass of the originally labelled conditions was higher than the critical cluster mass of this permutation distribution corresponding to a p-value $= .05$ (i.e. higher than the 950th biggest cluster mass of the random distribution; cluster-level criterion), the cluster was considered significant. Then, all significant spatiotemporal clusters were followed-up with repeated-measures ANOVAs including the within-factors Context (threat vs. safety), Facial Expression (fearful vs. happy), and Expressive Level (low vs. medium). To further test for hemispheric differences, significant cluster were mirrored (sagittal) and included as an additional factor Laterality (left vs. right hemisphere).

Testing the impact of threat versus safety context on neutral face processing (i.e. 0% emotional content), for neutral faces paired t-tests (threat vs. safety) were conducted for each estimated neural source and each time point. Positive (threat > safety) and negative (threat < safety) t-value distributions were tested by cluster permutation tests in the three time intervals convergent to the analysis of the three-way interaction described above ($p < .05$ on sensor and cluster level). Focusing on the neural correlates of recognition biases (e.g., misidentifying neutral faces as fearful; Kavcioglu et al., 2019), correlational analyses were performed between neural activation to neutral faces (difference threat-safe) and the false categorization of neutral faces as either fearful or as happy ($\text{FAR}^{\text{fearful}}$ and $\text{FAR}^{\text{happy}}$).

Greenhouse-Geisser corrections were applied where relevant, and the partial η^2 (η_p^2) is reported as effect size. Controlling for Type 1 error, Bonferroni correction was applied for post-hoc t-tests.

3. Results

3.1. Self-report data

3.1.1. Manipulation check

Ratings clearly confirmed previous research using the threat-of-shock protocol (Fig. 2). The instructed threat context was rated as more threatening, more arousing, and more unpleasant compared to the instructed safety Context, $Fs(1,28) = 24.8$, 33.96, and 16.4, $ps < .001$, $\eta_p^2 = 0.47$, 0.55, and 0.37.

3.1.2. Confidence ratings

As expected, overall confidence increased with increasing Expressive Level, $F(3,87) = 31.75$, $p < .001$, $\eta_p^2 = 0.52$. Regardless of threat or safety condition, participants were overall more confident in recognizing fearful compared to happy Facial Expression, $F(1,29) = 13.60$, $p = .001$, $\eta_p^2 = 0.32$. The main effect Context did not reach significance, $F(1,29) = 2.48$, $p = .13$, $\eta_p^2 = 0.08$, however, confidence ratings varied as a joint function of Context × Facial Expression, $F(1,29) = 5.13$, $p < .05$, $\eta_p^2 = 0.15$ (Fig. 3A). Follow-up tests revealed that confidence was lower for happy faces during threat condition (relative to safety), $p = .01$, but no differences emerged for neutral and fearful faces between threat or safety context, $ps = .30$ and .88. Moreover, the interaction Facial Expression × Expressive Level approached significance, $F(3,87) = 2.76$, $p = .057$, $\eta_p^2 = 0.09$. This interaction was driven by the fact that confidence was higher in recognizing fearful compared to happy faces for the more ambiguous expressive levels of emotion at 20% and 30%, $ps < .01$ and .001, but not for the most difficult (10%) and most easily categorized (40%) expressive levels, $ps = .46$ and .098. No further interaction reached significance, $F(3,87) < 1.16$, $p > .33$, $\eta_p^2 < 0.04$.

3.2. Behavioral data: recognition performance

3.2.1. False alarm rates (FAR)

Participants tended to falsely categorize neutral faces as emotional, Facial Expression $F(1,29) = 10.85$, $p < .01$, $\eta_p^2 = 0.27$, and these mistakes were particularly pronounced during threat relative to safety Context, $F(1,29) = 11.15$, $p < .01$, $\eta_p^2 = 0.28$ (Fig. 3B). Moreover, a significant

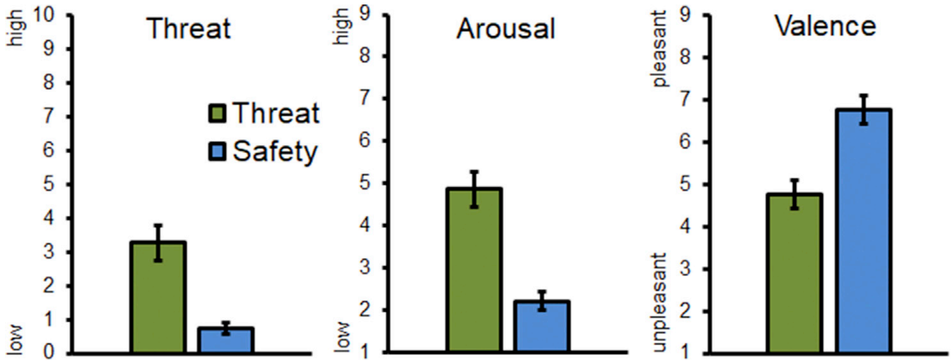

Fig. 2. Mean threat, arousal, and valence ratings as a function of instructed threat-of-shock or safety (SEM). Self-report data clearly confirm that contextual threat condition was perceived as more threatening, arousing, and unpleasant compared to the safety context.

