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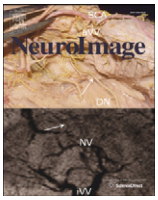

Emotional facial expressions evoke faster orienting responses, but weaker emotional responses at neural and behavioural levels compared to scenes: A simultaneous EEG and facial EMG study

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ABSTRACT

In the current study, electroencephalography (EEG) was recorded simultaneously with facial electromyography (fEMG) to determine whether emotional faces and emotional scenes are processed differently at the neural level. In addition, it was investigated whether these differences can be observed at the behavioural level via spontaneous facial muscle activity. Emotional content of the stimuli did not affect early P1 activity. Emotional faces elicited enhanced amplitudes of the face-sensitive N170 component, while its counterpart, the scene-related N100, was not sensitive to emotional content of scenes. At 220–280 ms, the early posterior negativity (EPN) was enhanced only slightly for fearful as compared to neutral or happy faces. However, its amplitudes were significantly enhanced during processing of scenes with positive content, particularly over the right hemisphere. Scenes of positive content also elicited enhanced spontaneous zygomatic activity from 500–750 ms onwards, while happy faces elicited no such changes. Contrastingly, both fearful faces and negative scenes elicited enhanced spontaneous corrugator activity at 500–750 ms after stimulus onset. However, relative to baseline EMG changes occurred earlier for faces (250 ms) than for scenes (500 ms) whereas for scenes activity changes were more pronounced over the whole viewing period. Taking into account all effects, the data suggests that emotional facial expressions evoke faster attentional orienting, but weaker affective neural activity and emotional behavioural responses compared to emotional scenes.

Introduction

In emotion research two kinds of stimuli are frequently used: facial expressions (e.g. a smiling or sad face) and emotionally evocative scenes (e.g. snakes, erotic pictures). But, do these forms of emotional stimuli undergo the same neural processing? Despite each being intrinsically emotionally evocative, only a few studies exist that have compared affective processing of faces and scenes in the same experiment and context.

A recent meta-analysis comparing 157 functional Magnetic Resonance Imaging (fMRI) studies that used either emotional faces or emotional scenes (Sabatinelli et al., 2011) revealed multiple clusters of brain activations unique to these different forms of stimuli even after the subtraction of neural activity related to basic visual processing. Although this suggests that both types of stimuli might be processed differently in the brain, direct comparisons of the time course of affective processing for faces and scenes are lacking and little is known about whether both stimulus classes elicit similar expressive behavioural reactions.

In other contexts it is obvious that faces and scenes are indeed quite different. For example, facial expressions elicit mimicry and facial feedback mechanisms might modify emotion-related processing (see Niedenthal et al., 2001). Facial expressions can be understood as interpersonal, facilitating social transactions, and require complex neural processing to translate these emotional cues into social meaning. Emotional scenes on the other hand are more intrapersonal and directly elicit motivational behaviours without needing to translate their meaning beyond knowing whether to approach or avoid. Different facial expressions are more similar to each other than different scene pictures are. Various processing differences between face and scene stimuli have been described. Hariri et al. (2002) found varying amygdala activity depending on whether a fearful face or a threatening scene was presented to their participants. In their fMRI study, Keightley et al. (2011) reported about their conclusion that the contextual information in emotional

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scenes may facilitate memory via additional visual processing, whereas memory for emotional faces may rely more on cognitive control mediated by rostrolateral prefrontal regions. Epstein et al. (2006) investigated differences between face and scene inversion. Their results demonstrate that both face and scene inversion cause a shift from specialised processing streams towards generic object-processing mechanisms, but this shift only leads to a reliable behavioural deficit in the case of face inversion.

The temporal characteristics of neural affective processing have been relatively well documented for emotional faces (Vuilleumier and Pourtois, 2007; Wieser and Brosch, 2012) and emotional scenes (Olofsson et al., 2008; Schupp et al., 2006a). Anatomically, visual information passes through the extrastriate visual cortex where low-lying physical stimulus properties such as luminance and spatial complexity determine which aspects of visual information receive rapid attentional capture and further processing (Clark and Hillyard, 1996; Givre et al., 1994; Hillyard and Anllo-Vento, 1998; Mangun et al., 1993; Rugg et al., 1987). This rapid-attentional capture is seen in scalp-recorded potentials as a prominent positively charged deflection in amplitude over lateral posterior occipital sites at approximately 100 ms post-stimulus (termed the P100 component, or P1 to represent the first positive peak in neural activity), where the size of the amplitude deflection indexes the degree of attentional capture of the related stimulus. Attended-to information then undergoes object recognition processing in neural circuits proceeding through bilateral ventral–lateral streams from the visual cortex into the temporal cortices (Allison et al., 1999). Here, the fusiform gyrus, a well-studied structure located in the inferior temporal lobes, facilitates face recognition via a highly specialised process of collating local facial features into a holistic global face representation (Rossion et al., 2003). This activity is observed in scalp-recorded potentials as a strong negatively charged deflection in amplitude over lateral temporal–occipital areas approximately 170 ms post-stimulus onset (Bentin et al., 1996; Deffke et al., 2007), hence the name N170. Other stimuli such as complex scenes also undergo category-specific processing across more widely distributed hierarchically organised circuits in the ventral–lateral streams, with this activity being observed as a more modest negative deflection in amplitude at around 150–200 ms after stimulus onset over lateral temporal-occipital scalp locations (termed the N100). From here, it has been posited that affective information of faces and scenes begins to influence neural activity, seen at lateral–occipital scalp recordings as a more stable negative shift in polarity when viewing emotionally-evocative relative to neutral stimuli. This posterior negativity (i.e. the early posterior negativity or EPN) typically emerges at the offset of the N100/N170, around 200 to 250 ms post-stimulus and has been found to be modulated as a function of increased attentional allocation and greater motivational relevance of the emotionally evocative stimuli (Bublatzky and Schupp, 2011; Foti et al., 2009; Schupp et al., 2006a; Weinberg and Hajcak, 2010).

There is however evidence that affective information can influence activity at earlier stages of processing relative to the EPN. Several studies have reported larger N170 amplitudes when viewing negatively-valanced facial expressions such as fear and anger (e.g. Batty and Taylor, 2003; Leppänen et al., 2008; Pourtois et al., 2005; Stekelenburg and de Gelder, 2004), which has been interpreted as an innate attentional 'negativity bias' (Carretie et al., 2009; Holmes et al., 2005). The same controversy exists for emotional scenes, with some studies reporting a negativity bias for highly unpleasant threatening or fearful scenes in the time window of the N100. Affective modulation has even been reported as early as 100 ms post-stimulus (Batty and Taylor, 2003; Eger et al., 2003; Eimer and Holmes, 2002; Holmes et al., 2003; Pizzagalli et al., 1999; Pourtois et al., 2005; Recio et al., 2014; Smith et al., 2013; Streit et al., 2003). Differences as well as similarities in affective stimulus processing may be better understood by directly comparing when these processes occur for emotional faces and scenes in a single experimental framework. This would also allow a direct comparison of behavioural reactions elicited by faces and scenes.

