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Fearful faces heighten the cortical representation of contextual threat

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Abstract

Perception of facial expressions is typically investigated by presenting isolated face stimuli. In everyday life, however, faces are rarely seen without a surrounding visual context that affects perception and interpretation of the facial expression. Conversely, fearful faces may act as a cue, heightening the sensitivity of the visual system to effectively detect potential threat in the environment. In the present study, we used steady-state visually evoked potentials (ssVEPs) to examine the mutual effects of facial expressions (fearful, neutral, happy) and affective visual context (pleasant, neutral, threat). By assigning two different flicker frequencies (12 vs. 15 Hz) to the face and the visual context scene, cortical activity to the concurrent stimuli was separated, which represents a novel approach to independently tracking the cortical processes associated with the face and the context. Twenty healthy students viewed flickering faces overlaid on flickering visual scenes, while performing a simple change-detection task at fixation, and high-density EEG was recorded. Arousing background scenes generally drove larger ssVEP amplitudes than neutral scenes. Importantly, background and expression interacted: When viewing fearful facial expressions, the ssVEP in response to threat context was amplified compared to other backgrounds. Together, these findings suggest that fearful faces elicit vigilance for potential threat in the visual periphery.

Keywords

fear; vigilance; facial expression; visual context; visual cortex

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²In order to exclude the possibility that the different tagging frequencies (12 and 15 Hz) affected the modulation of the ssVEPs, we also conducted an omnibus ANOVA containing the additional within-subject factor carrier frequency (12 vs. 15 Hz). No associated effects involving a frequency \times tagged stimulus interaction were revealed. However, the frequency \times facial expression \times visual context interaction was significant, $F(4,76) = 3.46, p = .012, \eta_p^2 = .15$. For the 12 Hz condition, a significant main effect context was observed, $F(2,38) = 3.29, p = .048, \eta_p^2 = .15$, whereas in the 15 Hz condition the interaction of facial expression and visual context is highly significant, $F(4,76) = 3.62, p = .009, \eta_p^2 = .16$, which points at the notion that at 15 Hz, the signal is more sensitive to the experimental conditions, regardless of which stimulus is tagged. Most likely, this is due to better signal to noise ratio of 15 Hz ssVEPs and the closer vicinity of the 12 Hz ssVEP to the alpha band.

1. Introduction

Viewing fearful facial expressions enhances basic perceptual processes, such as contrast sensitivity, orientation sensitivity, and spatial resolution (Bocanegra and Zeelenberg, 2009b, 2011a; Phelps et al., 2006). These effects are often attributed to the signal character of fearful faces: Fear in another person suggests the presence of a potential threat, but the source of threat is unclear (Whalen et al., 2009). Thus, a fearful face may act as a cue that prompts heightened perceptual sensitivity to threat in the environment. This notion is also in line with several theories of anxiety, which assume that anxiety enhances sensory sensitivity in general (Lang et al., 2000; McNaughton and Gray, 2000).

In this vein, visual search tasks have demonstrated that a fearful face can increase search efficiency for task-relevant objects, even when those objects are non-threatening (Becker, 2009; Olatunji et al., 2011). It has been demonstrated that facially expressing fear enhances sensory sensitivity (Susskind et al., 2008) as well, which concurs with Darwin's assumption that facial expressions modify preparedness for perception and action. In this perspective, expressing fear alters the sensory response, augmenting or diminishing the sensitivity to the environment (Darwin, 1872). Thus, cuing observers with depictions of a fearful face or experiencing fear both may result in heightened attention and visual processing. The question arises regarding the extent to which such changes also affect the processing of environmental cues in which the observer or the face cue is embedded.

Recent evidence suggests that concurrent contextual stimuli impact the processing of facial expressions in a content-specific fashion (for a recent review, see Wieser and Brosch, 2012). The most common finding in this field of research has been that congruent context facilitates and accelerates emotion recognition, whereas incongruent context interferes with emotion recognition (e.g., Aviezer et al., 2008; Carroll and Russell, 1996; de Gelder and Vroomen, 2000). The perception of emotional faces seems to depend on an interaction of facial expression and contextual information (Herring et al., 2011; Neta et al., 2011), and associations between context and faces are routinely established (Aviezer et al., 2011; Barrett and Kensinger, 2010; Hayes et al., 2010). Using the N170 component of the visually evoked brain potential as an index of face perception, it was shown that the presence of a face in a fearful context enhanced the N170 amplitude compared to a face in neutral contexts, but this effect was strongest for fearful faces (Righart and de Gelder, 2006, 2008a, b). These findings suggest that the context in which a face appears may influence how it is encoded. In addition, faces without any context showed the largest N170 amplitudes possibly reflecting competition for attentional resources between visual scene context and facial expressions (Righart and de Gelder, 2006). This effect was replicated in a later study where N170 amplitudes were increased for fearful faces in fearful scenes as compared to fearful faces in happy scenes (Righart and de Gelder, 2008a). These results show that the information provided by the facial expression is combined with the scene context during the early stages of face processing. However, from a methodological point of view, it should be noted that the larger N170 in response to expressive faces with simultaneously presented scenes reflects the brain response to both stimuli (face and scene), and thus cannot be taken as a pure index of face processing.

Electrophysiological testing of hypotheses concerning the relative amount of cortical processing of concurrent stimuli is typically made difficult by the fact that the neural responses to concurrent stimuli are not distinct. The steady-state visually evoked potential (ssVEP) methodology together with “frequency-tagging” allows researchers to separately quantify responses to multiple visual objects, which are simultaneously present in the field of view (e.g., Miskovic and Keil, 2013; Wang et al., 2007; Wieser and Keil, 2011; Wieser et al., 2011, 2012; Zhang et al., 2011). The ssVEP is an oscillatory response to stimuli periodically modulated in contrast or luminance (i.e., flickered), in which the fundamental frequency of the electrocortical response recorded from the scalp equals that of the driving stimulus (Müller et al., 1998; Regan, 1989). Of significant advantage, the driven oscillatory ssVEP is precisely defined in the frequency domain as well as time-frequency domain, and can consequently be reliably separated from noise (i.e., all features of the ongoing EEG that do not oscillate at the frequency of the stimulus train). Amplitude modulation of this signal reflects sustained sensory processing modulated both by intrinsic factors (e.g., Keil et al., 2003) and extrinsic, task-related processes (e.g., Andersen and Müller, 2010). Importantly, because the ssVEP is by definition a stationary and sustained oscillation in sensory neural populations, its modulation by tasks and goals is thought to be effected through sustained re-entrant processes (Keil et al., 2009). The effect of such re-entrant modulation can be observed through phase analyses (Keil et al., 2005) or by measuring the time-varying ssVEP amplitude in response to physically identical stimuli (e.g., Wieser and Keil, 2011). Generators of the flicker-evoked and contrast-reversal ssVEP have been localized to the extended visual cortex (Müller et al., 1997), with strong contributions from retinotopic areas, but also from cortices higher in the visual hierarchy (Di Russo et al., 2007). Similarly, source estimation has indicated an early visual cortical origin of the face-evoked flicker-ssVEP (Wieser and Keil, 2011). Frequency-tagging refers to the feasibility of assigning different frequencies to stimuli simultaneously presented in the visual field, whose signals can be separated in the frequency domain (Appelbaum et al., 2006; Wang et al., 2007; Wieser and Keil, 2011) and submitted to time-frequency analyses to provide a continuous measure of the visual resource allocation to a specific stimulus amid competing cues. As a consequence, this method is ideally suited for the investigation of competition between facial expressions and affective pictures. Recently, ssVEP studies have suggested that affectively engaging stimuli prompt strong competition effects, associated with reduction of the response amplitude elicited by a concurrent stimulus or task (Hindi Attar et al., 2010a; Hindi Attar et al., 2010b; Müller et al., 2011; Müller et al., 2008). Thus, one may hypothesize that prioritized processing of facial expressions is at the expense of processing the visual scene and vice versa, a fact that has been neglected in this line of research so far.

