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Threat-conditioned contexts modulate the late positive potential to faces—A mobile EEG/virtual reality study

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Abstract

In everyday life, the motivational value of faces is bound to the contexts in which faces are perceived. Electrophysiological studies have demonstrated that inherent negatively valent contexts modulate cortical face processing as assessed with ERP components. However, it is not well understood whether learned (rather than inherent) and three-dimensional aversive contexts similarly modulate the neural processing of faces. Using full immersive virtual reality (VR) and mobile EEG techniques, 25 participants underwent a differential fear conditioning paradigm, in which one virtual room was paired with an aversive noise burst (threat context) and another with a nonaversive noise burst (safe context). Subsequently, avatars with neutral or angry facial expressions were presented in the threat and safe contexts while EEG was recorded. Analysis of the late positive potential (LPP), which presumably indicates motivational salience, revealed a significant interaction of context (threat vs. safe) and face type (neutral vs. angry). Neutral faces evoked increased LPP amplitudes in threat versus safe contexts, while angry faces evoked increased early LPP amplitudes regardless of context. In addition to indicating that threat-conditioned contexts alter the processing of ambiguous faces, the present study demonstrates the successful integration of EEG and VR with particular relevance for affective neuroscience research.

KEYWORDS
contextualized face processing, fear conditioning, LPP, mobile EEG, virtual reality

1 | INTRODUCTION

In everyday life, faces do not appear isolated but are rather bound to contexts that influence how they are perceived. Accordingly, previous studies demonstrated that contexts yielding affective information may severely alter the processing of faces, with evidence emerging from fMRI and EEG (for review, see Wieser & Brosch, 2012). In particular, it has been shown that faces presented in inherently threatening contexts modulate ERPs compared to safe contexts (Righart & de Gelder, 2006, 2008a). However, thus far there is very limited research on the influence of threat-conditioned rather than inherently threatening contexts on cortical face processing. To address this issue, we investigated ERPs to faces embedded into threat-conditioned contexts by combining mobile EEG and fully immersive virtual reality (VR).

Contexts can be defined as complex compositions of events surrounding a certain stimulus. Contexts that are particularly relevant for face stimuli include external features surrounding faces like additional affective stimuli (Wieser & Brosch, 2012). In this line, it has been demonstrated that affective visual scenes increase or decrease reaction times to simultaneously presented faces when faces and contexts are congruent or incongruent, respectively (Righart & de Gelder, 2008b), indicating that inherently affective contexts affect face processing (Schmidt, Belopolsky, & Theeuwes, 2015).

However, in addition to inherently affective visual scenes, stimuli that have acquired a specific valence in the course of prior learning may also affect face processing. The responses to threat-conditioned stimuli have been extensively investigated in rodents and humans by using fear conditioning paradigms (Duits et al., 2015; Lissek et al., 2005; Milad & Quirk, 2012). In a differential fear conditioning paradigm, a neutral stimulus is paired with an aversive unconditioned stimulus (UCS) to become a threat stimulus, whereas another cue remains unpaired, serving as a safety stimulus. Studies in the field have shown that threat-conditioned stimuli lead to potentiated defensive reactions (Alvarez, Chen, Bodurka, Kaplan, & Grillon, 2011; Grillon & Baas, 2003; Öhman, 2005; Sperl et al., 2018) and effectively capture and hold attention (Cisler & Koster, 2010; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Koster, Crombez, Verschuere, Vanvolsem, & De Houwer, 2007), which makes them suitable external features for the investigation of electrocortical responses to faces in threat versus safe contexts.

With regard to cortical face processing, previous studies have shown that early and late stage ERPs are enhanced by both noncontextualized affective versus neutral faces (Eimer & Holmes, 2007; Hinojosa, Mercado, & Carretié, 2015; Pizzagalli, Regard, & Lehmann, 1999; Santesso et al., 2008; Schupp et al., 2004) and faces presented in inherently threatening versus safe contexts. For instance, threatening versus happy and neutral contexts, operationalized as affective visual scenes around faces, increased the amplitudes of the face-sensitive N170 (Righart & de Gelder, 2006, 2008a, 2008b), suggesting a more effective face structure encoding in threat contexts. In another paradigm, self- versus other-related threatening imaginations enhanced the amplitudes of the P100 to subsequently presented angry faces (Muench, Westermann, Pizzagalli, Hofmann, & Mueller, 2015). It has further been demonstrated that the late positive potential (LPP) is enhanced in response to faces that follow self- versus other-related (McCrackin & Itier, 2018; Wieser et al., 2014) as well as negative versus positive/neutral labels (Wieser & Moscovitch, 2015; Xu, Li, Diao, Fan, & Yang, 2016). From a functional perspective, the modulations of P100 and LPP amplitudes may reflect increased selective and sustained attention, respectively (Hajcak, MacNamara, & Olvet, 2010). Together, these results indicate that inherently affective contexts modulate attentional aspects of neural face processing.

Although a considerable amount of research has been devoted to either face processing or fear conditioning in isolation, there are only few findings on how threat-conditioned contexts affect cortical face processing. Kastner and colleagues (Kastner, Flohr, Pauli, & Wieser, 2016) provided tentative evidence that threat-conditioned contexts modulate ERPs to faces, as indicated by a trend for enhanced LPP amplitudes to faces in threat versus safe olfactory-conditioned contexts. Moreover, it has been shown that threat contexts, operationalized as threat-conditioned colored background, increase the startle response to fearful faces (Grillon & Charney, 2011), which have been shown to particularly increase vigilance for contextual threat (Wieser & Keil, 2014).

The presentation of visual contexts on a monitor screen has some disadvantages with respect to ecological validity, such as (a) the two-dimensionality of the stimulus array, which diminishes the spatial distinctness of the face and the context, or (b) the size of the monitor, which constrains the experimentally manipulated context to a small part of the laboratory room. Whereas recent VR studies in threat research have provided promising measurements of behavioral and physiological parameters, such as the startle, heart rate, and skin conductance responses (Diemer, Alpers, Peperkorn, Shiban, & Mühlberger, 2015; Glotzbach-Schoon, Andreatta, Mühlberger, & Pauli, 2013; Huff et al., 2011; Notzon et al., 2015), there is no study in threat research known to the authors that has assessed EEG activity in a fully immersive VR (i.e., three-dimensional vision using a head-mounted display).

To increase the ecological validity of contextualized face research, the goal of the present study was to examine electrocortical responses to contextualized faces by assessing brain activity in virtual environments. In this novel methodological approach, we implemented mobile EEG (Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Ladouce, Donaldson, Dudchenko, & Ietswaart, 2017) within fully immersive VR (Blascovich et al., 2002). Based on prior studies, we hypothesized that threat versus safe contexts presented in VR enhance the amplitudes of (a) early stage ERP components (P100, N170), and (b) the LPP in response to faces.