In the current study, we were interested in investigating how affective neural activity during emotional face and scene perceptions translates into emotional behaviour, building on the idea that emotional behaviour should be understood as a consequence of subcortical affective neural activity (Walla and Panksepp, 2013). Spontaneous facial muscle activity is an emotion-related behavioural phenomenon that is thought to play a crucial role in social emotion recognition, whereby perceiving an emotional facial expression elicits a rapid or spontaneous micro-simulation of the perceived facial expression by the perceiver less than 1000 ms post onset (Achaibou et al., 2008; Dimberg et al., 2000a; Grèzes et al., 2013; Korb et al., 2010; Moody et al., 2007). By utilising the excellent temporal resolution offered by electromyography to measure facial muscle activity (fEMG), these studies have shown that zygomaticus major 'cheek' muscles rapidly and spontaneously contract in response to smiling faces while corrugator supercilii 'eyebrow' muscles rapidly and spontaneously contract in response to angry or fearful faces. The phenomenon is thought to facilitate emotion recognition by triggering the reactivation of specific neural regions that are involved in producing that same emotion in the perceiver, leading to a realisation of the other person's emotional state (e.g. Barsalou, 2003a; Barsalou et al., 2003b; Clark et al., 2008; Niedenthal, 2007). Moreover, empirical evidence suggests that spontaneous facial reactions play a causal role in emotion recognition whereby selectively preventing movement in facial muscle/s required to simulate an expression leads to poor recognition ability for that facial expression in another person (Foroni and Semin, 2011; Niedenthal et al., 2001; Oberman et al., 2007; Ponari et al., 2012).

However, emotional scenes have also been shown to evoke spontaneous facial reactions (Dimberg et al., 1998). In contrast to faces emotional scenes often do not contain any third-party emotion to recognise. This raises the question of whether and in what ways spontaneous facial muscle activity may differ when elicited by emotional faces compared to scenes, such as in latency or strength of the response. To this extent, the objective of the current study was to investigate differences in emotional responses evoked by happy, fearful and neutral faces versus positive, neutral and negative scenes: (1) during early visually-evoked stages of neural activity including the P1, N100/N170, and EPN; and (2) in spontaneous zygomatic and corrugator facial reactions; and (3) to examine correlations between affective neural activity and emotional behaviour.

When considering motivationally-relevant emotion processing, arousal must be taken into consideration, because stimuli that evoke heightened arousal have been shown to modulate both neural and facial muscle activity independent of emotional valence or stimulus type (Cacioppo et al., 1986; Cuthbert et al., 2000; Feng et al., 2014; Lang et al., 1993). For this reason the face and scene stimuli chosen for the current study were relatively low-arousing (see Fig. 1 bottom right graph). However, it was still possible that face and scene stimuli could evoke different degrees of arousal. Therefore, arousal responses to pictures were also recorded via the skin conductance response (SCR), a neurophysiological measure of sweat gland activity which is controlled by the sympathetic part of the autonomic nervous system. SCRs could therefore be used to differentiate neural and behavioural effects associated with enhanced levels of arousal from those associated with emotional valence or stimulus type.

A secondary aim of this study was to examine whether or not early emotion processing is influenced by the depth of conceptual emotion processing, and, if so, whether such effects might suppress or enhance spontaneous facial reactions. Traditionally, the delayed match-to-sample task involves the 'passive' presentation of a first stimulus (e.g. an emotional facial expression) followed by an 'active' presentation of a second stimulus, at which point some judgement must be made regarding the second stimulus as a function of the first, usually whether or not they express the same type of emotion. In the current study, we varied the semantic format of emotion recognition between three 'delayed match-to-sample' emotion-matching tasks. A consistent

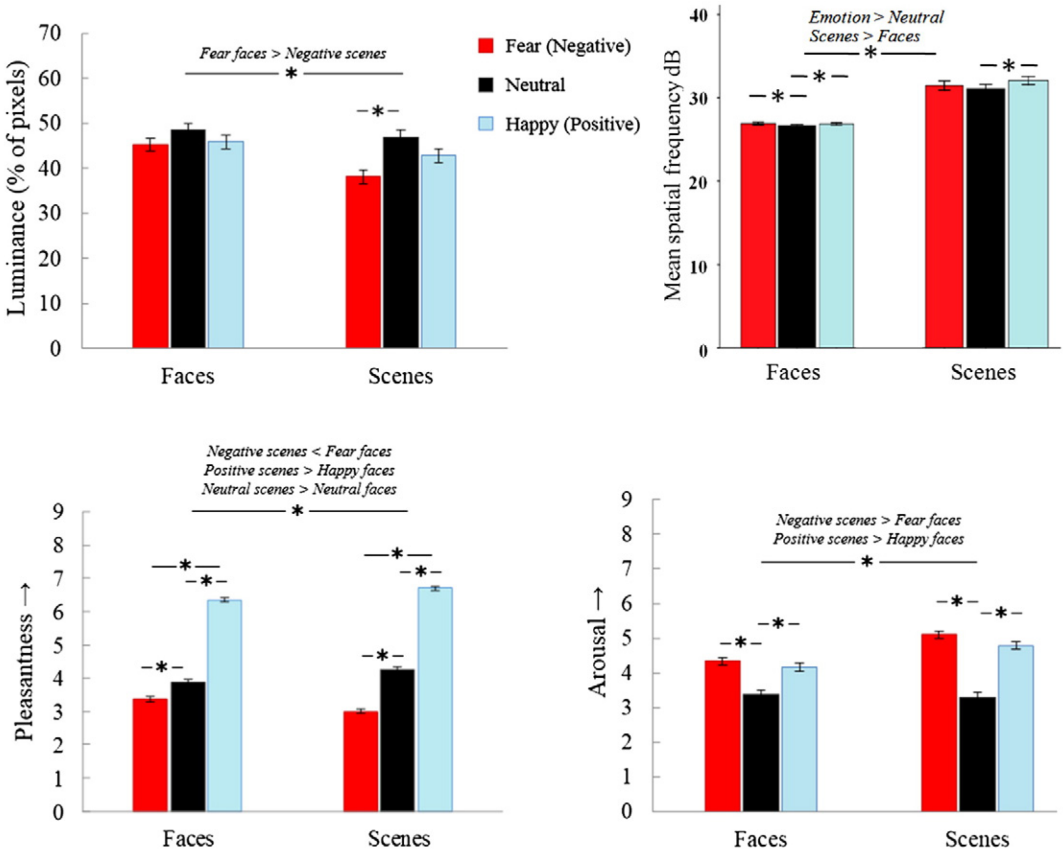


Fig. 1. Mean luminance and spatial frequency values (top) and pre-evaluated pleasantness (bottom left) and arousal (bottom right) ratings for the final collection of stimuli. Pleasantness was rated on a scale of 1 (very unpleasant) to 9 (very pleasant). Arousal was rated on a scale of 1 (very calm) to 9 (very arousing). Error bars represent one standard error of the mean.* = The differences are significant at .05 alpha level.

presentation format was always used for the first emotional stimulus (i.e. always an emotional picture) while for the second emotional stimulus, the presentation format was varied across tasks to be either another emotional picture, an emotional word or to freely label the depicted emotion (see Fig. 2 for examples of each task). Hence, one version of the task was to compare an emotional picture with another emotional picture; the second version was to compare an emotional picture with an emotional word; and the third task had no second emotional stimulus to compare the first emotional picture with, instead participants had to freely label the depicted emotion.