Recently, studies in the cognitive and affective neurosciences have increasingly used the steady-state visual evoked potential (ssVEP) to study different aspects of face processing, including processing of emotional expression as well as face identification (e.g., Ales et al., 2012; Gruss et al., 2012; McTeague et al., 2011; Rossion and Boremanse, 2011; Rossion et al., 2012). Of note, these studies revealed different sensor locations for maximal resonating oscillatory responses in the visual cortex, which were either predominantly expressed over medial-occipital sensors (Gruss et al., 2012; McTeague et al., 2011) or over right temporo-occipital clusters approximately at sensor locations where the face-sensitive N170 in the

ERP is normally maximally expressed (e.g., Ales et al., 2012; Rossion and Boremanse, 2011, Rossion et al., 2012). These differences are mostly due to differences in stimulus presentation or experimental design as the ssVEP can be driven in lower-tier visual cortices using high contrast luminance modulation with square-wave stimulation (e.g., Gruss et al., 2012) or in higher order cortices such as the fusiform cortex using sinusoidal modulation of face-specific contrast (e.g., Rossion and Boremanse, 2011).

The main goal of the present study was to examine the effects of viewing facial expressions on the cortical processing of contextual cues and vice versa. To this end, steady-state visually evoked potentials (ssVEPs) together with frequency-tagging were employed, yielding separate continuous estimates of sensory cortical engagement for the face and the context stimulus. We examined the following alternative hypotheses: 1) If competition between faces and visual scenes takes place, the ssVEP signal evoked by faces should be reduced when the face is embedded in affective compared to neutral scenes, whereas at the same time, cortical processing of the background visual scenes should be reduced when emotional compared to neutral facial expressions are presented. 2) If fearful facial expressions enhance attentional sensitivity, then enhanced ssVEP amplitudes for background scenes should be observed when a fearful face is present. Specific enhancement of the threat context during fearful face viewing would indicate that peripheral sensitivity is enhanced to amplify threat features selectively, rather than any content.

2. Materials and Methods

2.1. Participants

Twenty participants (20–27 years old, $M = 22.80$, $SD = 2.46$; 10 females, right-handed) were recruited from general psychology classes at the University of Würzburg who received course credit for participation. All of the participants had no family history of photic epilepsy, and reported normal or corrected-to-normal vision. Written consent was obtained from all participants. All procedures were approved by the institutional review board of the University of Würzburg.

2.2. Design and Procedure

Twenty-four pictures (12 female; 12 male) were taken from the Radboud Faces Database (Langner et al., 2010) with fearful, happy, and neutral facial expressions. All stimuli were converted to grayscale, cropped to a size of 225×315 pixel (visual angle = 4.2×5.9 degrees), and rearranged such that for each face, the eyes were positioned in the middle of the picture. Serving as visual context stimuli, 36 pictures (12 pleasant, 12 neutral, 12 threat; 1024×768 pixel, visual angle = 19.1×14.4 degrees) were selected from the International Affective Picture System (Lang et al., 2005)¹. The luminance of the gray background was

¹IAPS catalog numbers for pictures used in this study are: pleasant scenes: 1604, 1731, 5200, 5260, 5480, 5628, 5660, 5811, 5814, 7410, 7508, 8170; neutral scenes: 5520, 7000, 7002, 7041, 7042, 7052, 7100, 7140, 7233, 7242, 7491, 7547; threat scenes: 5970, 6000, 9000, 9001, 9010, 9440, 9471, 9495, 9600, 9622, 9911, 9920. Only pictures without human faces were selected to avoid competition of facial expressions with the target face stimuli. Based on normative ratings, it was ensured that pleasant pictures did not differ with regard to emotional arousal from threat pictures (pleasant $M = 4.72$, $SD = 0.99$; threat $M = 5.04$, $SD = 0.91$; $t(11) = 0.81$, $p = .44$). Neutral pictures were less arousing ($M = 3.01$, $SD = 0.50$). In addition, pictures were converted to grayscale, and entropy was computed for each picture as a statistical measure of randomness (complexity). Mean entropy scores per categories did not differ, $F(2,22) = 0.23$, $p = .80$. (pleasant: $M = 7.08$, $SD = .48$; neutral: $M = 6.93$, $SD = .34$; threat: $M = 7.00$, $SD = .69$).

27 cd/m² and the average luminance of the face and the background pictures was adjusted to the same mean luminance (i.e., 27 cd/m²). Contrast was approximated by calculating the variance, which was standardized across all IAPS pictures and in a separate step for the Radboud faces.

In each experimental trial, a face picture was presented at the center of the screen for 3,000 ms. Faces were shown in a flickering mode either at a frequency of 15 Hz or 12 Hz to evoke ssVEPs. In the background of this flickering face stimulus, a visual scene picture was presented, flickering at either 12 Hz or 15 Hz, respectively (see Figure 1). Using presentation software (Neurobehavioral Systems, Inc., Albany, CA, USA), stimuli compounds were displayed on a 19-inch computer monitor (resolution = 1280 × 1024 pixel) with a vertical refresh rate of 60 Hz, located approximately 80 cm in front of the participant. The driving frequencies of the face stimulus and the IAPS stimulus were different to ensure distinct frequency tagging of each stimulus stream.

A central fixation point was present at the center of the screen throughout the experiment. Participants were asked to maintain gaze on the fixation cross and to avoid eye movements. In order to facilitate central fixation, a simple change detection task was introduced, for which participants were asked to press a button whenever the color of the fixation cross changed from white to gray. Color changes appeared very rarely (3–5 times per session), and occurred only during inter-trial intervals, in order to avoid contamination of ongoing ssVEP by motor potentials and transient responses to the task stimulus. Inter-trial intervals, in which the fixation cross was presented against a gray background, had durations between 2,500 and 3,500 ms.

Presentation was in blocks. In each block, 6 male and 6 female faces from one condition were combined with the 12 IAPS pictures from one condition, resulting in 12 trials per condition. Two blocks per condition were created with the other half of the female and males faces in the second block. Thus, twenty-four stimulus pairs were created per condition in total. In one half of the trials of each condition, the face picture was presented at 15 Hz, and vice versa. All expressions were combined with neutral, pleasant and threat background IAPS pictures and were fully crossed over driving frequencies, resulting in nine conditions (fearful-pleasant, fearful-neutral, fearful-threat, neutral-pleasant, neutral-neutral, neutral-threat, happy-pleasant, happy-neutral, happy-threat). This resulted in a total of 216 trials (24 trials × 9 conditions). The order of blocks was pseudo-randomized across participants.

After the EEG recording, each participant viewed 12 trials of each face-IAPS compound again in a randomized order and was asked to identify the facial expressions (forced-choice) and to rate the respective face on the dimensions of hedonic valence and emotional arousal on the 9-point Self-Assessment Manikin (SAM, Bradley and Lang, 1994). The SAM is a language-free scale on which observers indicate how pleasurable and how intense their emotional experience is when exposed to a given stimulus. In this block, participants viewed each face-IAPS compound for 500 ms (without flickering) before the identification task and SAM was presented.

2.3. EEG Recording and data analysis

The EEG was continuously recorded from 129 electrodes using an Electrical Geodesics System (EGI, Eugene, OR, USA), referenced to Cz, digitized at a rate of 250 Hz, and on-line band-pass filtered between 0.1 and 100 Hz. Electrode impedances were kept below 50 k Ω , as recommended for the Electrical Geodesics high-impedance amplifiers.