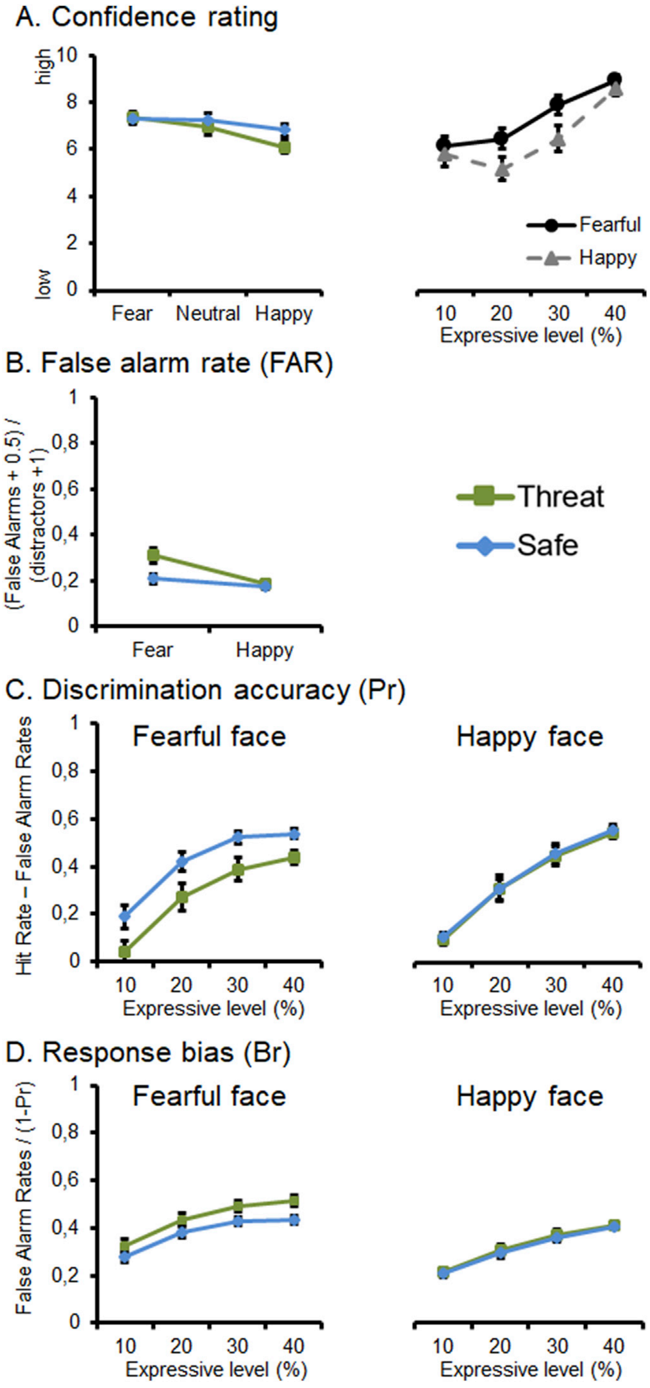

Fig. 3. Facial emotion recognition as a function of expressive level during threat-of-shock and safety condition. (A) Confidence ratings for categorizing happy, neutral, and fearful faces during threat or safety (left side), and as a function of expressive level (right side). (B) False alarm rates reflect misclassification of neutral faces as either fearful or happy. Building upon this (C) discrimination accuracy and (D) response biases vary specifically for fearful faces.

interaction Context × Facial Expression, $F(1,29) = 6.27$, $p < .05$, $\eta_p^2 = 0.18$, showed that threat-enhanced false alarms occurred significantly more often towards fearful facial expression, $p = .005$, but not towards happy faces, $p = .33$.