Most research using the match-to-sample paradigm focuses on neural or behavioural activity associated with the second 'active' stimulus (e.g. Hirai et al., 2008; Narumoto et al., 2001). However the focus of the current study was neural and behavioural activity associated with the first passively viewed stimulus. This design specifically allowed us to examine whether, when emotional pictures are viewed under exactly the same presentation conditions, does passive emotion processing and responding vary as a function of the semantic level of emotion recognition? Due to unresolved muscle-related artefact issues in the picture-labelling task, we here focus on EEG and fEMG effects associated with the 'picture–picture matching' and 'picture–word matching' tasks.

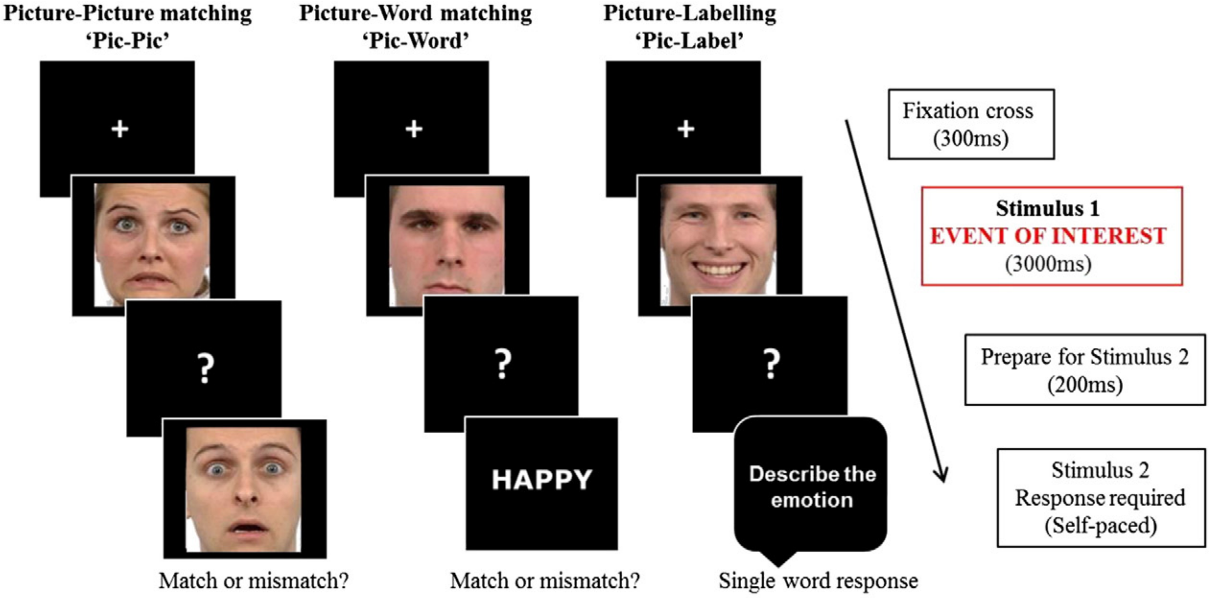
Methods

Participants

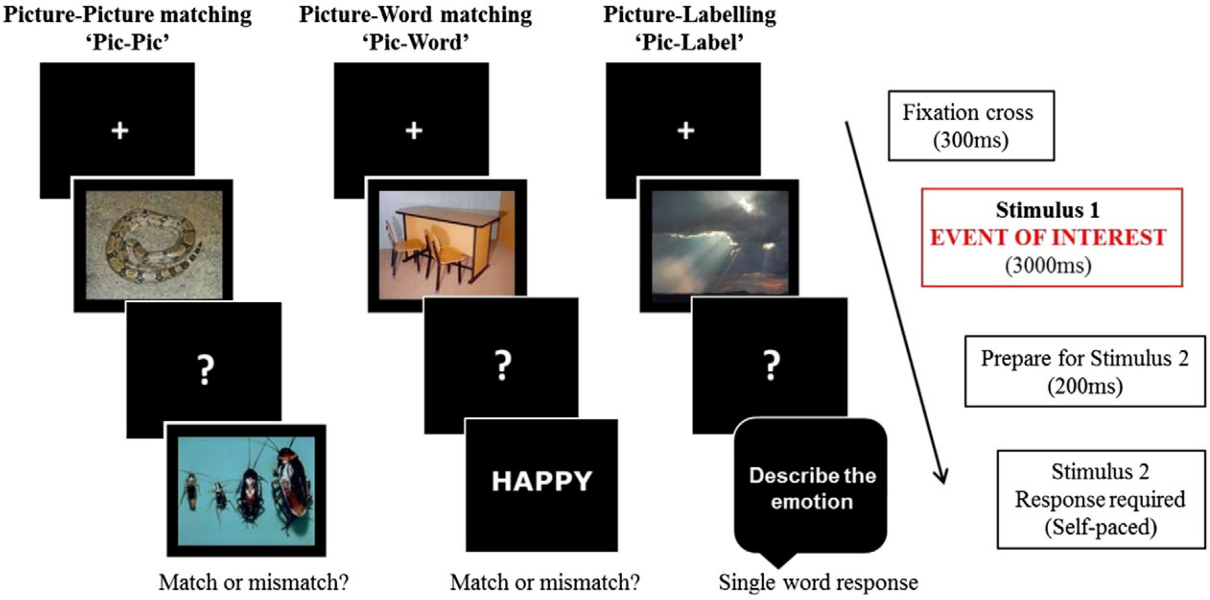
Participants were 27 undergraduate students enrolled at the University of Newcastle. Data of four participants were excluded from the analysis due to technical issues with the EMG and skin conductance recording equipment (two females and one male) and too few remaining EEG trials after artefact removal (one female). The mean age of the remaining 23 participants is 21 years (SD = 1.72) (17 females). Participants were native speakers of English, right-handed, non-smokers, had no known history of neuropathology and were not taking central nervous system targeted medication such as antidepressants or stimulants at the time of testing. Participants provided written informed consent and the project was approved by the University of Newcastle Human Research Ethics Committee [H-2012-0229].

Stimuli

The 270 happy, fearful and neutral face stimuli were taken from the Radboud Faces Database (RAFD; Langner et al., 2010) and Set A of the Karolinska Directed Emotional Faces Database (KDEF; Lundqvist et al., 1998). For face stimuli, each face was cropped to remove hair, ears, clothing etc. from the image, leaving only the necessary elements of the face for distinguishing an emotional expression. The 270 positive, negative and neutral scene stimuli were taken from the Geneva Affective Picture Database (GAPED; Dan-Glauser and Scherer, 2011) and the International Affective Picture System (IAPS; Lang et al., 2005). Positive scenes included nature scenes, baby animals, appetising food and erotic scenes depicting a male and female embrace. Negative scenes were specifically selected based on a study by Mikels et al. (2005), which categorised IAPS stimuli into discrete emotion categories including fear. Obvious thematic characteristics of the discrete IAPS fear collection, such as spiders and snakes, were then used as a basis for selecting negative (mainly fearful) scenes from the GAPED database, for which no discrete emotional categorisation exists. For neutral scenes, we specifically chose stimuli that visually represented neutrality (e.g. a stair case, computer, light bulb), because valence ratings are not accurate predictors of emotional categorisation (Blairy et al., 1999).



a. Face stimuli emotion recognition tasks



b. Scene stimuli emotion recognition tasks

Fig. 2. An example of the trial structure for each emotion recognition task. The top figure illustrates examples for the versions using emotional faces, and the bottom figure illustrates the same trial examples, but using emotional scenes. From the left to right of each figure is an example of the Picture–Picture matching task; the Picture–Word matching; and the Picture-Labelling task. Notice that each task begins exactly the same, with a fixation cross followed by a passively viewed picture (Stimulus 1; a happy, neutral or fearful picture (face or scene, depending on the task version)). After this, the trial structure changed according to type of task being completed. Neural and facial muscle activity during the 3000 ms time window corresponding to Stimulus 1 was analysed in this study to determine whether processing of emotional information is differently influenced by the way that information needs to be used.