Using EMEGS (Peyk et al., 2011), a low-pass filter of 40 Hz was applied off-line. Epochs of 600 ms pre-stimulus and 3,600 ms post-stimulus onset were extracted off-line. Artifact rejection was also performed off-line, following the procedure proposed by Junghöfer, Elbert, Tucker, and Rockstroh (2000). Using this approach, trials with artifacts were identified based on the distribution of statistical parameters of the EEG epochs extracted (absolute value, standard deviation, maximum of the differences) across time points, for each channel, and - in a subsequent step - across channels. Sensors contaminated with artifacts were replaced by statistically weighted, spherical spline interpolated values. The maximum number of approximated channels in a given trial was set to 20. Such strict rejection criteria also allowed us to exclude trials contaminated by vertical and horizontal eye movements. Due to the long epochs and these stringent rejection criteria, the mean rejection rate across all conditions was 34.7%. The number of remaining trials did not differ between experimental conditions, $F(8,152) = 1.50$, $p = .208$. For interpolation and all subsequent analyses, data were arithmetically transformed to the average reference. Artifact-free epochs were averaged separately for the 9 conditions of stimulus pairs to obtain ssVEPs containing both driving frequencies.

To ensure that the ssVEP signal in this study represented robust phase-locked driving of cortical networks at the flicker frequencies, time-domain averaging was performed before frequency-domain analysis. This method amplifies the so-called "evoked" (time and phase-locked to the oscillatory stimulus) part of the brain signal and suppresses "induced" (not phase-locked) activity. Reliability of the ssVEP at both driving frequencies was then quantified by means of the circular T-square statistic (Mast and Victor, 1991), which formally tests the stability of the evoked signal at a given driving frequency.

The raw ssVEP for a representative electrode (Oz), the Fast Fourier Transformation on this ssVEP, and the spatial topography of the two driving frequencies averaged across all subjects and conditions are shown in Figure 2.

The time-varying ssVEP amplitude for each condition was determined by means of complex demodulation of the averaged potentials, which extracts a modulating signal from a carrier signal (Regan, 1989) using in-house written MATLAB scripts (for a more detailed description, see Müller et al., 2008). The analysis used the driving frequencies of the stimuli, 12 and 15 Hz, as target frequencies, and a third-order Butterworth low-pass filter with a cut-off frequency (3dB point) at 1 Hz (time resolution 140 ms full width at half maximum) was applied during complex demodulation. Prior to complex demodulation, a baseline interval of 240 ms (from -380 until -140 ms) was subtracted, and a cosine square window with 20 points rise/fall (80 ms) applied to each averaged potential, to minimize on and offset artifacts. The overall mean ssVEP amplitude was calculated for the time window between 200 and 3,000 ms after picture onset. For each frequency, the face tagged with that same

frequency was considered the target, and the picture tagged with the other frequency was considered the competitor background stimulus. Fully crossing faces and IAPS pictures with stimulation frequencies, all permutations of target faces and competing stimuli were extracted from the compound ssVEP signal. Thus, a time-varying measure of the amount of processing resources devoted to one stimulus in presence of another stimulus (competitor) was obtained. In order to examine the time course of early and late stages of attentional engagement and to explore whether any effects were sustained and stationary in nature, ssVEP amplitudes were averaged across time points in two time regions, between 200–1,500 ms and 1,500–2,800 ms after picture onset in addition to the mean interval over the whole time window. As was seen in previous work (e.g., Müller et al., 2008; Wieser and Keil, 2011), amplitudes of the ssVEPs were most pronounced at electrode locations near Oz, over the occipital pole. We therefore averaged all signals spatially, across a medial-occipital cluster comprising Oz and its 7 nearest neighbors (EGI sensors 70, 71, 72, 74, 75, 76, 82, 83, see Figure 3).

2.4. Statistical analysis

Mean ssVEP amplitudes (200–3,000 ms) were analyzed by repeated-measures ANOVAs (PASW Statistics 18, Version 18.0.2, Chicago, IL, USA) containing the within-subjects factors tagged stimulus (face vs. IAPS picture), facial expression (fearful vs. neutral vs. happy), and visual scene (threat vs. neutral vs. pleasant). Significant effects were followed up by separate repeated-measures ANOVAs for each stimulus (face vs. IAPS). To analyze the time course, separate ANOVAs were carried out for two time intervals (200–1,500 vs. 1,500–3,000 ms).

SAM ratings were averaged per condition and submitted to separate ANOVAs for valence and arousal ratings, containing the within-subject factors of facial expression (fearful vs. neutral vs. happy) and valence of IAPS (threat vs. neutral vs. pleasant). Correct identification rates were also averaged across conditions and examined using the same repeated-measures ANOVA design.

A significance level of .05 (two-tailed) was used for all analyses. Throughout this manuscript, the uncorrected degrees of freedom, the corrected p values, the Greenhouse-Geisser (GG) ϵ , and the partial η^2 (η_p^2) are reported (Picton et al., 2000).

3. Results

3.1. Steady-state visually evoked potentials (ssVEPs)

The analysis over the whole time period (200–3,000 ms) revealed a significant interaction of tagged stimulus \times visual scene \times facial expression, $F(4, 82) = 4.19$, $p = .039$, $\eta_p^2 = .12$. This effect was followed up by ANOVAs performed for faces and visual scenes, separately. For faces, no significant effects of facial expressions were observed, except of a tendency of higher activity for happy facial expressions, $F(2, 38) = 2.96$, $p = .064$, $\eta_p^2 = .14$ (Figure 4). Simple contrasts highlighted this difference for happy compared to neutral faces, only, $F(1, 19) = 6.93$, $p = .016$, $\eta_p^2 = .27$.

In contrast, ssVEP amplitudes in response to visual scenes were significantly larger for emotional (pleasant and threat) compared to neutral pictures, $F(2,38) = 4.81, p = .014, \eta_p^2 = .20$. However, this effect was further qualified by the significant interaction of facial expressions and visual scene, $F(4,76) = 4.19, p = .016, \eta_p^2 = .15$ (Figure 5 and 6). Interestingly, mean ssVEP amplitudes were only enhanced for threat scenes, when fearful compared to neutral as well as happy faces were present, $F(1,19) = 6.13, p = .023, \eta_p^2 = .24$, and $F(1,19) = 4.38, p = .049, \eta_p^2 = .18$, respectively. Post-hoc comparisons for all other conditions did not yield any significant effects (all $F < 2.8, p > .11$)

The analysis of the two time intervals revealed a significant three-way interaction of tagged stimulus \times facial expression \times visual scene for both time intervals, $F(4,76) = 2.81, p = .031, \eta_p^2 = .13$, and $F(4,76) = 3.37, p = .014, \eta_p^2 = .15$ (see Figure 7). As a follow-up, ANOVAs were conducted for each time window for the averaged ssVEPs for faces and IAPS pictures, separately. In the first time window, the signal evoked by the visual scenes was modulated by facial expression and visual scene, $F(4,76) = 4.49, p = .003, \eta_p^2 = .19$. Planned contrasts showed that only for threat scenes, the cortical signal was enhanced when fearful compared to neutral as well as happy faces were present, $F(1,19) = 3.04, p = .043, \eta_p^2 = .20$, and $F(1,19) = 5.92, p = .025, \eta_p^2 = .24$, respectively. In contrast, for pleasant visual scenes, the overall signal was enhanced when a happy face was present compared to when a neutral face was present, $F(1,19) = 4.46, p = .048, \eta_p^2 = .19$. No differences were observed in the signal evoked by the facial expressions. For the second time interval, analysis of the signal evoked by the visual scene revealed a significant main effect of visual scene and a significant interaction of facial expression and visual scene, $F(2,38) = 3.81, p = .031, \eta_p^2 = .167$, and $F(4,76) = 4.49, p = .003, \eta_p^2 = .19$. Here, the signal was amplified only for threat visual scenes when a fearful face was present compared to either happy or neutral face, $F(1,19) = 5.88, p = .025, \eta_p^2 = .24$, and $F(1,19) = 3.99, p = .060, \eta_p^2 = .17$. Again; no effects were found for the face-evoked ssVEP amplitude (all $F < 2.74, p > .11$)

3.2. Affective Ratings and emotion recognition

Mean affective ratings are given in table 1. Participants rated the facial expressions embedded in visual background context scenes as differentially pleasant regardless of visual background, $F(2,38) = 59.12, \text{GG-}\varepsilon = .61, p < .001, \eta_p^2 = .757$. Planned contrasts revealed that fearful faces were rated as more threat than neutral and happy faces, $F(1,19) = 33.56, p < .001, \eta_p^2 = .638$, and $F(1,19) = 65.23, p < .001, \eta_p^2 = .774$, respectively. Also, happy faces were rated as more pleasant than neutral faces, $F(1,19) = 69.61, p < .001, \eta_p^2 = .786$. Background visual scenes also influenced the valence ratings of the facial expressions, $F(2,38) = 14.71, \text{GG-}\varepsilon = .57, p = .001, \eta_p^2 = .436$. Faces were rated as more threatening when a threat compared to either neutral or pleasant visual background was present, $F(1,19) = 8.66, p = .008, \eta_p^2 = .313$, and $F(1,19) = 15.57, p = .001, \eta_p^2 = .466$. Also, faces in pleasant contexts were rated as more pleasant than in neutral visual background, $F(1,19) = 24.35, p < .001, \eta_p^2 = .562$.