3.2.2. *Discrimination accuracy (Pr)*

Overall, contextual threat reduced discrimination accuracy of facial expressions relative to safety Context, $F(1,29) = 6.82$, $p < .05$, $\eta_p^2 = 0.19$ (Fig. 3C). The main effect Facial Expression was not significant, $F(1,29) = 0.001$, $p = .98$, $\eta_p^2 < 0.01$, however, an interaction with Context was observed, $F(1,29) = 6.25$ $p < .05$, $\eta_p^2 = 0.18$. Follow-up analyses revealed that fear recognition performance decreased during threat compared to safety, $p < .01$, but no difference was observed for happy faces, $p = .81$. Moreover, discrimination accuracy improved with increasing Expressive Level, $F(3,87) = 110.08$, $p < .001$, $\eta_p^2 = 0.79$, however, neither the two-way interactions Expressive Level × Context, $F(3,87) = 0.10$, $p = .94$, $\eta_p^2 < 0.01$, nor Expressive Level × Facial Expression, $F(3,87) = 2.37$, $p = .09$, $\eta_p^2 = 0.08$, nor the three-way interaction Expressive Level × Facial Expression × Context reached significance, $F(3,87) = 0.21$, $p = .83$, $\eta_p^2 = 0.01$. Because we predicted better recognition of fearful (but not happy) faces in a threatening context (cf. Kavcioglu et al., 2019), we compared threat versus safety conditions for all facial emotions and expressive levels. Opposite to our hypotheses, follow-up tests revealed trend wise or significantly better recognition of fearful faces during safety compared to threat condition for each expressive level, $ps^{10\%\text{-}40\%} = 0.06$, 0.03, 0.02, and 0.01, but not for happy facial expressions, $ps^{10\%\text{-}40\%} = 0.68$, 0.93, 0.86, and 0.68.

3.2.3. *Response biases (Br)*

Biased responding towards categorizing facial expressions as emotional (rather than neutral) was observed during threat compared to safety Context, $F(1,29) = 7.34$, $p = .01$, $\eta_p^2 = 0.20$ (Fig. 3D). This bias was more pronounced with increasing Expressive Level, $F(3,87) = 109.25$, $p < .001$, $\eta_p^2 = 0.79$. Importantly, participants tended to categorize ambiguous facial expressions as fearful, Facial Expression $F(1,29) = 18.43$, $p < .001$, $\eta_p^2 = 0.39$. The interaction Context × Facial Expression did not reach significance, $F(1,29) = 2.87$, $p = .10$, $\eta_p^2 = 0.09$. No further interaction reached significance, $Fs(3,87) < 1.87$, $ps > .15$, $\eta_p^2 < 0.06$.

3.3. *Neural data*

3.3.1. *Estimated neural sources L2-MNE*

Based on previous research, a priori defined time intervals of interest (early: 80–130 ms; mid-latency: 100–300 ms; late: 300–600 ms) were tested focusing on the of-interest three-way interaction of Context × Facial Expression × Expressive Level. For the *early time interval (80*–130 ms*)*, two left sided spatio-temporal clusters reached significance (centro-parietal and anterior; see Figs. 4A and 5A). Because the time boundaries of cluster significance (centro-parietal: 80–127 ms; anterior: 100–130 ms) were in part limited by the a priori defined interval, an exploratory post-hoc inspection was performed within a broader time interval 50–160 ms (i.e., ± 30 ms) post-stimulus. Please note, the post-hoc extension of the temporal search interval was performed solely to better estimate the onset and offset of the found effects; the described cluster revealed significance within the a priori defined intervals. In fact, these exploratory analyses revealed an earlier onset of the centro-parietal cluster (63 ms), and a later offset of the anterior cluster (157 ms). This post hoc inspection also revealed the left anterior cluster with a broader spatial expansion.

The a priori *mid latency analysis (100*–300 ms*)* substantiated the found left anterior cluster within the identical time interval 103–157 ms (see Fig. 5A). The left-sided cluster expanded from the ventrolateral prefrontal cortex (vlPFC) to the anterior temporal pole region, and a right-sided prefrontal cluster revealed significance. For the *late time window (300*–600 ms*)*, no first-level significant cluster reached cluster-level significance.

For neutral faces, paired *t*-tests did not reveal any spatio-temporal cluster with significant differences between threat and safety context within the a-priori defined time intervals. However, visual inspection showed distinctly enhanced neutral face processing during threat compared to safety in an earlier LPP time interval. In fact, restriction of the LPP search interval between 300 and 400 ms resulted in a significant right hemispheric occipito-temporal cluster in a time interval between 310 and 397 ms. Again, an analysis for effects of laterality revealed