Scene stimuli featuring a forward-facing face were excluded from the scenes collection.

The stimuli collections were rated on levels of valence and arousal in a pilot study of a larger pool of images using an independent group of 42 participants (23 females) with a mean age of 25 years (*SD* = 4.61). Participants rated equal samples of face and scene stimuli using the Self-assessment manikin (SAM; Bradley and Lang, 1994). Pictures with ratings that best balanced valence and arousal levels across stimulus categories were then chosen to be included in the study. Mean valence and arousal ratings in addition to luminance and spatial frequency values for the final collection are displayed in Fig. 1.

There is existing empirical evidence showing that low level physical features of visual stimuli such as luminance and spatial frequency modify early brain activities (e.g. Alorda et al., 2007; De Cesarei and Codispoti, 2012; Delplanque et al., 2007), a phenomenon also known as exogenous brain activity effects (Donchin, 1978). Since our motivation was focused on early brain activity effects related to emotion-specific content of faces versus scenes it is important to look at physical features of all visual stimuli, in particular luminance and spatial frequency and to test whether or not potential differences in luminance and spatial frequency across stimuli could theoretically explain any early brain activity differences that are described in the frame of this paper.

For this purpose we ran a spatial frequency analysis of all our images and calculated analytic statistics to test whether or not spatial frequencies differed between stimulus categories (faces and scenes) and also between emotion categories. An ANOVA including all spatial frequency values was run and revealed a highly significant main stimulus category effect ($p < .001$) and a significant main emotion category effect ($p = .009$). However, the interaction of both factors was not significant ($p = .097$) (all Greenhouse–Geisser corrected). The pattern of these results is understood as demonstrating that mean spatial frequencies of our images differ between faces and scenes. In addition, spatial frequencies of our images differ as a function of emotion category, but the way they differ between emotion categories does not depend on stimulus category. Descriptive statistics shows that scenes had overall higher spatial frequencies than faces (reflected in the main stimulus category effect), which we interpret as a result of higher complexity of scenes compared to faces. In both stimulus categories it can be seen that neutral images are associated with lower spatial frequency values compared to both positive and negative emotion categories (reflected in the main emotion category effect and the not significant interaction of both factors).

Further, t-tests revealed significant differences between spatial frequencies of neutral and negative faces ($p = .010$; $T = 2.618$), also neutral and positive faces ($p = .047$; $T = -2.009$), but not negative and positive faces ($p = .557$; $T = .590$). Spatial frequencies of negative scenes don't differ from those of neutral scenes ($p = .312$; $T = 1.017$), but they do differ between neutral and positive scenes ($p = .009$; $T = -2.679$). No differences are found between positive and negative scenes ($p = .107$; $T = -1.626$).

In summary, positive and negative stimuli are associated with higher spatial frequencies than neutral stimuli, which is true for both stimulus categories. In general, scenes are associated with higher spatial frequencies compared to faces (see Fig. 1).

It also turned out that luminance differences exist. An ANOVA revealed a significant main stimulus category effect on luminance values ($F = 10.106$; $p = .002$). There is also a highly significant emotion category effect ($F = 15.911$; $p < .001$), but a not significant interaction of those two factors ($F = 2.931$; $p = .058$) (all Greenhouse–Geisser corrected). Similar to spatial frequency data luminance data also demonstrate that differences exist between emotion categories, but that these differences do not depend on stimulus category. Paired-sample T-Tests revealed that image luminance differs significantly between fearful faces and negative scenes ($t = 4.177$; $p < .001$). No other differences were found to be significant (see Fig. 1).

Overall, we can summarise that both physical features show similar patterns in terms of how they differ across stimulus and emotion categories. There are emotion-specific differences in physical features, but those differences are independent from stimulus category. In other words, any stimulus category effect on brain activities can theoretically be explained by differences in physical image features, but stimulus-specific emotion category effects cannot.

For instance, taking a closer look at the present early EEG effects we notice that the P1 stimulus category effects could theoretically be explained by spatial frequency and/or luminance differences of our stimuli, but this is not the case for the task-dependent effects and also not for all of the emotion-specific brain activities that differ between faces and scenes as they were found in later time windows.

Tasks and procedure

During individual testing sessions, participants sat in a reclining chair under dim lighting and positioned in front of a display monitor to allow 9.9° × 8.5° of visual angle (300 × 399 pixels). After being connected to the recording equipment, participants completed three delayed match-to-sample emotion recognition tasks in random order. Each task was completed once with face stimuli and once with scene stimuli (blocked sessions randomised within tasks; Figs. 2a and b). At the beginning of the session participants were informed of what each task involved so as to minimise potential practice effects of task order bias. Then for each task, instructions for that task were repeated and six practice trials were completed. Practice trials were not included in the analyses.

Trials in each task always began with a fixation cross followed by a happy, neutral or fearful picture (Stimulus 1; ‘S1’) for 3000 ms, which required no overt response from the participant other than to simply view the picture. S1 was proceeded by a second stimulus (Stimulus 2; ‘S2’) which required an active response. For one of the tasks (Picture–Picture matching; ‘Pic–Pic’), the S2 was another happy, neutral or fearful picture, while for another one (Picture–Word matching; ‘Pic–Word’), the S2 was one of the three emotion category labels ‘fear’, ‘neutral’ or ‘happy’ presented in block white letters against a black background. The active response for the Pic–Pic and Pic–Word tasks was a forced choice (match/mismatch) judgement of whether S1 and S2 represented the same emotion (happy, fear or neutral) by pressing one of two buttons (‘Z’ or ‘/’) with the corresponding index finger as quickly as possible without forgoing accuracy. For a third task (Picture labelling; ‘Pic-Label’), the S2 was the symbol ‘?’ which cued the participant to say out loud any one word that best described the emotion depicted in S1. For the Pic-Label task, participants continued to the next trial by pressing the space bar. Key responses at the end of each trial cued a 1000 ms inter-trial interval before the next trial began. It should be emphasised that the S1 presentation conditions were identical across the three tasks, i.e., the S1 was always a passively viewed picture. Hence, the S2 event served as the experimental manipulation to examine whether emotional information (S1) is processed differently depending on the emotion context of S2 and the task. Accordingly, the event of interest for the analysis was the 3000 ms time window corresponding to the S1 presentation.