For arousal ratings, also two significant main effects of facial expression, $F(2,38) = 7.54, p = .002, \eta_p^2 = .284$, and visual background IAPS, $F(2,38) = 8.75, p = .001, \eta_p^2 = .315$, were observed. Regardless of background scene, fearful faces were rated as more arousing as

neutral and happy ones, $F(1,19) = 12.05, p = .003, \eta_p^2 = .388$, and $F(1,19) = 6.27, p = .022, \eta_p^2 = .248$. In the same vein, all faces embedded in threat visual background scenes were rated as more arousing than the one in either neutral or pleasant visual background scenes, $F(1,19) = 11.00, p = .004, \eta_p^2 = .367$, and $F(1,19) = 11.13, p = .003, \eta_p^2 = .369$. Analysis of the emotion recognition rates did not yield any significant influences neither of facial expression, $F(2,38) = 1.05, p = .359, \eta_p^2 = .053$, nor visual background, $F(2,38) = 1.11, p = .342, \eta_p^2 = .055$. Recognition rates per condition are given in table 2.

4. Discussion

The present study investigated the interaction between facial expressions and surrounding context information in visuo-cortical processing using ssVEP frequency tagging. Flickering streams of facial expressions were overlaid on affective visual scenes flickering at a different frequency. This allowed us to obtain continuous electrocortical indices reflecting processing of each stimulus individually. Whereas electrocortical responses to facial expressions were not altered by visual background, facial expressions affected the electrocortical processing of the visual background. Specifically, the presence of a fearful face at fixation was associated with heightened electrocortical response amplitude in response to threat, compared to pleasant peripheral context. Importantly, this modulation was stable and sustained throughout the viewing period, as demonstrated by the lack of a change across the two segments examined here. Affective ratings of facial expressions embedded within an affective context did not co-vary with affective background. The results demonstrate that fearful facial expressions enhance concurrent processing of negative affective visual background.

The enhanced processing of threat cues, i.e. context features that may signal aversive information, when a fear face is present is consistent with evolutionary perspectives on the processing of facial affect. For instance, it has been proposed that widening of attention and enhancing visual perception is adaptive in an evolutionary sense: Seeing a fearful face signals that an expresser may perceive threat in the environment, leading others to localize and identify any such threat themselves. These findings are in line with studies demonstrating benefits from viewing facial expressions of fear in the spatial and temporal domain as well as with regard to enhanced contrast sensitivity (Bocanegra and Zeelenberg, 2009a; Bocanegra and Zeelenberg, 2009b, 2011a; Bocanegra and Zeelenberg, 2011b; Phelps et al., 2006). In the same vein, the perception of fear increases efficiency in visual search, even for non-threatening objects (Becker, 2009), which was recently replicated in a study where prior exposure to a fearful expression resulted in faster target identification in a subsequent visual search task, compared to exposure to other facial expressions. Further support for this line of reasoning comes from studies showing that fearful faces together with averted gaze are faster detected/identified, elicit higher affective responses and are processed more deeply (Adams and Kleck, 2005). It is assumed that the combination of averted gaze and fearful expressions prompts the observer to search for potential sources of threat and increase vigilance and attention. Consequently, further studies need to include gaze (direct vs. averted) as a variable to address this issue (Olatunji et al., 2011). Interestingly, it has been proposed that fear-related facilitation of attention is also observed in the expresser: When participants are instructed to pose expressions of fear, they tend to

have a subjectively larger visual field, faster eye movements during target localization, and an increase in nasal volume and air velocity during inspiration (Susskind et al., 2008).

Together, this demonstrates that distinct sensory features of facial expressions in relation to the physical world may reflect important differences in the communicative functions of the expressions. The present results support the notion that threat evaluation produces increased arousal that leads to hypervigilance (Phelps and LeDoux, 2005). Contextual enhancement in response to fear faces is also consistent with Whalen's (1998) "threat-ambiguity" hypothesis, which postulates that facial expressions of fear should prompt vigilance for their target, directing attention away from the face. The current research extends the work summarized above by suggesting that fear-induced amplification in lower-tier visual cortex specifically affects contextual cues that are consistent with threat and danger. A limitation of the current approach however is, that the ssVEP does not allow any inferences about the initial sensory sweep following the onset of the flickering face-scene compound stimulus, which conversely is an advantage of ERP studies. Thus, the present method does not allow testing hypotheses regarding the initial temporal sequence of electrocortical events accompanying stimulus evaluation. ERP work as conducted previously is better suited to address these issues. In this context, constraints of the present study should be mentioned regarding the physical stimulus properties associated with placing a face stimulus in the middle of an IAPS picture. To the extent that the present research builds on ERP work employing similar stimuli, the present design and material helped comparing the present results with previous work. However, because the compound stimuli used here were artificial in nature, edges appeared between the face and the context (see Figure 1), potentially acting as prominent cues signaling the presence of a discontinuity between face and context, as well as driving visual neuron populations themselves. Such constraints can be overcome in future work using ssVEP frequency tagging with more naturalistic picture stimuli, where faces are in integral part of the scene.

Interestingly, no modulation of face-evoked ssVEPs by context was detected, which appears at odds with findings of strong competition effects of emotional background scenes on a demanding visual foreground task. (Hindi Attar et al., 2010a; Müller et al., 2008). In the present study, affective pictures were selected to contain credible and meaningful context information, not to represent high arousing content. For instance, IAPS pictures highest in rated arousal typically contain persons/bodies (i.e., mutilations/erotica), and were not included in this study. It is conceivable that the resulting lower level of rated arousal is associated with diminished prioritization of the picture context and thus less distraction.

In terms of potential neurophysiological mechanisms for the enhanced processing of background threat cues when viewing fearful faces, connections involving the amygdala are key candidates (Pourtois et al., 2013). It has been hypothesized that the bilateral amygdala is sensitive to emotional value of sensory events –particularly faces— and, among other efferent events boosts perceptual processing (Amaral et al., 2003). In the context of the present study, it is noteworthy that the amygdala is more strongly activated in response to fearful compared to other threatening faces (angry faces), perhaps due to their uncertainty aspect -- i.e. the source of danger is unknown (Whalen et al., 2009). Electrophysiological and tracer studies have converged to demonstrate that the amygdaloid complex possesses

strong efferent connections to visual cortex, which may serve to alter sensory cortical processing (Kapp et al., 1994; Sabatinelli et al., 2009; Shi and Davis, 2001). In humans, this notion has also been supported by studies in which the amygdala and extrastriate cortex correlated in their responses to images of fearful faces (Morris et al., 1998; Pasley et al., 2004), whereas this modulation was attenuated in patients with amygdala damage (Vuilleumier et al., 2004). Moreover, diffusion tensor imaging has confirmed connections between the amygdala and visual cortical parts of the occipital lobe (Catani et al., 2003). To the extent that scalp recorded ssVEPs are not sensitive to deep structures such as the amygdaloid complex, any conjectures regarding the neurophysiology underlying modulation of sustained sensory processing are speculative in nature. In addition, limitations of the ssVEP technique as applied here include the fact that the initial sweep of processing is not reflected in the frequency domain representation of the driving frequency. Although ssVEP power is directly related to activity in sensory neurons, it can be considered an average across time points and the fine-grained temporal sequence information as contained in event-related potentials is therefore not available in ssVEPs.