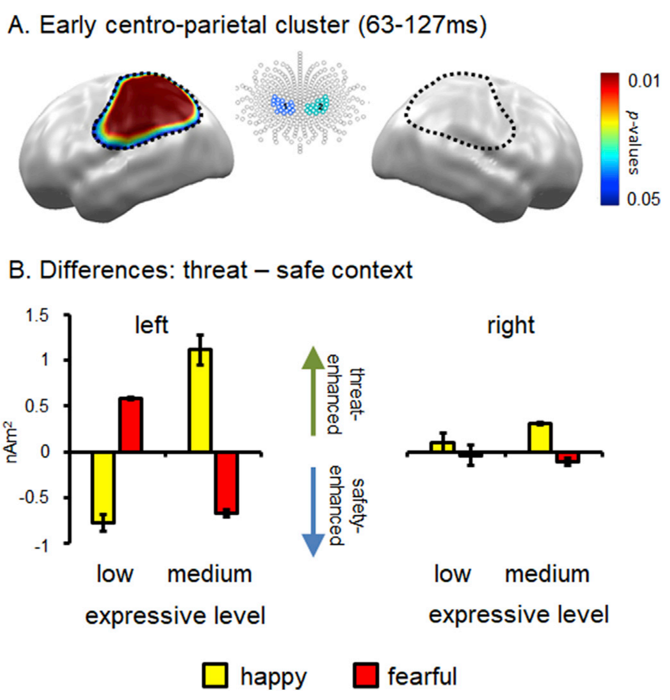

Fig. 4. Interaction of Context × Facial Expression × Expressive Level for estimated neural activity. (A) Significant spatio-temporal cluster covering left parietal regions in the time interval between 63 and 127 ms post face onset. A sagittal mirrored cluster (dotted black lines) is used for the right hemisphere and involved sensors are shown. (B) Bar-graphs illustrate difference scores (threat-safety condition, ±SEM) of neural activity for happy and fearful faces as a function of low and medium emotional expressive level. Positive values indicate threat-enhanced cluster activity, negative values indicate safety-enhanced activity.

qualitatively identical effects in a mirrored left hemispheric spatio-temporal cluster (Fig. 6).

3.3.2. Early centro-parietal cluster (63–127 ms)

The overall post-hoc ANOVA confirmed the significant interactions of Context × Facial Expression × Expressive Level, $F(1,28) = 8.36, p < .01, \eta_p^2 = 0.23$, and revealed hemispheric specificity based on a significant four-way interaction, Context × Facial Expression × Expressive Level × Laterality, $F(1,28) = 5.79, p < .05, \eta_p^2 = 0.17$ (Fig. 4B). Follow-up analyses were calculated for each hemisphere separately. The left-sided cluster confirmed the interaction Context × Facial Expression × Expressive Level, $F(1,28) = 22.96, p < .001, \eta_p^2 = 0.45$. For low-expressive fearful faces, activity tended to be more pronounced during threat compared to safety context, $p = .061$, at medium-expressive level activity was more pronounced during safety context, $p = .057$. The reversed pattern was observed for happy faces: safety-enhanced activity for low- and threat-enhanced for medium-expressive faces, $ps < .05$ and .01. Moreover, the interaction Facial Expression × Expressive Level approached significance, $F(1,28) = 3.72, p = .06, \eta_p^2 = 0.12$, indicating more activity for medium-expressive happy compared to fearful faces, $p = .02$, but no difference for low-expressive facial emotions, $p = .83$. Regarding the right hemisphere, no main effect or interaction reached significance, $Fs(1,28) < 2.69, p > .11, \eta_p^2 < 0.09$.

3.3.3. PFC-temporal pole cluster (103–157 ms)

Across the left sided and laterally mirrored right sided cluster significantly more activity was observed for the threat compared to the safety Context, $F(1,28) = 4.37, p < .05, \eta_p^2 = 0.14$ (Fig. 5). Importantly, interactions emerged for Context × Facial Expression, $F(1,28) = 4.39, p < .05, \eta_p^2 = 0.14$, and Context × Facial Expression × Expressive Level, $F(1,28) = 12.79, p = .001, \eta_p^2 = 0.31$. Separate analyses were conducted for each hemisphere.