To test these hypotheses, two virtual rooms were established in a differential fear conditioning procedure and subsequently used as contexts in a contextualized faces paradigm using our novel VR/mobile EEG setup. Two rooms with different colorings (violet, teal) were paired with a white noise burst of 95 dB (threat context) or 80 dB (safe context), respectively. Thereafter, avatars expressing neutral and angry faces were presented within the contexts while EEG was recorded. In short, ERP analyses revealed that threat versus safe contexts enhanced the early LPP amplitude to neutral faces.

2 | METHOD

2.1 | Participants

Twenty-nine students from the University of Marburg participated in this study. Participants were included only if they were native speakers with normal or corrected-to-normal vision with contact lenses, were right-handed, and reported no present or past psychiatric or neurological condition. Because faces may be differentially processed in individuals with social phobia (Mueller et al., 2009), a screening for

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social phobia was conducted with a structured clinical interview (SCID; Wittchen, Zaudig, & Fydrich, 1997), and participants were excluded when social phobia criteria were met. Two participants were excluded due to technical problems, another due to excessive artifacts in the EEG, and a fourth did not comply with instructions. The final sample consisted of 25 participants (13 male; 20–31 years of age, mean age 24.56 years). Written informed consent was obtained from each participant. The study was approved by the local ethics committee.

2.2 | VR environment

A VR environment was composed using Vizard (WorldViz, Santa Barbara, CA). As shown in Figure 1a, the environment was designed to resemble the actual laboratory room, which consisted of two chairs and a table. It was displayed via an Oculus Rift Development Kit 2 (960 × 1,080 pixel resolution per eye, Oculus DK2; Oculus, Irvine, CA) head-mounted display (HMD). Head position and head movements were monitored with the manufacturer's HMD tracking sensor.

2.3 | Fear conditioning

Two different colorings of the room (violet, teal) were cue conditioned, serving as threat-conditioned (CXS+) and safe (CXS−) context (Figure 1b). As we have previously demonstrated the suitability of white noise bursts for EEG fear conditioning research (Mueller, Panitz, Hermann, & Pizzagalli, 2014; Sperl, Panitz, Hermann, & Mueller, 2016), the UCS was a 95 dB white noise burst with a duration of 1 s. The UCS was presented via two speaker boxes (Z533 of Logitech, Lausanne, Switzerland). To control for general auditory stimulation, a nonaversive 1 s 80 dB white noise burst instead of the UCS was presented during CSX−.

2.4 | Avatars

Using the Vizard complete characters set, virtual angry faces were generated in a reverse-correlation procedure (see online supporting information, Appendix S1) and cross-validated ($N = 41$; 18–33 years of age, mean age 24.44 years) as part of a pilot study. Based on this pilot study, one neutral and

FIGURE 1 VR stimulus material including (a) the virtual simulation of the real laboratory room, (b) the colored rooms (violet, teal), which served as CXS+ and CXS− in the contextual threat conditioning procedure, and (c) contextualized faces, showing the neutral face (left) and the angry face (right) presented in the contexts while EEG was recorded

one angry facial expression were selected as stimuli for the main study (Figure 1c). The avatar was sitting on the virtual chair opposite the participant. To control for gaze effects, the avatar's view was directed to the participants' current head position at every frame.

2.5 | Procedure and paradigm

The participants sat on a chair in front of a wooden table in the VR Lab. After signing informed consent, the UCS was presented to the participants, who rated its unpleasantness on a scale from 0 to 8. The 95 dB white noise burst (UCS) was rated as more unpleasant ($M = 6.80$, $SEM = 0.26$) than the nonaversive 80 dB white noise burst ($M = 4.28$. $SEM = 0.22$), $t(24) = 13.71$, $p < 0.001$, $d = 2.10$. The height of the seat was adapted so that every participant was at the same eye level. In order to reduce movement artifacts in the EEG, the HMD was fixated to the EEG cap to avoid free-floating device parts affecting the electrodes (see Figure 2 for an illustration of the setup). The paradigm consisted of four phases: (a) exploration, (b) habituation, (c) acquisition, and (d) contextualized faces (Figure 3a). Self-reports were assessed directly after every phase in the VR.

In the exploration phase, participants were given 90 s to visually explore the room. During the habituation phase, each CXS was presented 10 times without white noise bursts. The CXS were presented for 2 s in a randomized order. The interstimulus interval consisted of a gray background and lasted between 1 and 4 s. During the acquisition phase, the CXS+ was simultaneously presented with the 95 dB UCS and the CXS− with the 80 dB UCS in 25 trials each (i.e., the UCS was presented for the first second of the CXS presentation, total of 2 s). The CXS room colors were counterbalanced across participants. During the habituation and acquisition phase, participants performed a CXS one-back task in which they had to respond with a left mouse button press if the current trial showed the same context as the previous trial.

The contextualized faces phase consisted of two blocks during which the CXS+ or CXS− was presented together with the face stimuli (see Figure 3b for an example). The sequence of blocks (CXS+ first vs. CXS− first) was randomized across participants. Within each of these blocks, the avatar was presented 40 times with a neutral facial expression and 40 times with an angry facial expression simultaneously with the CXS+ or CXS− for 2 s in randomized order (1–4 s jittered interstimulus interval). To ensure that participants attended the faces during this phase, they also performed a face type one-back task in which they had to respond with a left mouse button if the current trial showed the same facial expression as the trial before. Moreover, self-reports were assessed after every contextualized faces block.

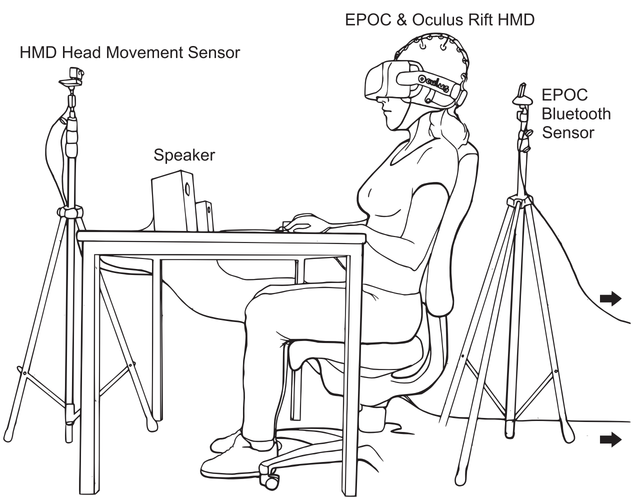

FIGURE 2 Experimental setup, which included the integration of mobile EEG with VR head-mounted display (HMD). EEG data were received via a Bluetooth sensor. Participants' head positions were tracked by the HMD movement sensor and translated to the position within the VR. Speakers were used to present the UCS. The arrows indicate the connection to the EEG recording device (top arrow) and the stimulus presentation computer (bottom arrow)

2.6 | Self-report variables

After every experimental phase, the participants rated the perceived threat of presented stimuli. One bipolar scale was used for assessing perceived threat of each CXS during habituation and acquisition (−4 to +4, secure/safe/protected vs. threatening/dangerous/disturbing: "How strong was this feeling present in the [teal/violet] room?"). Another but similar bipolar scale was used during the contextualized faces phase, which assessed the perceived threat of the entire situation as opposed to the teal/violet room (−4 to +4, secure/safe/protected vs. threatening/dangerous/disturbing: "How threatening did you perceived the entire situation?"). Moreover, a unipolar scale was used to measure the perceived threat of the faces during the contextualized faces phase (0 to 8: "How threatening was the person with the [neutral/emotional] facial expression?).