As an alternative to this classic two-route model for emotion processing, it has also been proposed (Vuilleumier, 2005), that the same cortical pathways (i.e. along occipito-temporal areas) might be recruited by an early and rapid feed-forward propagation of inputs to various areas (e.g. frontal, parietal, and possibly amygdala), followed by re-entrant modulations acting on sensory areas which may be necessary for full perceptual processing and access to conscious awareness (Lamme, 2003; Lamme and Roelfsema, 2000). As has been demonstrated before, modulations of ssVEPs in response to emotional stimuli are likely caused by such re-entrant projections from cortical areas such as parietal and frontal cortices (Keil et al., 2012; Keil et al., 2009). Via efferent projections, the amygdala might be able to increase general cortical arousal, which may be one correlate of hypervigilance (Kapp et al., 1992).

5. Conclusion

The present study capitalized on frequency-tagging in order to disentangle mutual influences of facial expressions and affective context scenes. This novel approach provides evidence that the presence of fearful faces increases vigilance specifically for threatening visual scenes, which may contain information about potential sources of threat in the environment. Vigilance to threat is reflected in increased large-scale (neural mass) electro-cortical activity in visual cortices. Taken together, these findings further illustrate the signal character of facial expressions of fear, where fear faces act as a cue, prompting heightened perceptual processing of potential threat in an observer's surroundings.

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Highlights

We investigated mutual effects of faces and affective context on visual processing.

Frequency-tagging allows separating visuo-cortical processing of faces vs. context scenes.

Presence of fearful faces heightens cortical processing of threatening visual context.

Fearful faces signal danger and lead to vigilance for threat in the observer.

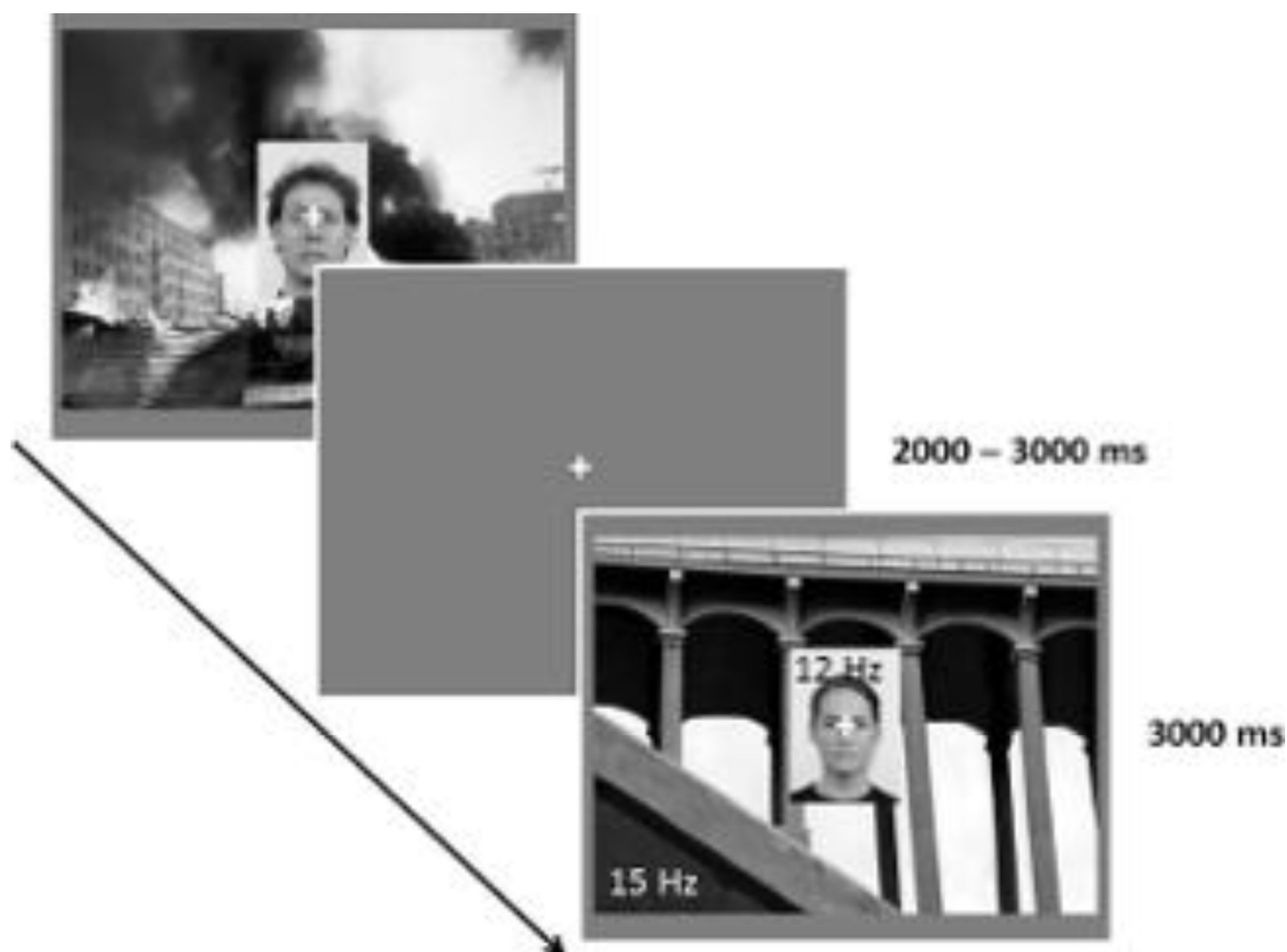


Figure 1. Schematic representation of 2 experimental trials. A fixation point in the center of the screen was present at all times during the experiment. Inter-trial intervals varied randomly between 2,500 and 3,500 ms. In each trial, two stimuli (facial expression overlaid on a visual scene), flickering at 12 Hz and 15 Hz, were presented for 3,000 ms.