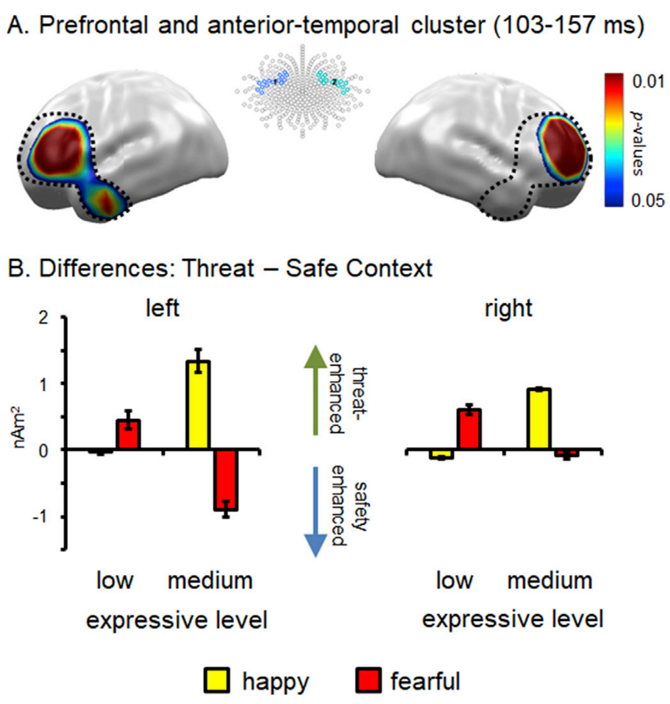

Fig. 5. Interaction of Context × Facial Expression × Expressive Level for estimated neural activity. (A) Bilateral spatio-temporal clusters covering prefrontal and anterior temporal pole regions in the time interval between 103 and 157 ms post face onset. Sagittal mirrored clusters were used (dotted black lines) and involved sensors are shown. (B) Bar-graphs illustrate difference scores (threat-safety condition, ±SEM) of neural activity for happy and fearful faces as a function of low and medium expressive level. Positive values indicate threat-enhanced cluster activity, negative values safety-enhanced activity.

For the left vlPFC and temporal pole cluster, activity varied as a function of Context × Facial Expression, $F(1,28) = 7.86, p < .01, \eta_p^2 = 0.22$, and Context × Facial Expression × Expressive Level, $F(1,28) = 12.4, p = .001, \eta_p^2 = 0.31$. No threat effects were observed for low-expressive fearful and happy faces, $ps = .22$ and .91. With regard to the medium-expressive level, however, fearful faces were associated with significantly less activity during threat relative to safety context, $p < .05$. The opposite pattern was true for happy faces, showing pronounced threat-enhanced activity, $p = .001$.

For the right vlPFC and temporal pole, cluster effects were qualitatively similar to the left cluster: Enhanced activity was observed for threat relative to safety context, $F(1,28) = 7.56\ p < .05, \eta_p^2 = 0.21$, and the interaction Context × Facial Expression × Expressive Level reached significance, $F(1,28) = 7.26, p < .05, \eta_p^2 = 0.21$. Follow-up tests showed threat-enhanced activity for low-expressive fearful faces, $p < .05$, but no differences at the medium-expressive level, $p = .76$. Happy faces did not show threat effects at low-expressive level, $p = .64$, however, threat-enhanced activity at medium-expressive level, $p = .001$.

3.3.4. Occipito-temporal cluster (303–397 ms) for neutral face processing

Enhanced neural activity was observed for neutral faces during threat relative to the safety context (Fig. 6), $F(1,28) = 9.28, p < .05, \eta_p^2 = 0.18$. On the descriptive level this effect seemed to be more pronounced over the right hemisphere, however, neither the main effect of Laterality, $F(1,28) = 0.08, p = .79, \eta_p^2 < 0.01$, nor the interaction Context × Laterality reached significance, $F(1,28) = 1.22, p = .28, \eta_p^2 = 0.04$.

Correlational analyses between neural activation to neutral faces (difference threat-safe) and their false categorization as either fearful or as happy were performed (i.e. false alarm rates). Threat-enhanced neural

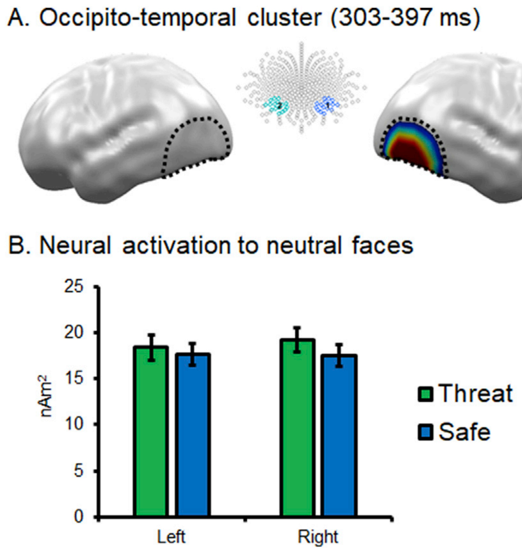

Fig. 6. Main effect of Context for estimated neural activity during perception of neutral faces. (A) Bilateral spatio-temporal clusters covering occipito-temporal regions in the time interval between 303 and 397 ms post face onset. Sagittal mirrored clusters were used (dotted black lines) and involved sensors are shown. (B) Bar-graphs illustrate neural activity for neutral faces as a function of threat and safety context (±SEM).

activity was associated with more false alarm rates towards fearful (FAR$^{\text{fearful}}$ $r = 0.37$, $p < .05$), and marginally towards happy facial expressions (FAR$^{\text{happy}}$ $r = .35$, $p = .06$), within the right hemisphere cluster, but not within the left hemisphere cluster FAR$^{\text{fearful}}$ $r =$ -.12, $p = .53$ and FAR$^{\text{happy}}$ $r = .11$, $p = .58$. Thus, the bigger the right-sided neural activation during threat (relative to safety) condition, the more likely were neutral faces falsely classified as fearful.