There were 90 trials for each face and scene version of the tasks (30 fearful (negative), 30 neutral and 30 happy (positive) S1 presentations). All S1 pictures were novel (i.e., no picture was presented more than once) and were presented in colour (as were the S2 Pic–Pic pictures). S1 stimuli were randomly presented within tasks, and for the Pic–Pic and Pic–Word tasks, S2 items were also randomised. Hence, each S1–S2 pairing was randomly generated, however the frequency of match/mismatch and S1–S2 emotion category combinations was balanced. Participants were given a short break midway and at the end of each 90-trial task. The experiment took approximately one hour to complete.

Measures and data reduction

Due to the different nature and dynamics of biosignals recorded in the frame of this study we chose different epoch lengths for the different measures. Since we focus on early brain activity changes we set maximum epoch length to 1 s, but actually display ERPs only until 400 ms post stimulus, because during this period early changes occur. Facial EMG epochs were set to 1.5 s to potentially capture later effects and skin conductance epochs were set to 4 s, because of their less dynamic nature and their delay (see more details below).

EEG recordings

Scalp EEG, measured in micro Volts (μV), was recorded using a 64 channel Biosemi cap and amplifier (http://www.Biosemi.com) sampled continuously at 2048 Hz using an electrode layout corresponding to the 10-10-electrode placement standard, and referenced to a common-mode signal. The data was down-sampled offline to 256 Hz and filtered from 0.1 to 30 Hz using EEG Display software. Eye blink artefacts were corrected using a set of linear regression weights at each EEG electrode derived from an averaged eye blink (Semlitsch et al., 1986). Segments of the EEG record containing gross artefact were detected by an automated procedure that applied amplitude thresholds within a number of frequency bands. For each S1 stimulus, EEG epochs were extracted from 100 ms pre-stimulus to 1000 ms post-stimulus, and baseline corrected across the pre-stimulus interval. Trials containing artefact exceeding ± 100 μV were excluded. Finally, trials were averaged to produce the ERP for each image type.

Noisy channels were interpolated prior to data reduction for five participants, involving no more than one electrode within each analysed cluster. The first two trials completed during each face and scene recognition task were removed. On average, 14% of trials were removed (4/30 trials per condition for the 12 analysed conditions, SD = 2.92). Trials were then group-averaged to create a single waveform per condition at each electrode location and re-referenced to an average of all electrodes excluding the mastoid and ocular sites.

The event-related components of interest were identified by visual inspection of the electrode montage to identify clusters with prominent activity, and then by software-facilitated comparisons to verify the exact electrode locations of peak amplitude deflection. The high number of factors being analysed increased the likelihood of generating false positive effects. To reduce this risk, we employed procedures similar to those used by Schupp et al. (2003) for calculating the grand mean of activity evoked during experimental conditions for each component analysed. These included averaging the activity of two electrode locations showing the greatest peak deflection, and then averaging over a time interval of at least 10 data samples (40 ms) centred over the peak. The P1 component peaked over posterior–occipital electrodes PO7/O1 and PO8/O2at 130 ms on average for face stimuli, approximately 20 ms earlier than for scene stimuli, which had an average latency of 150 ms. For each participant a single mean amplitude for each of the 12 experimental conditions was calculated for the 120–160 ms time interval. At temporal–occipital regions face stimuli elicited a prominent N170 component, while scene stimuli elicited only a small N100. These components were immediately followed by a slower progressive negative shift, the so called early posterior negativity (EPN). The N100/N170 and EPN were most prominent over temporal–occipital electrode locations P7/P9 and P8/P10. For each experimental condition, a single mean amplitude was again calculated for each participant for the 150–190 ms time interval corresponding to the N100/N170 and for the 220–280 ms time interval corresponding to the EPN.

fEMG recordings

The corrugator supercilii (CS) muscles, which furrow the eyebrows, were used to reference muscle potential changes corresponding to face and scene stimuli of negative content (see Ekman and Friesen (1978)). The zygomaticus major (ZM) muscles, which lift the cheeks and lips were used to reference muscle potential changes corresponding to face and scene of positive content. fEMG of the CS and ZM, measured in micro Volts (μV), was recorded using a NeXus-10 wireless amplifier (http://www.Mindmedia.com) connected via Bluetooth to a PC laptop, and output measurements were recorded using the NeXus-customised Biotrace + Software. A NeXus Trigger Interface was used to synchronise the onset of trial events between the continuous EEG and EMG recordings to within less than 1 ms accuracy (http://www.Mindmedia.com).

Bipolar electromyography (EMG) was used to record muscle potential changes of both muscles on both sides of the face. We used dual channel electrode cables with carbon coating and active shielding technology for low noise and an additional ground electrode cable attached to the back of the neck (see Reaz et al., 2006; Wand, 2015). The EMG sampling rate was 2048 Hz. A band pass filter from 20 Hz to 500 Hz was applied during online recording. Raw EMG data were then recalculated by using the root mean square (RMS) method (epochsize = 1/16 s) to transform EMG signals into amplitudes.

The resulting amplitudes were then subject to statistical analysis. Using a Matlab based program (www.mathworks.com), a single 1750 ms epoch time-locked to 250 ms preceding the onset of each S1 stimulus presentation was then extracted and divided into seven 250 ms time intervals by averaging across data points. The first time window (−250–0 ms) served as a baseline correction for the six following intervals (0–250, 250–500, 500–750, 750–1000, 1000–1250, 1250–1500 ms) which were the subject of the analysis. After the removal of gross artefacts, the time windows were baseline corrected and the first two trials for each face and scene recognition task were removed from analysis. An inspection of within-trial and across-trial variance was carried out for each data set using an outlier criterion of 3.5 SD or greater. On average, 18% of trials were removed from the ZM data (5/30 trials per condition for the 12 analysed conditions, SD = 3.56) and 13% of trials were removed from the CS data (4/30 trials per condition, SD = 3.35).

Skin conductance recordings

Skin conductance was recorded at a rate of 32 Hz with a Nexus-10-SC/GSR sensor (Two finger sensor) connected to the Nexus-10 recording system with a 24 bit resolution which is able to register changes of less than 0.0001 μS. Because the galvanic skin response is slow-changing, a 4250 ms epoch was extracted, time-locked to 250 ms preceding the onset of S1, with −250 to 0 ms serving as the baseline correction interval. The residual was divided into four 1000 ms time intervals for further analysis (0–1000, 1000–2000, 2000–3000, 3000–4000 ms). Like with EMG data, after the removal of gross artefacts, the time windows were baseline corrected and the first two trials for each face and scene recognition task were removed from analysis. An inspection of within-trial and across-trial variance was carried out for each data set using an outlier criterion of 3.5 SD or greater. On average, 22% of trials were removed (7/30 trials per condition, SD = 3.56).