2.7 | EEG recording and data reduction

During the contextualized faces phase, EEG was recorded at 128 Hz using a customized version of the consumer Emotiv EPOC 1.0 system (Emotiv Systems, Sydney, Australia). In short, the EPOC was reworked as described elsewhere (Debener, Minow, Emkes, Gandras, & de Vos, 2012) and attached to an EasyCap with 13 Ag/AgCl ring electrodes (EASYCAP, Etterschlag, Germany). Previous studies have provided evidence for the satisfactory data quality of the reworked EPOC (Barham et al., 2017; de Lissa, Sörensen, Badcock, Thie, & McArthur, 2015; De Vos, Kroesen, Emkes, & Debener, 2014). Eleven electrodes were used for

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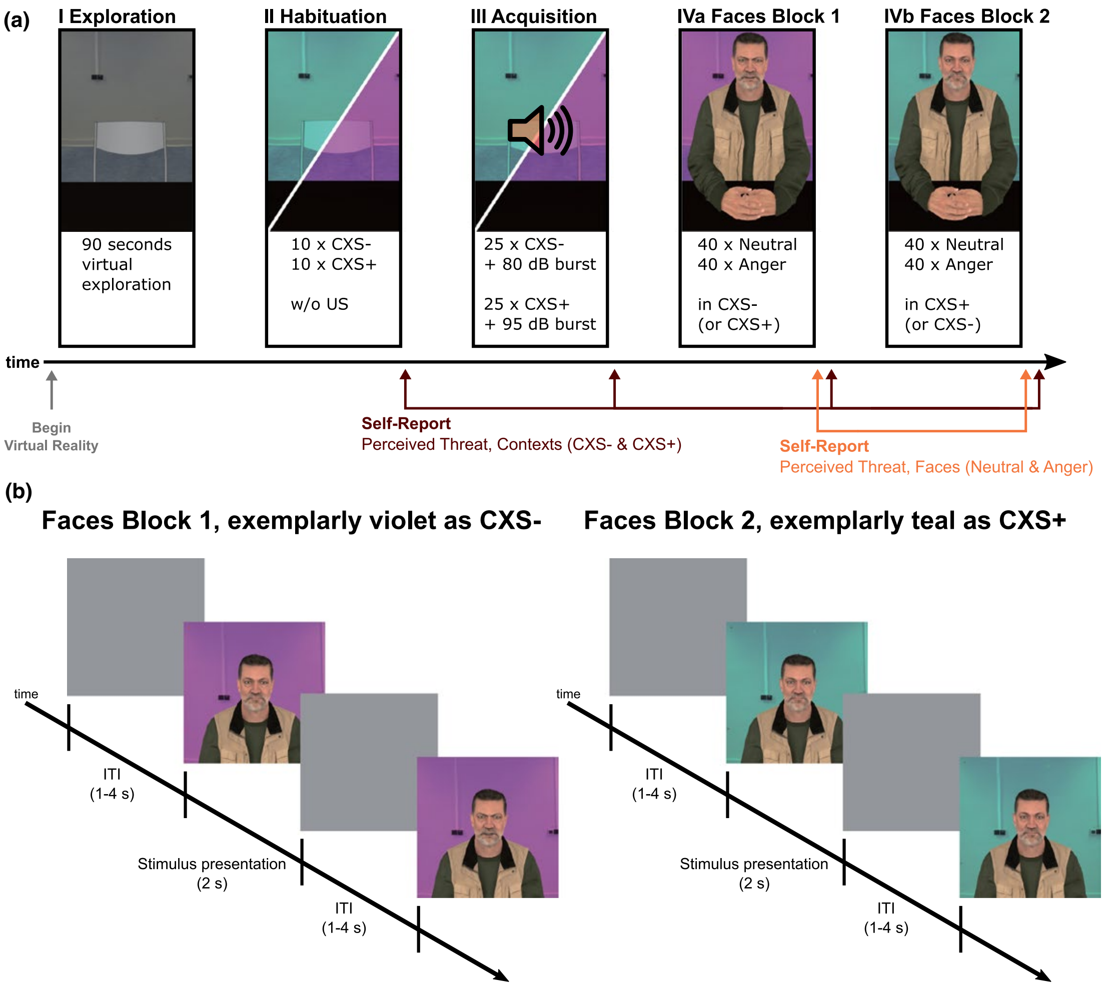

FIGURE 3 Paradigm used in the present study. (a) Timeline of the four phases and the measurements of self-reports and EEG. In the acquisition phase (III), 95 and 80 dB white noise bursts were presented with the respective CXS in all trials. The contextualized faces phase (IV) consisted of two blocks in a randomized sequence, whereas neutral and angry faces were presented in the safe (CXS−) or threat (CXS+) context. (b) Timeline of two trials in the contextualized faces phase (IV) with an exemplary block sequence beginning with CXS− and the following CXS+

EEG acquisition according to the International 10–20 system (AFz, Fz, F3, F4, FCz, Cz, C3, C4, Pz, PO7, PO8), two electrodes were used as right eye and right ear lobe electrode, respectively, and one pin was reserved for marker input. Common mode sense (CMS) was at position POz and driven right leg (DRL) at CPz. A digital-to-analog converter was built and attached between the parallel port of the VR presentation PC and the EEG amplifier, to send TTL markers into the EEG stream. EEG was filtered online with an effective 0.2 to 43 Hz band-pass, and recorded with a sampling rate of 128 Hz. Offline EEG analysis was performed by custom MATLAB (version R2015a) scripts based on the EEGLAB toolbox (Delorme & Makeig, 2004). Data containing muscle artifacts were manually rejected prior to and after an infomax independent component analysis (ICA). ICA components reflecting clear eyeblink artifacts were removed by a trained rater. On average, 9.5 trials per condition were rejected due to artifacts, so that the ERPs were scored with the following amount of effective trials per condition: 30 (75%) trials in the neutral face CXS−, 30 (75%) trials in the angry face CXS−, 31 (77.5%) trials in the neutral face CXS+, and 31 (77.5%) trials in the angry face CXS+condition. The artifacts were excessive eyeblinks and head movements, which were not pruned by removing the relevant ICA components and occurred prominently at electrode sites near the HMD, especially the eye electrode. To a lesser degree, there were artifacts at F3/F4 and C3/C4 that may represent horizontal head movement artifacts. Two participants showed some episodes (<300 ms) of noisy artifacts at PO7/PO8, probably due to a suboptimal placement of the HMD head bandage or forward motions of the head.