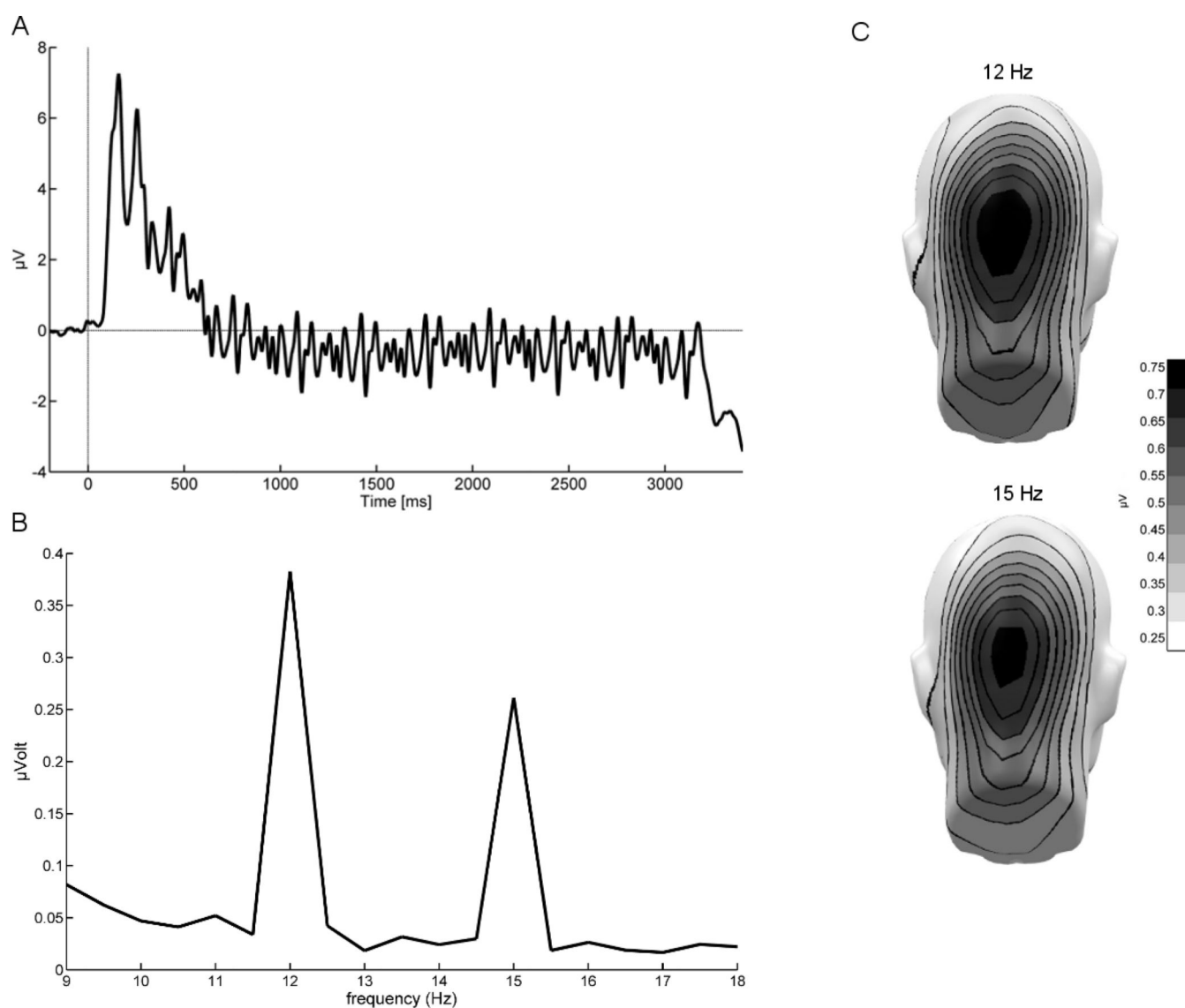


Figure 2.

A) Grand mean steady-state visually evoked potential averaged across all participants and conditions, recorded from a medial occipital electrode (Oz). The ssVEP in the present study contains a superposition of two driving frequencies (12 Hz and 15 Hz), as shown by the frequency domain representation (B) of the same signal (Fast Fourier Transformation of the ssVEP in a time segment between 200 and 3,000 ms). C) The mean scalp topographies of both frequencies show clear medial posterior activity over visual cortical areas.

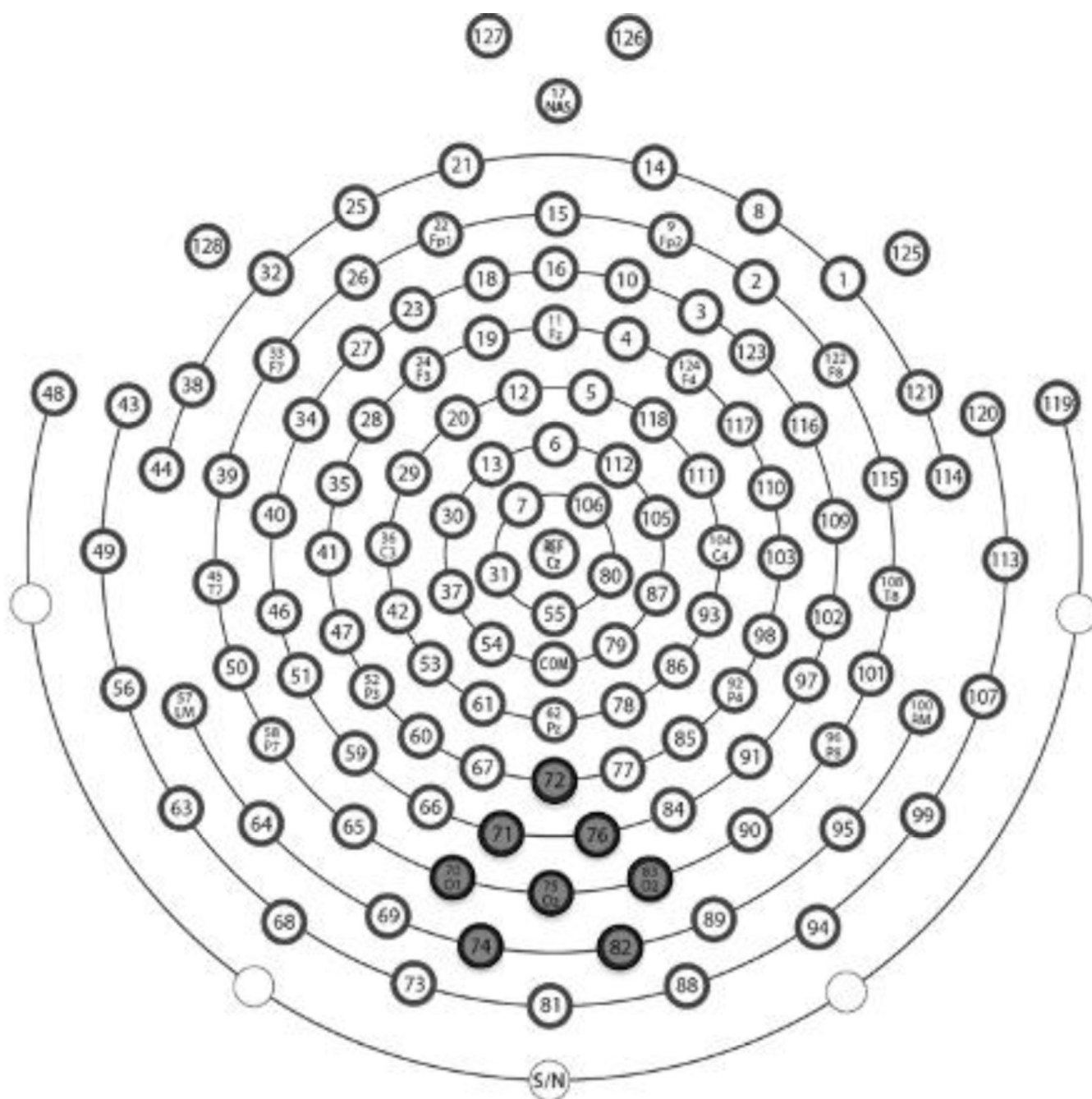


Figure 3.

Layout of the dense electrode array. Locations of the electrodes grouped for regional means (used for statistical analysis) are in gray. Sensor #75 corresponds to Oz of the International 10–20 System.