Statistical analyses

The analysis was a fully within-subjects design with three factors: Stimulus type (Faces, Scenes) × Emotion (Fear (negative), Neutral, Happy (positive)) × Task (Pic–Pic, Pic–Word). Note again that the Pic-Label task was not included in the current analysis. For each event-related potential (ERP) component of interest, condition grand means for the extracted time intervals were subject to a 4-way Stimulus type × Emotion × Task × Hemisphere (Left, Right) repeated measures analysis of variance (RM ANOVA). For the ZM, CS and SCR analyses, condition grand means for each time interval (six time intervals for ZM and CS, and four for SCR) were subject to 3-way Stimulus type × Emotion × Task RM ANOVAs. Significant interactions between Stimulus type and Emotion ($p < .05$) were further investigated where appropriate with secondary RM ANOVAs, conducted separately for each stimulus type. All other significant interactions involving the factor Stimulus type ($p < .05$) were further investigated with paired-samples *t*-tests with bonferroni alpha corrections. For Sphericity violations ($p < .05$), Greenhouse–Geisser epsilon adjustments were applied if $\epsilon < .75$, otherwise Hyundt–Feldt. All main effects are reported, however because the primary objective of the analysis was to investigate differences in emotional face and scene processing, only the interactions involving the factor Stimulus type are reported.

Results

EEG data

P1 component

Emotional content did not affect P1 amplitudes, however the type of stimulus and task did. In addition to the different latencies at which the P1 emerged for faces and scenes, significant main effects also emerged for the factors Stimulus type ($F\,(1, 22) = 15.64$, $p = .001$, $\eta 2 = .42$) and Task ($F\,(1, 22) = 24.89$, $p < .001$, $\eta 2 = .53$). As can be seen in the top left and right waveforms in Fig. 3, scenes evoked a larger mean P1

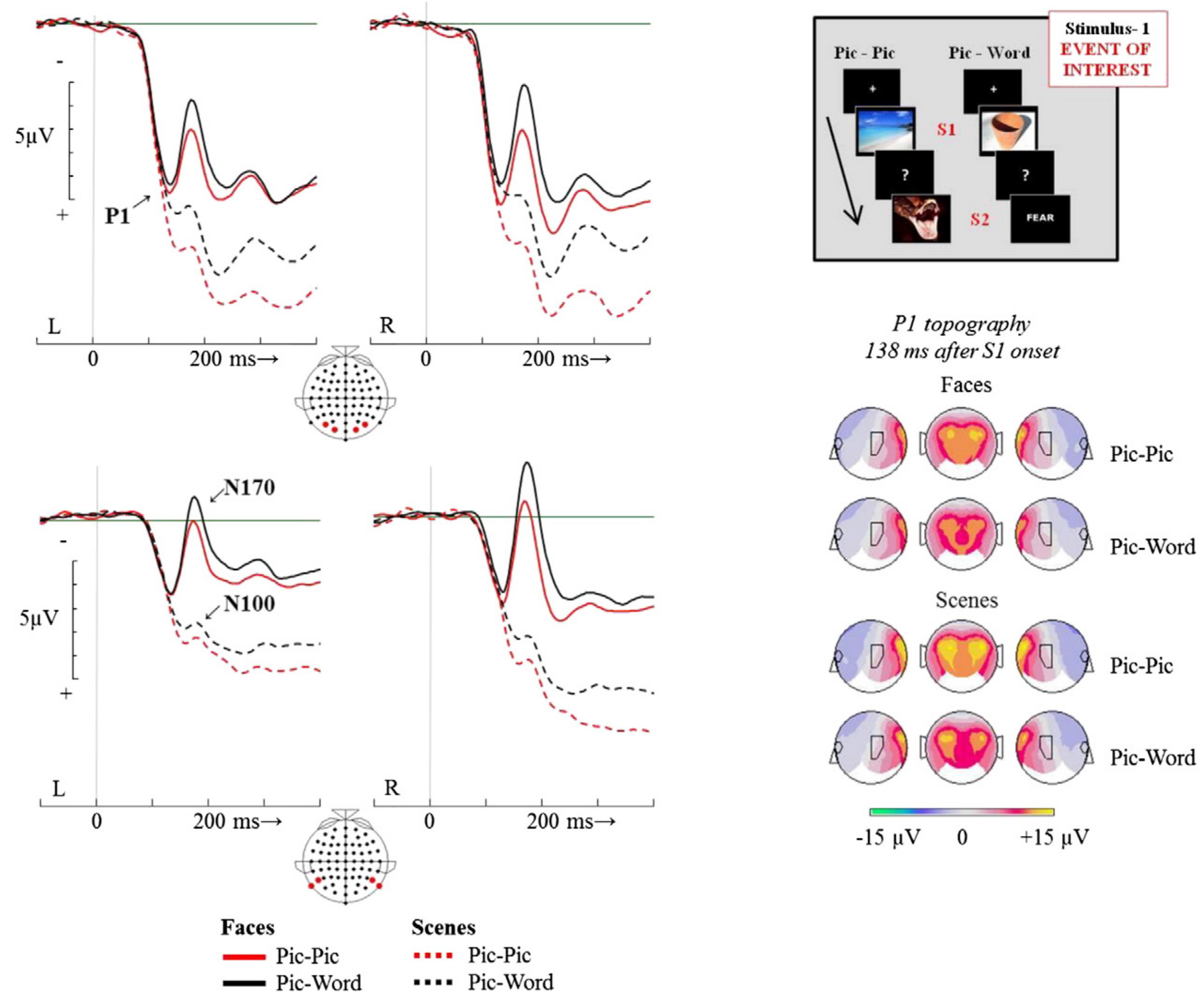


Fig. 3. Effects of the Pic–Pic and Pic–Word tasks on early visual processing of emotional faces and scenes. For quick reference, examples of the tasks are shown in the top right corner. Waveforms show grand-averaged ERPs collapsed across emotion categories and time-locked to the onset of the passively viewed Stimulus 1 (onset = 0 ms). Waveforms in the top panel represent brain activity recorded at left and right posterior–occipital electrode regions. At the far right are corresponding topographic maps of P1-related brain activity. Waveforms in the bottom panel represent brain activity recorded at left and right lateral occipital electrode regions. L = Left hemisphere. R = Right hemisphere.

deflection compared to faces, while pictures viewed during the Pic–Pic task produced larger mean P1 deflections compared to the Pic–Word task. The factors Stimulus type and Task also interacted significantly ($F\,(1, 22) = 5.43$, $p = .029$, $\eta 2 = .20$), indicating that the effect of the Pic–Pic task on P1 amplitudes was greater for scenes than for faces (see also topography maps in Fig. 3, far right).

N170 component (faces)/N100 component (scenes)

The factor Stimulus type produced a strongly significant main effect ($F\,(1, 22) = 324.22$, $p < .001$, $\eta 2 = .94$) indicating that, in line with past research, faces evoked a much larger negative deflection in the N100 time window, the so called N170 component, compared to scenes. A significant main effect of Task was also observed ($F\,(1, 22) = 33.60$, $p < .001$, $\eta 2 = .60$), indicating that pictures viewed during the Pic–Word task produced larger mean N100/N170 deflections compared to the Pic–Pic task (Fig. 3 bottom left and right waveforms).