EEG data were segmented into epochs ranging from −200 ms to 2 s relative to CXS onsets. Finally, data were re-referenced to the right earlobe, baseline-corrected (200 ms to 0 ms relative to stimulus onset), and averaged for every phase. To obtain P100 and N170 measurement latencies in the present sample, we computed minima and maxima of grand average ERPs across all phases using the min() and max() function of MATLAB in custom scripts. P100 peak latency was defined as the maximal positive peak between 50 ms and 160 ms after stimulus onset at pooled channels PO7/PO8 (S. Yoon, Shim, Kim, & Lee, 2016), which was at 125 ms. Following the same rationale, N170 peak latency was defined as the maximal negative peak between 125 to 220 ms, again at PO7/PO8, which was at 164 ms. Individual P100 and N170 amplitudes were scored as averages in the area ±16 ms around the respective grand average peaks (P100: 109–141 ms; N170: 148–180 ms). The time windows of the LPP strongly vary between studies, and, further, the LPP is often reported without considering separate time windows. In order to enhance the comparability with other studies and to examine the time course of contextualized face processing, we analyzed the entire LPP from 300 to 2,000 ms and three different time windows. Consequently, the LPP component was divided into an early LPP (300–600 ms), midlatency LPP (600–1,000 ms), and late LPP (1,000–2,000 ms) and scored as the average magnitude in the respective time window at electrode sites Fz, FCz, Cz, and Pz (Duval, Moser, Huppert, & Simons, 2013; Hajcak et al., 2010).

2.8 | Statistical analysis

Perceived threat of the CXS was analyzed with an analysis of variance (ANOVA) including the factors phase (habituation vs. acquisition) and context (CXS+ vs. CXS−). The reaction times (RTs) in the CXS one-back task during the acquisition phase were compared with a *t* test. A *t* test was performed to compare the perceived threat of the contexts during the contextualized faces phase. Analyses of the RTs in the face one-back task were subjected to ANOVAs containing the factors context (CXS+ vs. CXS−) and face type (neutral vs. anger). For the early ERP components (P100, N170), ANOVAs were calculated with the factors electrode site (PO7 vs. PO8), context (CXS+ vs. CXS−), and face type (neutral vs. anger). Four separate ANOVAs were conducted for the entire LPP and three different LPP time windows. The results of the ANOVAs are reported with Greenhouse-Geisser correction. Post hoc *t* tests were performed in case of a significant Context × Face Type interaction and reported with Bonferroni adjusted *p* values for multiple comparisons ($p = 0.0125$). Results were reported with partial eta squared (η_p^2) and Cohen's *d* as effect sizes. For all statistical analyses, SPSS Statistics Version 21 (IBM, Armonk, NY) was used.

3 | RESULTS

3.1 | Self-report of perceived threat and RTs

3.1.1 | Habituation and acquisition phase

The ANOVA on the perceived threat of contexts revealed a significant main effect of context (CXS+ vs. CXS−), $F(1, 24) = 14.10$, $p = 0.001$, $\eta_p^2 = 0.37$, and a significant main effect of phase (habituation vs. acquisition), $F(1, 24) = 17.25$, $p < 0.001$, $\eta_p^2 = 0.42$; Figure 4a. The Phase × Context interaction was significant, $F(1, 24) = 10.41$, $p < 0.01$, $\eta_p^2 = 0.30$. The CXS+ was not rated as more threatening than the CXS− during habituation, $t(24) = 1.66$, $p = 0.11$, $d = 0.27$ but was during acquisition, $t(24) = 4.34$, $p < 0.01$, $d = 1.07$. Mean values of perceived threat ratings for contexts are provided in Table 1. There was no significant difference in RTs to the CXS− ($M = 527.47$ ms, $SEM = 0.25$) versus CXS+ ($M = 543.82$ ms, $SEM = 0.26$) in the CXS one-back task, $t(24) = 1.31$, $p = 0.20$, $d = 0.13$.

3.1.2 | Contextualized faces phase

When asked to rate how threatening participants found the overall situation (context) in the contextualized faces phase, there

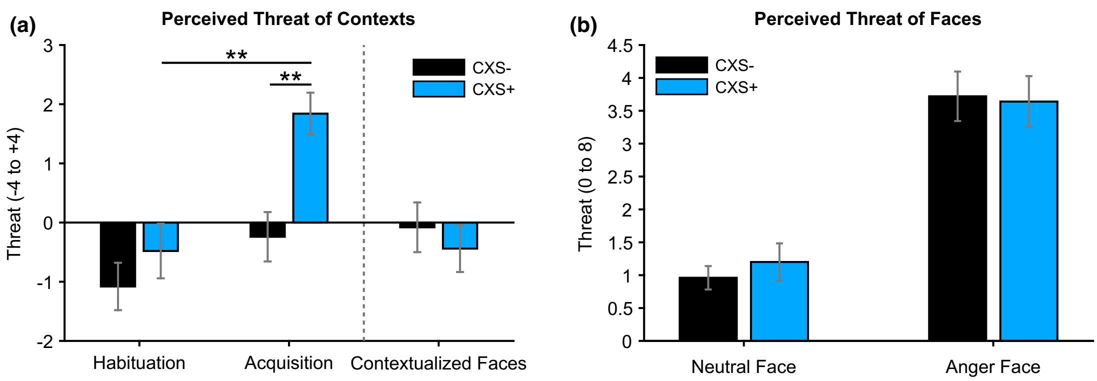

FIGURE 4 (a) Mean (*SEM*) ratings of perceived threat of contexts for the habituation and acquisition phases and for the entire situation of the contextualized faces phase. (b) Mean (*SEM*) ratings of perceived threat of faces are presented in the contextualized faces phase

TABLE 1 Mean ratings (*SEM*) of the perceived threat of contexts

	Habituation	Acquisition	Contextualized faces
CXS−	−1.08 (0.40)	−0.24 (0.42)	−0.08 (0.42)
CXS+	−0.48 (0.46)	1.84 (0.35)	−0.44 (0.40)

TABLE 2 Mean ratings (*SEM*) of the perceived threat of faces

	CXS−	CXS+
Neutral face	0.96 (0.18)	1.20 (0.28)
Angry face	3.72 (0.38)	3.64 (0.39)

TABLE 3 Mean reaction times in ms (*SEM*) to contextualized faces (face one-back task)

	CXS−	CXS+
Neutral face	653.58 (27.07)	667.30 (33.11)
Angry face	645.07 (27.32)	636.55 (28.48)

was no significant difference between CXS+ versus CXS− blocks, $t(24) = 0.86$, $p = 0.40$, $d = 0.18$; Figure 4b.