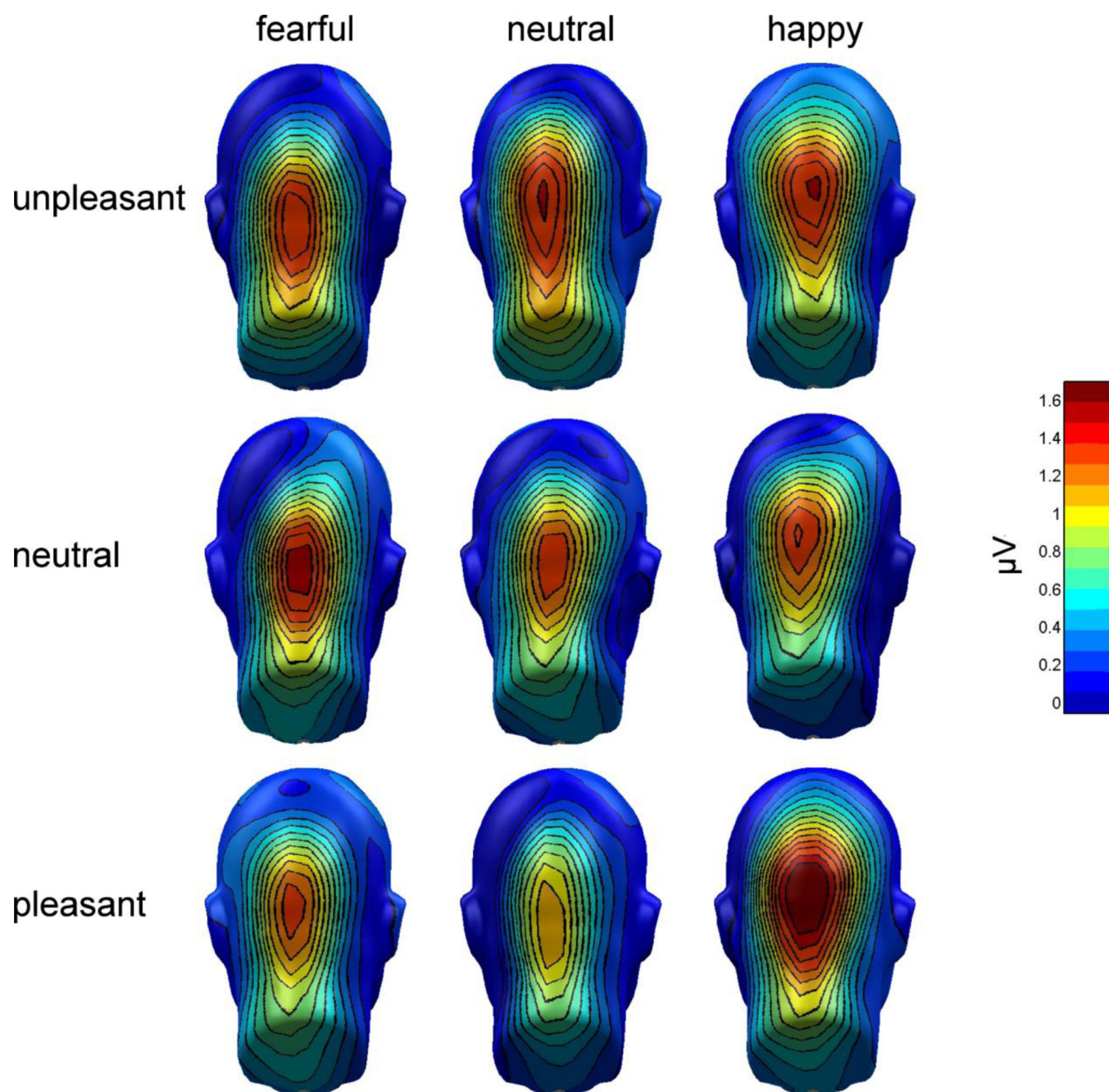


Figure 4. Mean scalp topographies of ssVEP amplitudes (200–3,000 ms) elicited by fearful, happy, and neutral facial expressions as a function of visual background pictures.

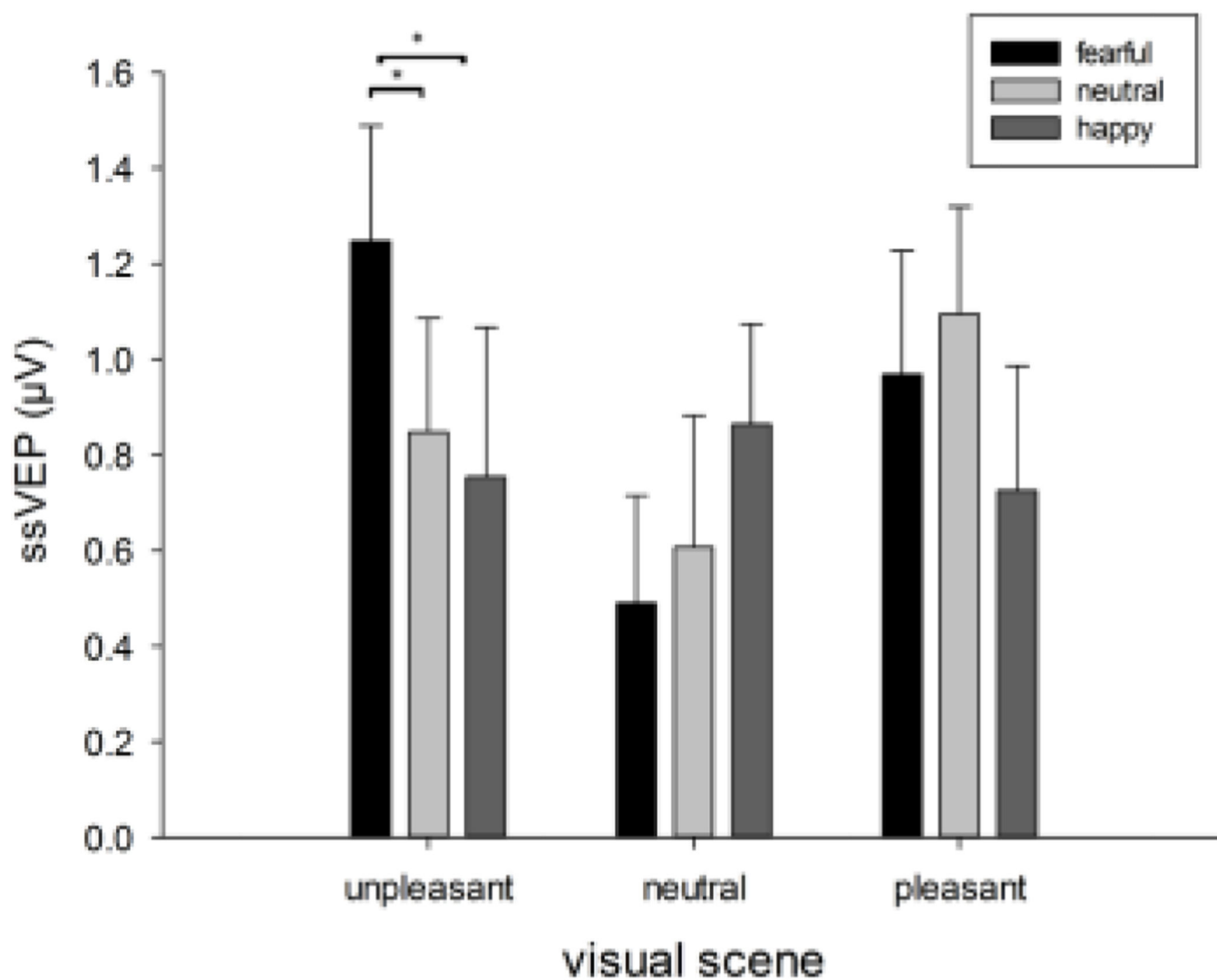


Figure 5. Mean ssVEP amplitudes (200–3,000 ms) +SEM evoked by threat, neutral, and pleasant visual background scenes as a function of facial expression foreground picture. Amplitudes are averaged across a medial-occipital cluster comprising Oz and its 7 nearest neighbors.