4. Discussion

The present study provides a detailed analysis of how subtle nuances of emotional facial expressions are recognized during times of threat and safety. Whereas verbal instructions effectively established context conditions, behavioral performance revealed detrimental effects of threat-of-shock on the recognition of facial emotions. Within a threatening context, participants tended to mistake neutral faces as fearful, leading to threat-enhanced false alarm rates and reduced discrimination accuracy of emotional facial expressions. This recognition bias was associated with enhanced occipito-temporal activity (303–397 ms). Moreover, neural network activity varied as a function of facial emotion and contextual threat or safety. Significant spatio-temporal clusters emerged in the left parietal cortex (63–127 ms), bilateral prefrontal cortices and temporal pole regions (103–157 ms). Importantly, early parietal activity revealed a double dissociation of face–context information (fearful/happy faces and contextual threat/safety) as a function of the emotional expressive level. Specifically, for facial expressions, which were very difficult to recognize (low expressive), contextual threat enhanced neural activity to fearful faces. In contrast, the processing of smiling faces was enhanced by contextual safety. Regarding more easy recognizable facial emotions (medium-expressive), pronounced left sided neural activity (parietal cortex, vlPFC, and temporal pole) was observed to incongruent face–context compounds (i.e., happy faces during threat and fearful faces during safety). Thus, early processing stages revealed contextual priming effects for hard-to-recognize facial emotions (left parietal cortex) and later vlPFC and temporal pole activity was associated with the integration of affectively incongruent face–context information reflecting more in-depth processing of unexpected environmental conditions.

4.1. *Early context-congruent perceptual processing*

Viewing a fellows' facial emotion in a potentially threatening environment provides important extra information to facilitate appropriate (defensive) behaviors. The present results revealed a double dissociation of the contextual settings and emotional facial expressions as a function of the emotional expressive level. In parietal processing areas (63–127 ms), contextual threat specifically amplified cortical activity to low-expressive fearful facial expressions, and contextual safety selectively enhanced the processing of subtle smiling faces. This result pattern complements behavioral data from a previous companion study (Kavcioglu et al., 2019). Focusing on recognition performance and psychophysiological responding, we observed improved emotion recognition for 20% fearful faces during threat and 20% happy faces during safety. Thus, contextual settings provide baseline information for the occurrence of facial fear during threat, and smiling faces during safety conditions. In the case of ambiguous low-expressive facial emotions, such a context-congruent default-processing mode (e.g., reduced salience threshold to identify a face as fearful) appears highly adaptive to recognize predictable emotions. That is, in a threatening situation it is more likely to encounter a fear-expressing person than a smiling one. Following this reasoning, the present MEG findings might reflect the workings of motivational circuits (appetitive and aversive) guiding perceptual-attentive processing and somatic-autonomic response systems. According to the motivated attention and motivational priming hypotheses (Lang et al., 1997), for instance, defensive reflexes are more readily activated in a threatening context. This logic has been transferred also to the perceptual domain suggesting that attentional processes are guided by motivational relevance of foreground and contextual information (e.g. Bradley et al., 2003; Schupp et al., 2004; Moratti et al., 2004). Thus, a threatening context might selectively enhance the recognition of threat-cues whereas a safe context enhances recognition of appetitive information (e.g. a smiling person during safety).

In fact, previous research showed such congruency effects in person perception with regard to multimodal integration of emotional faces, voices and body language (e.g., de Gelder and Vroomen, 2000; Müller et al., 2011). For instance, regarding emotional face–body compounds, Meeren et al. (2005) observed enhanced P1 effects as early as 115 ms after stimulus onset. The authors suggest a rapid neural mechanism, which is sensitive to the degree of congruence between concurrent facial expression and emotional body language. Moreover, viewing fearful faces presented with fear-related scenes as a backdrop (e.g., picture of a car accident) led to pronounced left sided N170 amplitudes of the event-related electrocortical activity (Righart and de Gelder, 2008). This occipito-temporal negativity has been more pronounced for increasing levels of emotion intensity of fearful expressions (Leppänen et al., 2007) as well as angry and disgusted faces (Sprengelmeyer and Jentzsch, 2006), and varies with the affective congruency of temporally preceding information (i.e. affective priming; e.g. Diéguez-Risco et al., 2015; Hietanen and Astikainen, 2013). The N170 component has been suggested to predominantly originate from fusiform gyrus (Pizzagalli et al., 2002; Iidaka et al., 2006), having direct connection to the amygdala, which has long been shown to be sensitive to facial emotions (e.g., Morris et al., 1996). Here, the present results suggest a very early onset (<100 ms) of context-enhanced face processing, which may originate from prediction-based perceptual priming effects driven by contextual settings and anticipatory processes (Dolan et al., 2001; Engel et al., 2001; Bublatzky and Schupp, 2012).