With regard to the ratings on the perceived threat of faces, there was a significant effect of face type (neutral vs. anger), $F(1, 24) = 63.87$, $p < 0.001$, $\eta_p^2 = 0.73$, with higher means for angry ($M = 3.68$, $SEM = 0.33$) compared to neutral ($M = 1.08$, $SEM = 0.21$) faces; Figure 4b. There was no significant effect of context on face ratings, $F(1, 24) = 0.09$, $p = 0.77$, $\eta_p^2 < 0.01$, and no Context × Face Type interaction, $F(1, 24) = 1.03$, $p = 0.32$, $\eta_p^2 = 0.04$. Mean values of perceived threat ratings for faces are provided in Table 2.

Regarding the RTs to contextualized faces in the face one-back task, there were no significant effects of context, $F(1, 24) = 0.03$, $p = 0.86$, $\eta_p^2 < 0.01$, and face type, $F(1, 24) = 1.18$, $p = 0.29$, $\eta_p^2 = 0.05$. The interaction of Context × Face Type was significant, $F(1, 24) = 6.19$, $p < 0.05$, $\eta_p^2 = 0.21$. However, post hoc *t* tests did not reach significance (*t*s < 1.46 and *p*s > 0.63). The reaction times are provided in Table 3.

3.2 | EEG measures

3.2.1 | P100 and N170

As shown in Figure 5, a visually evoked potential with the expected latencies and polarities could be recorded with our novel VR/mobile EEG setup. The P100 evoked by the contextualized avatar showed a latency of 125 ms with an occipital topography, and the N170 showed a latency of 164 ms with a temporal negativity. However, in contrast to our hypotheses, there were no significant effects of context or face type on the P100 (all $Fs \leq 3.46$, $ps \geq 0.08$) or N170 (all $Fs \leq 2.22$, $ps \geq 0.15$).[1] The ERPs and scalp topographies of the early components are provided in Figure 5. The mean amplitudes of all assessed ERP components are provided in Table 4.

3.2.2 | Early LPP

The time windows for the LPP are shown in Figure 6a. For the early LPP, there was a significant effect of face type (neutral vs. anger), $F(1, 24) = 8.42$, $p < 0.01$, $\eta_p^2 = 0.26$, with increased amplitudes following angry ($M = 7.03$, $SEM = 0.69$) compared to neutral ($M = 5.93$, $SEM = 0.69$) faces. Importantly, this main effect was further qualified by a significant interaction of Context × Face Type, $F(1, 24) = 6.98$, $p < 0.05$, $\eta_p^2 = 0.23$; see Figure 6b. Post hoc comparisons with Bonferroni correction revealed that neutral faces evoked a potentiated early LPP in threat (CXS+) versus safe (CXS−) contexts, $t(24) = 3.47$, $p < 0.05$, $d = 0.43$, but this effect was absent for angry faces, $t(24) = −0.39$, $p = 1.00$, $d = −0.06$. Moreover, angry compared to neutral faces significantly enhanced the early LPP in the safe context (CXS−), $t(24) = 4.75$, $p < 0.001$, $d = 0.54$, but there was no significant effect of face type in the threat (CXS+) context, $t(24) = 0.33$, $p = 1.00$, $d = 0.05$. The main effect of context did not reach significance (CXS+ vs. CXS−), $F(1, 24) = 2.84$, $p = 0.11$, $\eta_p^2 = 0.11$. The ERPs and topographies are provided in Figure 6.

To provide a more comparative hypothesis testing of the observed interaction of Context × Face Type on the early LPP, we computed the Bayes factor (BF) of H_1: "The mean early LPP in response to neutral faces in the safe context (CXS−) is less than that of the other conditions, which have equal mean" versus H_0: "The mean early LPP of all conditions is equal," assuming that all conditions have equal variance. We assumed uniform priors on the means of all conditions in the interval [0,20], subject to the mean of the early LPP in response to neutral faces in the CXS− being smaller under H_1, and uniform priors on the variances in the interval [0.1,100.0]. The prior on the mean was chosen to cover the observed means of our recording system with a wide margin; the prior on the variance results from a distribution with maximum variance in the same interval as the means. The BF was greater than 8, corresponding to a posterior probability of H_1 greater than 0.98 given uniform prior over hypotheses. According to Kass and Raftery (1995), this constitutes "strong evidence" in favor of H_1.

[1]Since an earlobe reference is suboptimal for scoring the N170 (Joyce & Rossion, 2005), we rereferenced the data to the most frontal electrode AFz, and calculated an ANOVA including the factors context and face type. However, there were also no significant effects on the N170 in this analysis ($Fs \leq 1.97$, $ps \geq 0.17$).