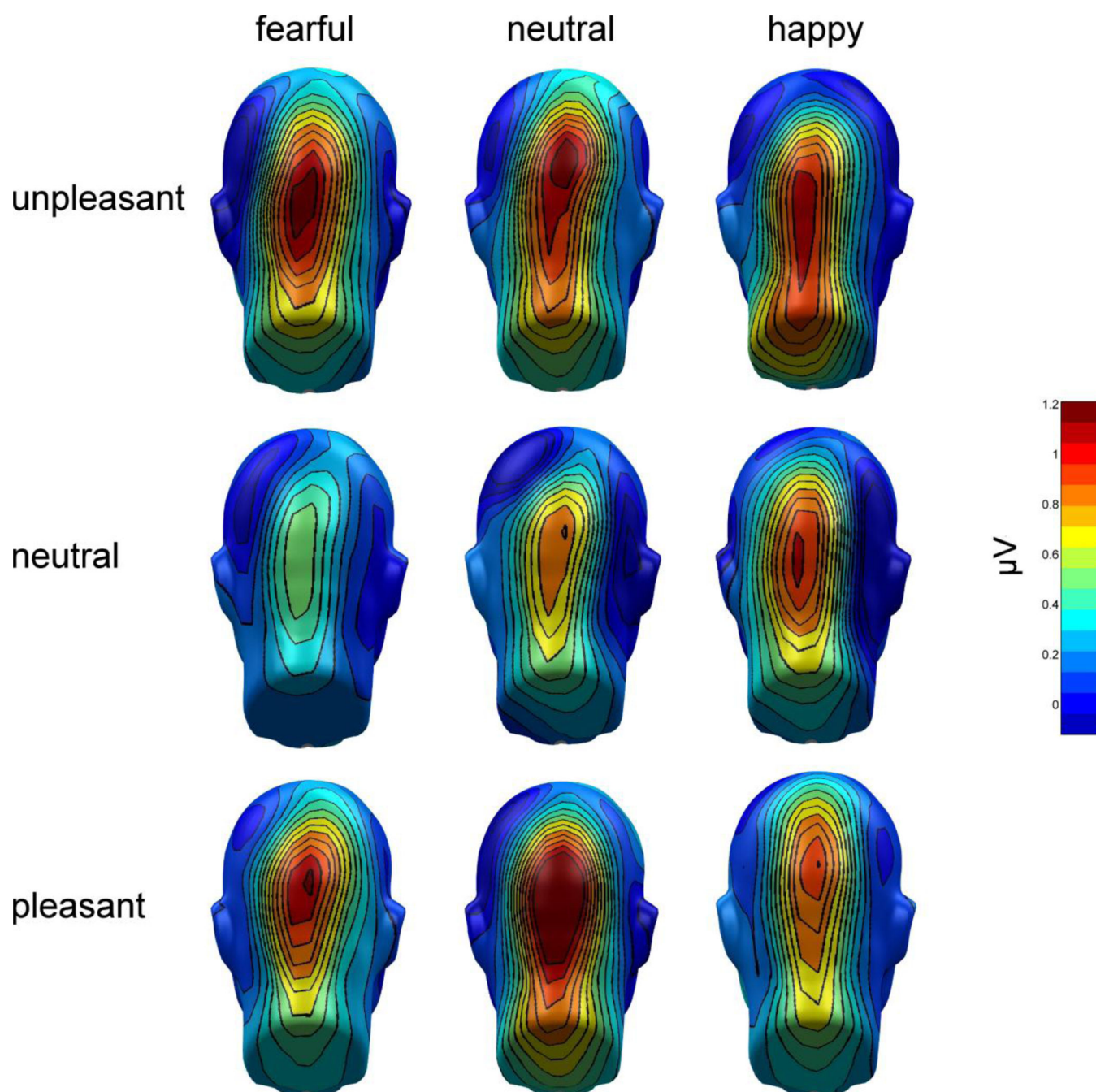


Figure 6. Mean scalp topographies of ssVEP amplitudes (200–3,000 ms) elicited by threat, neutral, and pleasant visual scenes as a function of facial expression foreground picture.

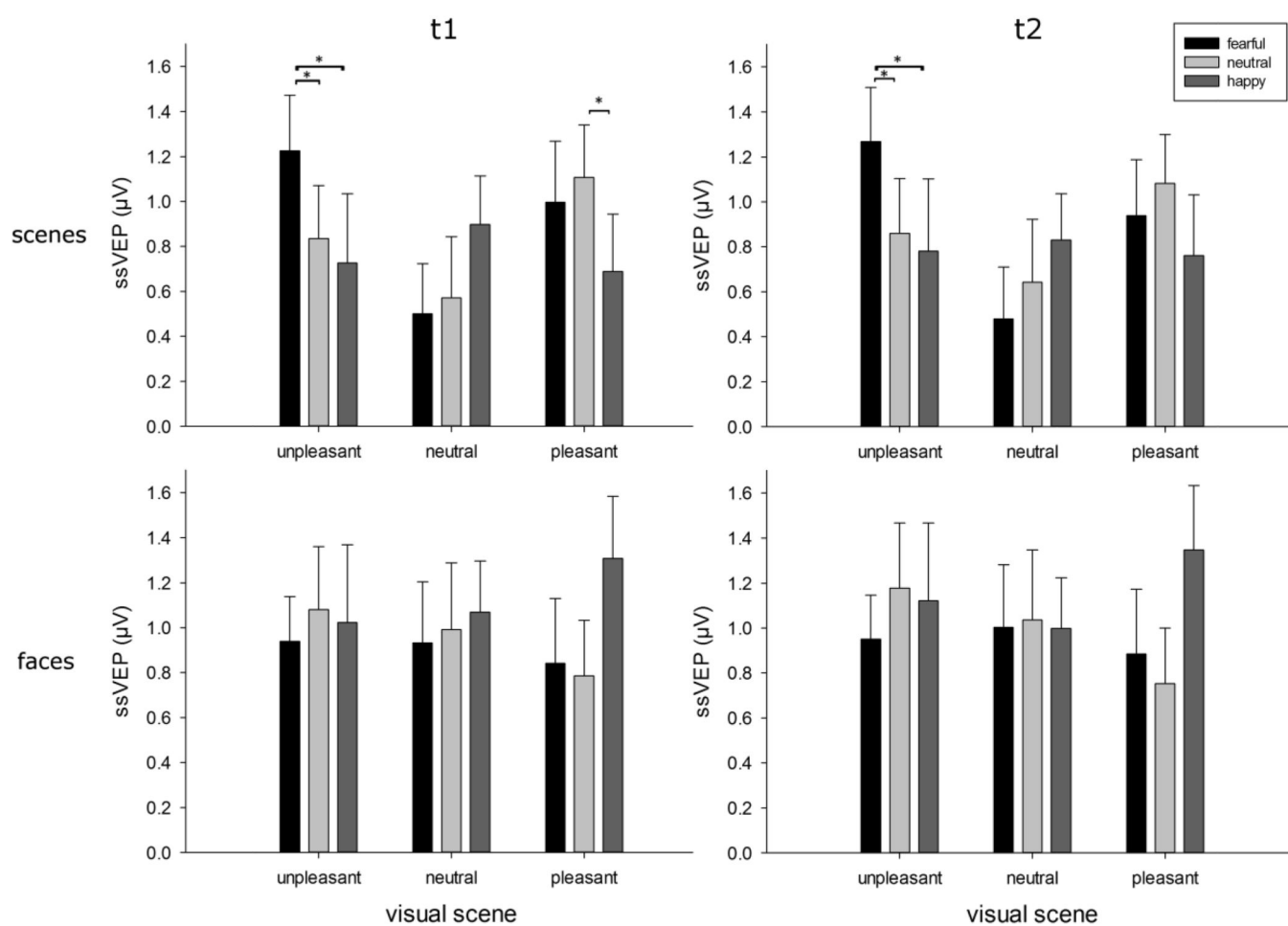


Figure 7.

Mean ssVEP amplitudes (+ SEM) evoked by visual scenes and faces in the two time intervals (t1: 200–1,500 ms; t2: 1,501–3,000 ms).

Table 1

Mean valence and arousal ratings (+ SD) of facial expressions embedded in three visual contexts (threat, neutral, pleasant).

facial expression	visual background					
	pleasant		neutral		threat	
	Valence	Arousal	Valence	Arousal	Valence	Arousal
happy	6.6 (0.6)	4.4 (1.4)	6.3 (0.7)	4.4 (1.4)	5.9 (1.1)	4.7 (1.4)
neutral	5.1 (0.5)	3.9 (1.3)	4.9 (0.3)	3.7 (1.4)	4.5 (0.6)	4.3 (1.4)
fearful	4.1 (1.0)	5.0 (1.6)	3.8 (0.9)	5.0 (1.8)	3.4 (0.8)	5.4 (1.7)

Note. Valence: 1 = very threat, 9 = very pleasant; arousal: 1 = not arousing, 9 = very arousing.

Table 2

Mean recognition rates in percent (+ SD) for facial expressions embedded in three visual contexts.

facial expression	visual context		
	pleasant	neutral	threat
happy	94.2 (15.1)	92.9 (13.6)	93.8 (15.3)
neutral	96.3 (9.9)	93.8 (15.0)	95.0 (8.3)
fearful	91.7 (20.4)	90.8 (21.3)	92.9 (22.2)