4.2. *Elaborate processing of deviant information*

In contrast, when viewing clear-cut facial expressions at a medium-expressive level, the left parietal cortex was most active for incongruent face–context compounds. Specifically, pronounced neural activity was observed for smiling persons during threat and fearful faces during safety conditions. For the integration of such rather unexpected and deviant information, more elaborate processing is required. Ample evidence points to a mismatch detection mechanism, triggered by physical, semantic, or affective violation of expectations (e.g., Näätänen et al., 2007; Kutas and Federmeier, 2000; Woldorff et al., 1998). For instance, specifically pleasant scenes were associated with selective attention processes when undergoing aversive anticipations (Bublatzky et al., 2010), and triggered pronounced defensive responding when cueing threat (Bradley et al., 2005). Moreover, two recent MEG studies showed threat effects involving the superior temporal gyrus and parietal cortex, as well as a feedforward coupling between auditory cortex and a temporo-frontal network in an auditory oddball task while undergoing threat-of-shock (Cornwell et al., 2007, 2017). The authors suggest that the balance in reciprocal network communication (between sensory and temporo-frontal cortical network) was temporally skewed by aversive shock anticipations (Cornwell et al., 2017). Interestingly, the present pattern of incongruence processing was also observable in spatio-temporal clusters at bilateral ventrolateral PFC and left temporal pole regions (103–157 ms; see also supplementary materials), which both has been suggested to be involved in emotion-perception integration (Olson et al., 2007). Taken together, this widespread neural activation pattern suggests ongoing elaborate stimulus analyses possibly driven by a re-entrant processing flow from anterior to inferior-temporal and parietal brain areas (Keil et al., 2009; Sabatinelli et al., 2005; Moratti et al., 2004).

These result patterns – the context-congruent default processing of ambiguous faces and context-incongruent processing of emotions that are more clear-cut – suggest the workings of distinct but concurrent processes focusing on the prediction-based recognition and integration of rather unexpected information. In both cases, face–context compounds require more elaborate processing, either because of low-expressive subtle expressions or because of deviant facial emotions. In other words, undergoing aversive anticipations, a smile might pop out because of affective incongruence between cue and context, and/or due to elevated affective meaning (e.g., a mean person smiling at me while undergoing threat). Alternatively, viewing a fearful face during safety is more informative as it signals 'the situation is not totally safe'. In contrast, viewing a fearful face during threat is more redundant and requires less higher-order processing resources. To test these opposing explanations, future research might implement explicit task instructions (e.g., count all fearful faces presented during threat/safety; cf. Schupp et al., 2007) in compound social–anticipatory situations (e.g. expecting to meet a person; Bublatzky et al., 2014a,b). Here, the gradual variation of emotional expressivity and/or perceived intensity might help detailing congruency effects in spatial versus temporal contextual settings (e.g. background frames or preceding pictures), as a function of the pre-knowledge of the perceiver (e.g. information about a situation or person).

4.3. Verbal communication of threat and safety

As expected, the mere verbal instruction about imminent but unpredictable threat of electric shocks was highly effective to provoke aversive anticipation in the participants. These context-triggered apprehensions have been shown to prime defensive motor-behavioral reflexes (Bublatzky et al., 2013; Grillon and Charney, 2011), elicit behavioral avoidance (Bublatzky et al., 2017c; Clark et al., 2012; Dymond et al., 2012), and disrupt reward reversal learning in more complex decision-making tasks (Paret and Bublatzky, 2020). In the present study, behavioral performance revealed detrimental effects of contextual threat on the recognition of facial emotions. Within a threat context, participants tended to mistake ambiguous faces as fearful, leading to reduced discrimination accuracy of facial expressions. Interestingly, threat-enhanced false alarms were significantly more often towards recognizing fearful but not happy facial expressions, this recognition bias was associated with threat-enhanced neural activity (temporo-occipital, 303–397 ms), and participants were more confident about their decisions during threat. These behavioral findings add to a recent study that also showed biased recognition performance during a threatening context specifically towards fearful facial expressions. However, the direction of effects was opposite to the present findings, with improved discrimination accuracy for fearful faces (Kavcioglu et al., 2019). Moreover, other studies have observed more liberal recognition biases to fearful compared to perceiving happy or angry faces (Nummenmaa and Calvo, 2015; Leppänen et al., 2007), and such recognition and confidence effects have been associated with reduced gray matter density in dlPFC, a region linked to perceptual decision-making (Koizumi et al., 2016). Thus, labeling an ambiguous face as fearful may have prioritized access to conscious processing, especially during times of anticipated threat.