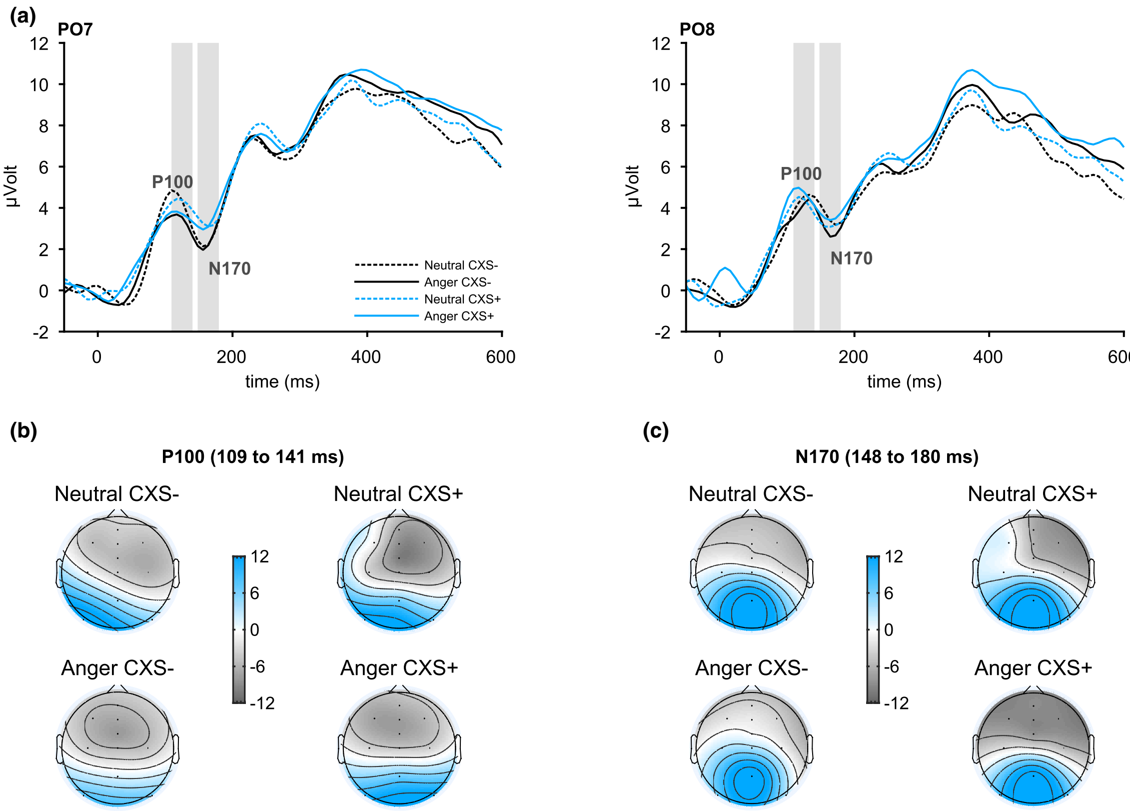

FIGURE 5 (a) ERPs at parietal-occipital (PO7, PO8) electrodes in response to neutral and angry faces presented in the safe (CXS−) and threat (CXS+) context. Labels indicate P100 and N170 components, and gray boxes show the time interval of averaging. (b) Scalp topography of the P100 time window (109–141 ms). (c) Scalp topography of the N170 time window (148–180 ms). Gross scalp topography maps are provided to facilitate comparisons with previous studies

TABLE 4 ERPs (*SEM*) to neutral and angry faces

	Neutral CXS−	Angry CXS−	Neutral CXS+	Angry CXS+
P100				
PO7	4.25 (0.92)	3.38 (0.92)	4.25 (0.96)	3.68 (0.77)
PO8	4.36 (0.79)	4.29 (0.81)	4.30 (0.71)	4.67 (0.84)
Pooled	4.31 (0.72)	3.84 (0.75)	4.28 (0.65)	4.17 (0.71)
N170				
PO7	2.53 (0.98)	2.47 (0.88)	3.30 (1.15)	3.33 (1.08)
PO8	3.54 (1.31)	2.94 (1.10)	3.20 (1.33)	3.57 (1.36)
Pooled	3.03 (1.05)	2.71 (0.91)	3.25 (1.13)	3.45 (1.13)
LPP				
Early	5.14 (0.76)	7.14 (0.72)	6.72 (0.70)	6.91 (0.78)
Midlatency	0.44 (0.70)	1.91 (0.60)	2.20 (0.76)	2.19 (0.75)
Late	−0.76 (0.62)	0.14 (0.62)	1.00 (0.53)	0.85 (0.62)

3.2.3 | Midlatency LPP

There were no significant main effects of context, $F(1, 24) = 3.14$, $p = 0.09$, $\eta_p^2 = 0.12$, or face type $F(1, 24) = 2.92$, $p = 0.10$, $\eta_p^2 = 0.11$, and no significant Context × Face Type interaction, $F(1, 24) = 2.79$, $p = 0.11$, $\eta_p^2 = 0.10$.

3.2.4 | Late LPP

There was a significant effect of context, which indicated an enhanced late LPP for CXS+ ($M = -0.92$, $SEM = 0.48$) versus CXS− ($M = -0.31$, $SEM = 0.50$), $F(1, 24) = 15.08$, $p < 0.01$, $\eta_p^2 = 0.27$. There were no significant effects involving face type (Fs ≤ 1.2, ps ≥ 0.28).

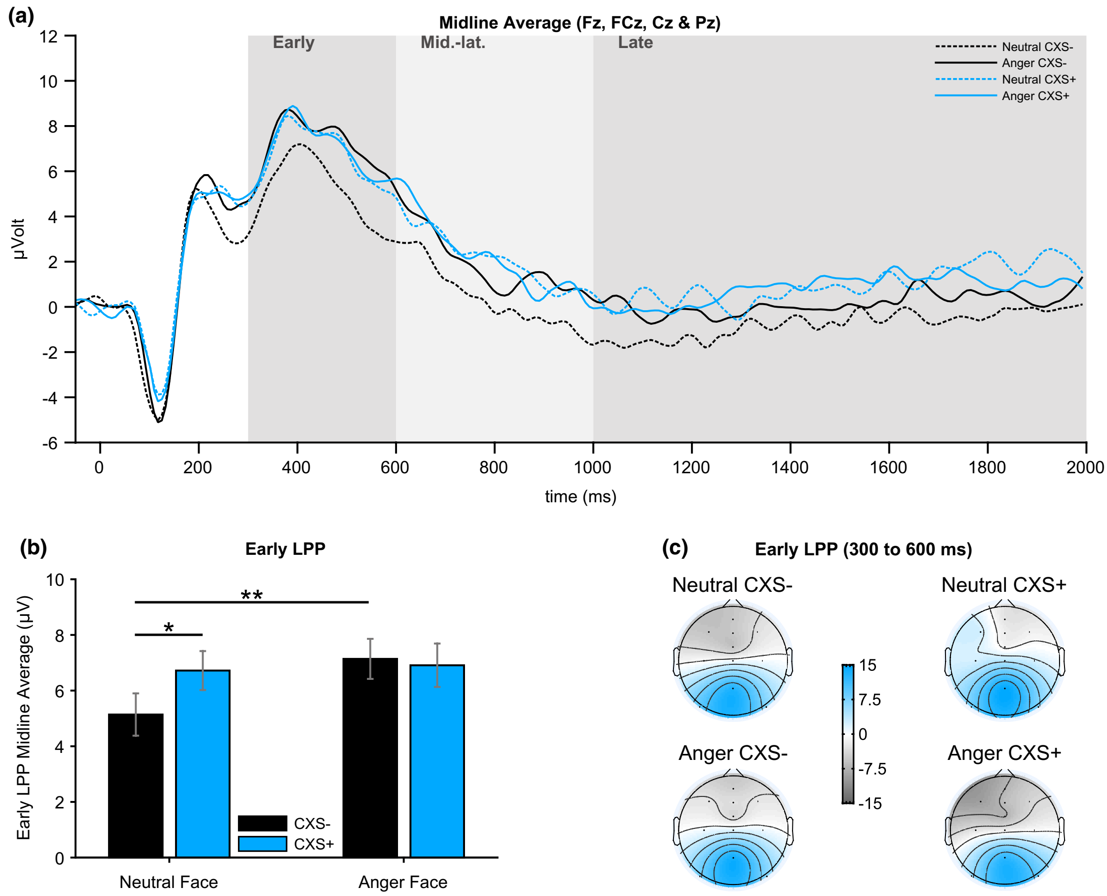

FIGURE 6 (a) ERP at sensors Fz, FCz, Cz, and Pz (pooled). LPP time windows are also highlighted: early and late LPP are indicated by dark gray and midlatency LPP by light gray boxes. (b) Mean (*SEM*) midline averaged early LPP amplitudes in response to faces (neutral, angry) in the safe (CXS−) and threat (CXS+) contexts. (c) Scalp topography of the early LPP (300–600 ms). Gross scalp topography maps are provided to facilitate comparisons with previous studies