Stimulus type also interacted separately with the factors Hemisphere ($F\,(1, 22) = 17.64$, $p = <.001$, $\eta 2 = .45$) and Emotion ($F\,(2, 44) = 7.63$, $p = .001$, $\eta 2 = .26$). Effects of emotion content are shown in Fig. 4 top left and right waveforms, and bar graphs depicting the mean activity across the categories are also displayed at the bottom left. The Stimulus type × Hemisphere interaction indicated that regardless of task or emotional expression, face stimuli produced greater activity over the right hemisphere relative to left compared to scenes, which produced no observable lateralised effects. However, note that when we followed up this effect by comparing the total mean activity produced by faces over left and right hemispheres (i.e. collapsing the means of emotion and task conditions), right hemispheric activity was only marginally greater than left ($p = .059$). More critically, the Stimulus type × Emotion interaction was further investigated using separate secondary ANOVAs for each stimulus type. These ANOVAs showed that the N100 was not sensitive to the emotional content of scenes ($F\,(2, 44) = 1.64$, $p = .206$, $\eta 2 = .07$), but that the N170 was differently modulated depending on the emotional facial expression ($F\,(2, 44) = 6.27$, $p = .004$, $\eta 2 = .22$). Contrasts confirmed that fearful faces evoked significantly ($p = .004$; $p = .043$) more negative N170 amplitudes compared to neutral and happy faces, respectively, while amplitudes for happy and neutral facial expressions were not different ($p = .131$).[1]

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[1] Given the critical nature of these findings, we reran the analysis using the 23 original participant data sets plus those for an additional three participants whose data were not included due to EMG recording issues. The analysis resulted in exactly the same interaction between Stimulus and Emotion even when applying a degrees of freedom correction ($p = .005$).

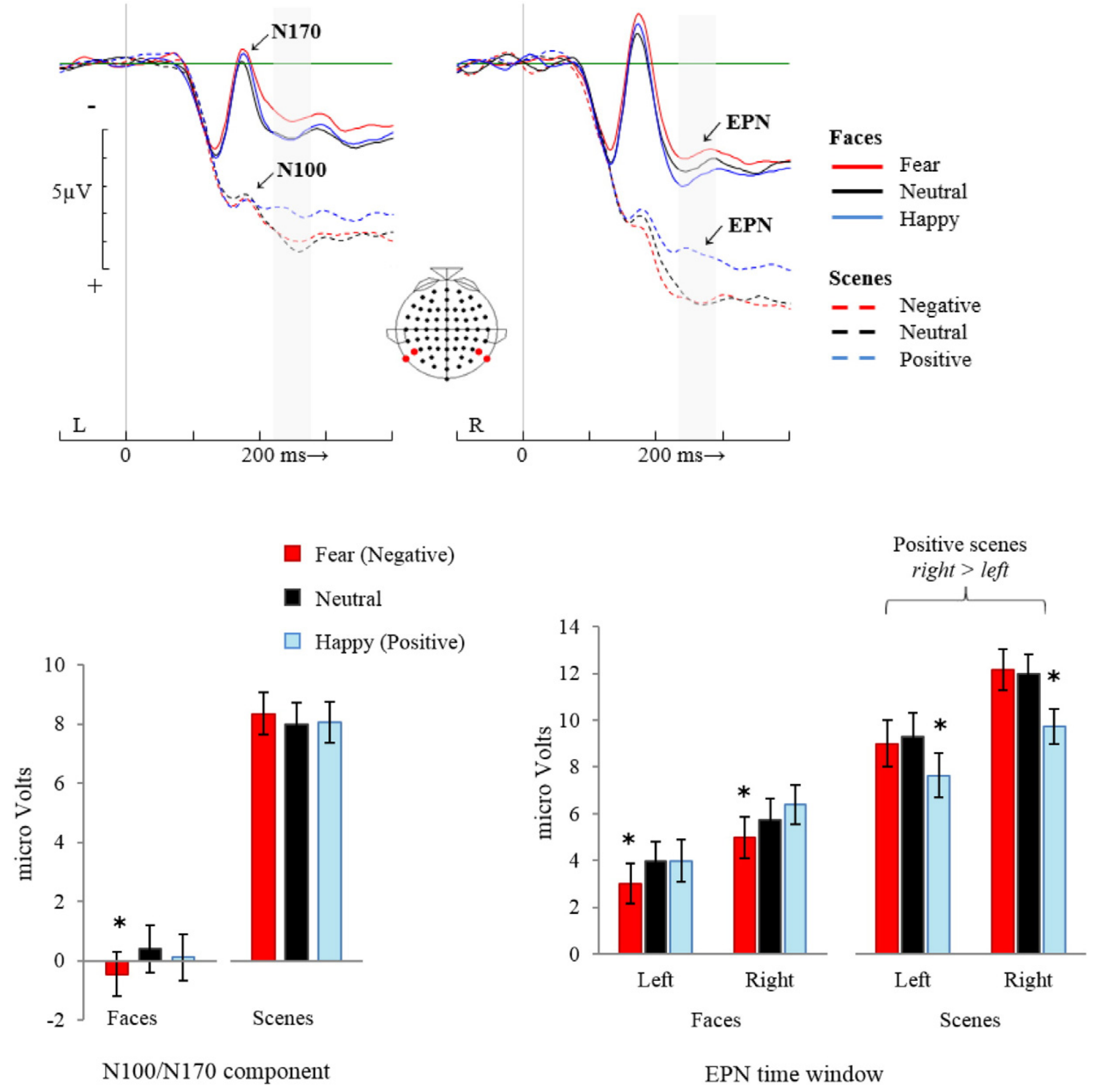

Fig. 4. Effects of emotion category on early visual processing of emotional faces and scenes. In the top panel, waveforms represent brain activity recorded at left and right lateral occipital regions and show grand-averaged ERPs collapsed across task categories and time-locked to the onset of the passively viewed Stimulus 1 (onset = 0 ms). The bar graph at the bottom left illustrates the mean N170-related activity averaged across left and right hemispheres. The bar graph at the bottom right illustrates EPN-related activity recorded over left and right hemispheres. Error bars represent one standard error of the mean. * = The differences are significant after Bonferroni corrections. L = Left hemisphere. R = Right hemisphere.

EPN time window

Waveforms corresponding to the EPN are also presented in Fig. 4 (top left and right waveforms), and bar graphs depicting the mean activity across the categories are displayed at the bottom right. Main effects of Stimulus type (F (1, 22) = 412.62, $p < .001$, $\eta2 = .95$), Task (F (1, 22) = 19.08, $p < .001$, $\eta2 = .46$), and Emotion (F (1.70, 37.38) = 11.60, $p < .001$, $\eta2 = .35$, with sphericity corrections $\chi2 = 6.16$, $\epsilon = .85$, $p = .046$) re-emerged, as did the interaction between Stimulus type and Emotion (F (2, 44) = 43.11, $p < .001$, $\eta2 = .66$). Additionally, a significant main effect of Hemisphere emerged (F (1, 22) = 5.70, $p = .026$, $\eta2 = .21$), which led to a three-way interaction between Stimulus type, Emotion, and Hemisphere (F (2, 44) = 5.54, $p = .007$, $\eta2 = .20$). Accordingly, secondary ANOVAs of each stimulus type were performed with Emotion and Hemisphere as within-subjects factors. For faces, Emotion (F (2, 44) = 11.63, $p < .001$, $\eta2 = .35$) and Hemisphere (F (1, 22) = 4.53, $p = .045$, $\eta2 = .17$) produced significant main effects but did not interact ($p = .171$). Contrasts confirmed that the negative-going shift in activity during fearful face presentations was significantly greater than during happy and ($p < .001$) and neutral ($p = .013$) face presentations. The effect of Hemisphere further indicated greater negative-going activity over the left hemisphere, but see

Table 1
Summary of significant factor main effects and/or significant factor interactions related to EEG data.