4.4. Potential clinical implications

In contrast to a 'classically' fear-conditioned threat context, in this experiment, participants never received aversive shocks contingent with the instructed threat context. This was done to address the impact of anticipated (but not experienced) threat, which has been suggested to be more relevant to anxiety-like symptomatology in response to sustained and diffuse threats (e.g. Davis et al., 2010; Grillon, 2008). Beyond testing healthy participants in the present study, relations between (in)accurate facial emotion recognition and psychopathology of interpersonal functioning are given. For instance, aversive anticipations and high levels of trait anxiety have been suggested to improve perceptual sensitivity and faster reaction times during threat (Doty et al., 2013; Sussman et al., 2016a,b). Moreover, in depressed patients, impaired recognition of mildly happy faces has been observed (Surguladze et al., 2004), and increased amygdala activation to expressions of sadness (Surguladze et al., 2005). Thus, impaired interpersonal functioning in depressed and/or anxious participants may rely on the inability to identify nuances of emotion displays during social interactions. Moreover, mood-congruent processing biases may critically contribute to maintain psychopathology by means of reinforcing emotional states (Bar-Haim et al., 2007; Elliott et al., 2002). Here, future research may follow up on prediction-based perceptual processing in hypervigilant states, for instance, with patients suffering from posttraumatic stress or social anxiety disorder.

4.5. Limitations and future directions

Some methodological aspects of the present study need to be considered. We chose an inverse source model that constrained inverse solutions to superficial regions (i.e. the cortex) and thus excluded subcortical structures from modeling. With the chosen inverse modeling, neural activation in deeper structures get projected to the cortex but due to the exponentially reduction of the magnetic field with depth and the additional reduction of depth resolution as consequence of the axial gradiometer system used here, we suppose projections of deeper structures as rather weak. Nevertheless, our analysis can thus not provide any inferences about subcortical structures. We also chose a spherical head model, which is a reasonable approximation of the cortical surface and circumvents the necessity for the regularization of quasi-radial sources in more realistic MEG head modelling. For visualization purposes, the L2-MNE results calculated on this spherical head model were eventually projected onto the 3d model brain. Thus, activities in source regions deviating from a sphere to a stronger degree (such as prefrontal activities in Fig. 5) could be mislocalized to a stronger degree than activities in regions with a better fit (e.g. clusters in Figs. 4 and 6).

Given the robust and stable nature of instructed threat effects shown in multiple studies and even across repeated test days (Bublatzky et al., 2014a) we decided to optimize the present study for MEG recordings forgoing additional peripheral physiology measures as further manipulation checks. Regarding presentation features, the blocked presentation of facial emotions might have simplified emotion recognition, however, enabled a good stimulus to noise ratio for the neural data. Building upon a companion study which focused on behavioral and psychophysiological responding to 20%–80% expressive happy, fearful and angry expressions (Kavcioglu et al., 2019), we also obtained only one recognition trial per emotion conditions (e.g., just one trial for recognizing 10% happy during threat). This limitation might explain diverging behavioral result patterns and actually prevented meaningful correlational analyses of neural data with the recognition data for happy and fearful facial expressions. Future research might use event-related designs with online shock expectancy ratings to better focus on the involved mechanisms of threat generalization and extinction learning (Dunsmoor et al., 2017; Lovibond and Shanks, 2002). Moreover, the motivational direction of facial expressions may be of particular relevance during times of threat or safety (Adams et al., 2003; Hess et al., 1997). For instance, comparing the recognition of approach-versus avoidance-related unpleasant facial expressions (e.g., anger vs. fearful) might be particularly interesting. Similarly, morphing different facial emotions and or identities might help clarify the impact of ambiguity on person perception during threat and safe conditions (e.g., Schweinberger et al., 1999).

5. Conclusions

The present study elucidate how environmental settings of threat or safety help recognize subtle nuances of happy and fearful faces. During the anticipation of aversive events, more false alarms occurred and participants tended to mistake low-expressive ambiguous faces as fearful. Regarding neural activity, false alarms were associated with more occipito-temporal activity (303–397 ms). Moreover, early processing stages revealed contextual priming effects for hard-to-recognize facial emotions (e.g. fearful faces during threat; 67–127 ms; left parietal cortex) and later vlPFC and temporal pole activity (100–160 ms) was associated with the integration of affectively incongruent face-context information reflecting more in-depth processing of unexpected environmental conditions (e.g., happy faces during threat). These findings indicate that contextual settings reduce the salience threshold and boost early face processing of low-expressive congruent facial emotions, whereas face–context incongruity drives neural activity for clear-cut facial emotions.

CRediT authorship contribution statement

Florian Bublatzky: Supervision, Conceptualization, Methodology, Formal analysis, Funding acquisition, Writing - original draft. **Fatih Kavcıoğlu:** Formal analysis, Methodology, Writing - review & editing. **Pedro Guerra:** Conceptualization, Methodology, Writing - review & editing. **Sarah Doll:** Formal analysis. **Markus Junghöfer:** Supervision, Conceptualization, Formal analysis, Methodology, Funding acquisition, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116814.

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