3.2.5 | Entire LPP

An ANOVA on the entire LPP without different time windows revealed a large significant effect of context (CXS+ vs. CXS−), $F(1, 24) = 7.18$, $p < 0.05$, $\eta_p^2 = 0.23$. The effect of face type, $F(1, 24) = 2.11$, $p = 0.16$, $\eta_p^2 = 0.08$, and the interaction of Context × Face Type, $F(1, 24) = 2.57$, $p = 0.12$, $\eta_p^2 = 0.10$, did not reach significance.

4 | DISCUSSION

The goal of the present study was to investigate the cortical processing of affective faces in threat contexts. To this end, an avatar with neutral and angry facial expressions was embedded into previously threat-conditioned contexts using highly ecological valid VR in conjunction with mobile EEG techniques. Consistent with our hypotheses, threat versus safe contexts enhanced the early LPP (300–600 ms) in response to neutral faces. In addition, threat versus safe contexts enhanced the late LPP (1,000–2,000 ms) regardless of face type. Furthermore, the early LPP was increased following angry versus neutral faces in a nonthreatening context, which agrees with previous findings on affective face processing without contextual manipulations. Notably, we found this effect in response to three-dimensional artificial avatar faces in VR rather than realistic two-dimensional photographs as in prior studies. Most importantly, the present study provides evidence that threat contexts influence the cortical processing of neutral and angry faces in the LPP time window, suggesting a stronger allocation of attentional resources to threat in ecologically valid situations as early as 300 to 600 ms. This effect was qualified by both a significant interaction effect of Context × Face Type and a Bayes factor that comparatively tested the hypothesis that the early LPP is lower in response to neutral faces in the safe context compared to the other conditions.

Threat versus safe contexts enhanced early LPP amplitudes in response to neutral faces. This converges with previous findings that threat-conditioned contexts modulate face processing at behavioral and cortical levels (Grillon & Charney, 2011; Kastner et al., 2016). Since the LPP has been reported to be highly sensitive for affective and motivational saliency (Hajcak et al., 2010), the observed increase of the early LPP to neutral faces in threat contexts may reflect the allocation of attentional resources toward threat. Consistently, it has been demonstrated that fear-conditioned versus neutral stimuli lead to enhanced LPP amplitudes (Nelson, Weinberg, Pawluk, Gawlowska, & Proudfit, 2015; Panitz, Hermann, & Mueller, 2015) and capture as well as bind attention (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2005; Koster, Crombez, Van Damme et al., 2004; Koster, Crombez, Verschuere, & De Houwer, 2004; Schmidt et al., 2015). Due to the task irrelevance of the contexts, our results further provide evidence that attentional capture of threat contexts is relatively immune to distraction (Bishop, 2008). This is in line with a recent study suggesting increased vigilance in threat versus safe contexts, as indexed by enhanced steady-state visually evoked potentials (ssVEPs) during both a fear acquisition and a test phase with distracting objects (Kastner, Pauli, & Wieser, 2015). Since the LPP has been demonstrated to be sensitive to manipulations of directed attention (Hajcak, Dunning, & Foti, 2009; Wiens, Sand, Norberg, & Andersson, 2011; Wiens & Syrjänen, 2013), it may be possible that our results reflect dynamic allocation of attentional resources to threatening stimuli. Due to the task relevance of the faces during the contextualized faces phase, it could be that the early LPP time window was more sensitive to integrative processing, whereas the present context-only effect on the late LPP with larger amplitudes in threat versus safe contexts may reflect that conditioned threat maintains its motivational importance in later processing stages.

The present context effects on the early LPP amplitudes were specific for neutral faces, suggesting that the processing of neutral or ambiguous faces is particularly vulnerable to contextual threat. In line with this observation, EEG and fMRI studies demonstrated that negative compared to neutral and positively valent contexts increase the cortical processing of neutral faces (Klein, Iffland, Schindler, Wabnitz, & Neuner, 2015; Ryan & Schwartz, 2013; Wieser & Moscovitch, 2015). Since neutral faces do not provide inherent motivational information, it is conceivable that threat contexts predominantly capture perceptual and attentional resources. This is in line with the suggestion that threat cues bind and hold attention as part of an effective defensive response (Fanselow, 1994; Öhman, Flykt, & Esteves, 2001). There is also evidence that the perception and cortical processing of neutral faces is influenced by state anxiety (Somerville, Kim, Johnstone, Alexander, & Whalen, 2004) and trait social anxiety (Cooney, Atlas, Joormann, Eugène, & Gotlib, 2006; Hagemann, Straube, & Schulz, 2016; Wieser et al., 2014; K. L. Yoon & Zinbarg, 2007, 2008). Together, these results indicate that the perception of neutral faces is sensitive to negative affective top-down biases (Sussman, Jin, & Mohanty, 2016).

The context effects on the early LPP, as reported for neutral faces, were not observable in response to angry faces. Since angry faces and threat contexts are both signals to threat, it is conceivable that angry faces and threat contexts are integrated in a nonadditive manner. The face-context compound may have received higher attention as soon as it is threat related, be it due to an angry face, a threat context, or both (Bishop, 2008; Fox, Russo, & Dutton, 2002; Vuilleumier, Armony, Driver, & Dolan, 2001). Future studies could address this issue, for example, by using eye tracking to explore the patterns of attentional shifts toward either angry faces or threat contexts.

From another perspective, angry versus neutral faces enhanced the early LPP in safe contexts, which replicates the results of prior studies on noncontextualized faces (Duval et al., 2013; Schupp et al., 2004; Smith, Weinberg, Moran, & Hajcak, 2013). Our initial findings may reflect enhanced sustained attention to threat, which is in line with the notion of angry faces as motivational relevant signals of conspecific threat (Öhman, 1986; Öhman & Mineka, 2001; Öhman, Soares, Juth, Lindström, & Esteves, 2012). This suggestion is further supported by higher threat ratings of angry versus neutral faces in the present study. Finally, convergent with the reports of Mühlberger et al. (2009), that LPP amplitudes were increased to virtual angry versus neutral faces presented on a computer screen, our results provide further evidence that ERPs to (and the neural processing of) virtual faces may be similar to those of realistic face stimuli.

There were no significant effects on early stage ERPs as indexed by the P100 and N170 components. This could be explained by habituation effects since only one pair of neutral and angry faces of the same avatar were presented repetitively (Heisz, Watter, & Shedden, 2006; Mercure, Cohen Kadosh, & Johnson, 2011; Schweinberger & Neumann, 2015). In contrast, it is likely that the affective modulation of the LPP by contexts and faces remained intact across repetitive trials (Codispoti, Ferrari, & Bradley, 2006, 2007; Ferrari, Codispoti, & Bradley, 2017). Moreover, the context-related one-back task during the acquisition phase may have marginally increased the distractibility by the contexts during the contextualized faces phase, which could have partly affected very early face processing. Future studies in mobile EEG/VR could overcome possible habituation effects in the early stage ERPs by using various avatars and a higher number of affective and neutral face stimuli. However, the present findings do reflect effects of threat-conditioned contexts on rather slow and complex visuocognitive integration and might not be indicative of early processing stages.

In contrast to many other fear conditioning studies in VR, we used a differential cued fear conditioning protocol rather than a contextual fear conditioning protocol (Glenn, Risbrough, Simmons, Acheson, & Stout, 2017; Lonsdorf et al., 2017; Maren, Phan, & Liberzon, 2013). Whereas in differential cue conditioning protocols discrete cues are paired with a UCS in a trial-by-trial fashion, contextual conditioning protocols commonly present unpredictable UCS during extended presentations of a visual context (Andreatta et al., 2015; Ewald et al., 2014; Glotzbach, Ewald, Andreatta, Pauli, & Mühlberger, 2012; Tröger, Ewald, Glotzbach, Pauli, & Mühlberger, 2012). In the present study, face-related contexts were defined as external features, that is, contexts that are visually and spatially distinct from the avatar. A threat-related learning experience in these contexts was obtained by cue conditioning. However, our results are comparable to those in the field of contextual fear conditioning, and we assume that our mobile EEG/VR setup would be highly suitable for future studies that investigate contextual face processing with different types of contexts in highly ecologically valid environments.

For the first time in contextualized faces research, mobile EEG has been successfully implemented with a full immersive VR technique, as our results demonstrate that avatar-evoked ERPs are modulated by virtual contexts. Thus, the present study can also be considered as a feasibility study on the combination of mobile EEG with fully immersive VR in emotion research. This novel methodological approach allows us to exploit the advantages of VR, such as the high degree of stimulus control and the assessment of behavioral responses in naturalistic scenarios, while measuring brain activity with high temporal resolution. In comparison to the common laboratory setup, which includes a monitor screen for stimulus presentation, VR potentially increases the chance to observe more ecologically relevant psychological and behavioral responses (Bohil, Alicea, & Biocca, 2011). As reported in a recent meta-analysis (Cummings & Bailenson, 2016), fully immersive VR outclasses the use of common monitor screens with respect to the experience of being involved in the experimental environment. Obviously, the experience of being involved is particularly relevant for research on emotions, which are often difficult to generate in conventional laboratory settings. Further applications of mobile EEG with VR in threat research could focus on neurobehavioral responses in highly naturalistic fear- and anxiety-related scenarios (Huff, Zeilinski, Fecteau, Brady, & LaBar, 2010; McCall, Hildebrandt, Hartmann, Baczkowski, & Singer, 2016). Moreover, mobile EEG/VR may be a valuable tool for the investigation of neurocognitive processes during virtual exposure therapy of anxiety disorders (e.g., Diemer, Mühlberger, Pauli, & Zwanzger, 2014; Krijn, Emmelkamp, Olafsson, & Biemond, 2004; Meyerbröker & Emmelkamp, 2010).

Our study demonstrates high quality EEG data assessed within fully immersive VR. While there is only a relatively low amount of trials were rejected due to artifacts, this may in part be due to the experimental setup of the present study, where participants were seated instead of actively moving. So far, even though recent research demonstrated high quality EEG data in moving subjects (Banaei, Hatami, Yazdanfar, & Gramann, 2017), future studies need to further examine EEG data quality in actively moving participants during stressful VR paradigms.

There are some limitations of the present study. First, since the Emotiv EPOC EEG includes only 14 electrodes, a unilateral right earlobe reference was chosen to have a maximum number of scalp electrodes. Depending on the research question, one could adapt the electrode positions and the reference of the Emotiv EPOC to examine a specific ERP component (for the N170, see de Lissa et al., 2015), and our specifications seemed to be better suited for the LPP than early stage ERPs. Nevertheless, it must be noted that the 0.2 Hz online high-pass filter of the EPOC amplifier is suboptimal for assessing slow waves like the LPP. Second, a potential limitation of the present study is the use of a simultaneous rather than delayed conditioning design as used in most fear conditioning studies (Andreatta et al., 2015; Ewald et al., 2014; Glotzbach-Schoon, Tadda, et al., 2013; Grillon, Baas, Cornwell, & Johnson, 2006; Wieser, Reicherts, Juravle, & von Leupoldt, 2016). As demonstrated in prior studies, delayed conditioning typically leads to larger conditioned responses than simultaneous conditioning (e.g., Jones, 1962). Thus, the present effects could have been even larger when using a delayed contextual fear conditioning procedure. Third, with regard to the subjective ratings, the perceived threat of the context only differed before but not after the contextualized faces phase presumably due to within-session fear extinction (Milad & Quirk, 2012; Mueller et al., 2014; Muench et al., 2015), which may have weakened the observed effects of context. This could also explain the absent modulation of the face ratings by contexts, as has been demonstrated in studies which used a different contextualized faces paradigm (Wieser et al., 2014; Wieser & Moscovitch, 2015). Future studies may consider reactivating conditioned fear of contexts by additional CS-US pairings during the contextualized faces phase.

Our study provides novel evidence that threat-conditioned contexts influence cortical face processing as demonstrated by context modulations of LPP amplitudes. Consistent with our hypotheses, threat versus safe contexts increased the early LPP in response to neutral faces, suggesting that contexts with threat-related learning experiences strongly capture attentional resources. Second, angry versus neutral faces enhanced the early LPP in safe contexts. Finally, our study provides a successful integration of mobile EEG with fully immersive VR as a useful tool for threat research. This approach allows us to investigate how the brain processes realistic threats with a high degree of experimental control and temporal resolution.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1

Figure S1

Table S1

Table S2

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