EEG	P1	N170/N100	EPN
Task		P < .001	P < .001
Emotion			P < .001
Stimulus	P < .001	P < .001	P < .001
Hemisphere			P = .026
*stimulus * task*	P = 0.29		
*stimulus * hemisphere*		P < .001	
*stimulus * emotion*		P = .001	P < .001
stimulus emotion * hemisphere*			P = .007

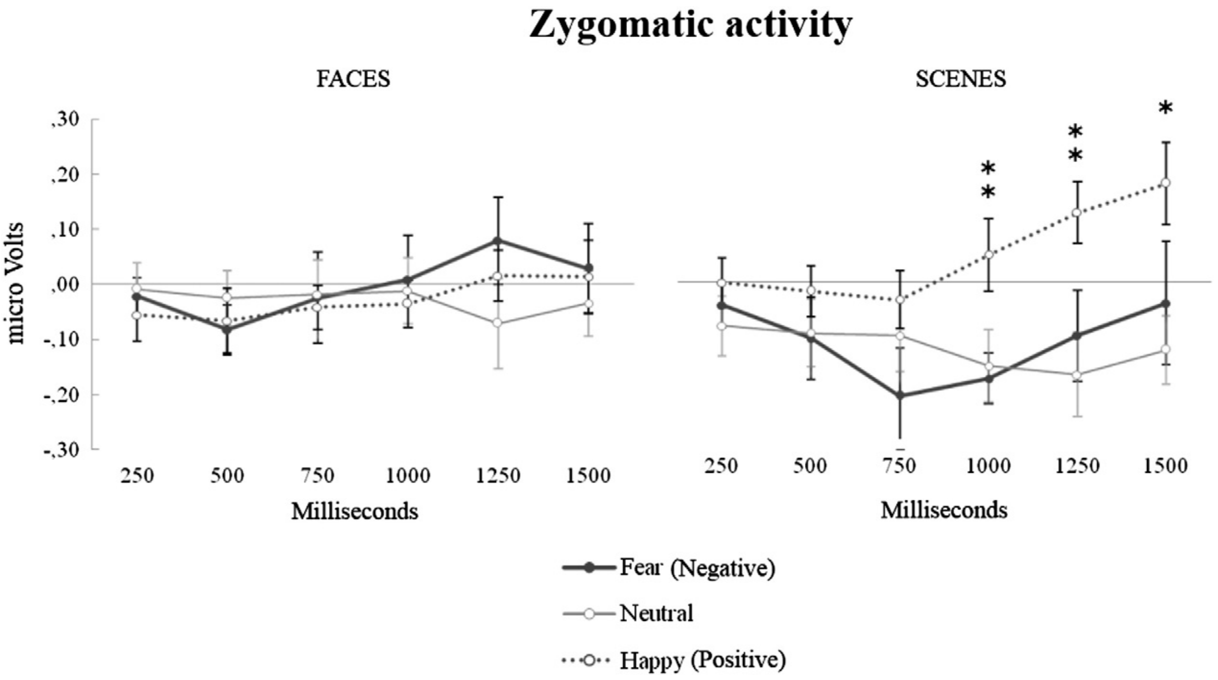

Fig. 5. Mean zygomatic muscle EMG amplitudes (μV) and error bars for 1 standard error, time-locked to the onset of the passively viewed Stimulus 1 (onset = 0 ms). * = The differences are significant after Bonferroni corrections.

below for a more thorough interpretation. For scene stimuli, Emotion (F (2, 44) = 41.96, $p < .001$, $\eta 2 = .66$) and Hemisphere (F (1, 22) = 5.95, $p = .023$, $\eta 2 = .21$) produced significant main effects and did interact significantly (F (2, 44) = 3.74, $p = .032$, $\eta 2 = .15$). The EPN was differently sensitive to emotional content in scenes than in faces however, with positive scenes eliciting significantly greater negative-going activity compared to negative and neutral scenes (both p's < .001). Critically, the interaction of Emotion and Hemisphere evoked by scenes revealed that although scenes (and faces) generated more negativity over the left hemisphere, there was greater discrimination of positive from negative scenes over the right hemisphere ($p = .005$), hence the EPN was more robust over the right hemisphere. In short, fearful faces and positive scenes elicited a stronger EPN overall compared to other emotional stimuli, but positive scenes also elicited a lateral difference in EPN magnitude whereas fearful faces did not. See Table 1 summarising all EEG-related statistical significancies.

EMG data

Zygomatic recordings

No main effects emerged from the six ANOVAs, however a significant three-way interaction between Stimulus type, Emotion and Task emerged at the third time interval corresponding to the time between 500 and 750 ms post-stimulus (F (2, 44) = 3.22, $p = .049$, $\eta 2 = .13$) followed by a sustained interaction between Stimulus type and Emotion over the next three time intervals (750–1500 ms; F (2, 44) = 4.54, 6.45, 4.85, $p = .016$, .003, .012, $\eta 2 = .17$, .23, .18, respectively). As seen in Fig. 5, these interactions collectively indicated that positive scenes evoked spontaneous ZM activity, while happy faces did not. The initial three-way interaction between Stimulus type, Emotion and Task also suggested that positive scenes elicited spontaneous activity earlier during the Pic–Word task compared to the Pic–Pic task. However, when the corresponding data for scene stimuli was submitted to a secondary ANOVA with Task and Emotion as the within-subjects factors, the modulatory effect of Task disappeared ($p = .202$), and, consistent with the effects at ensuing time intervals, was replaced with a significant Stimulus type × Emotion interaction (F (2, 44) = 3.62, $p = .035$, $\eta 2 = .14$). As expected, the secondary ANOVA for face stimuli revealed no effects of task or emotion (all p-values > .2)

Paired samples t-tests were used to determine significant fluctuations in ZM activity between emotional scene categories at each time interval for intervals three to six (corrected significance threshold = .017). From approximately 500–750 ms, positive scenes evoked significant differences in ZM activity relative to negative scenes ($p = .034$, .005, .019, .088 (trend), respectively for intervals 3–6). Significant differences between positive and neutral scenes did not emerge until 750–1000 ms, but were reliably strong across the epoch ($p = .228$, .004, .001, <.001, respectively for intervals 3–6). See Table 2 summarising all statistically significant zygomaticus effects.

Corrugator recordings

As shown in the top panel in Fig. 6, CS activity was characterised by a rapid reduction in muscle activity from stimulus onset to 750 ms during all face and scene S1 presentations, however the rate of this decline was faster when faces were viewed compared to scenes, which led to a significant main effect of Stimulus type in the 250–500 ms time window ($F(1, 22) = 5.58, p = .027, \eta^2 = .20$).[2] This apparent relaxation of corrugator muscles at the point of stimulus onset has been demonstrated by others (e.g. Achaibou et al., 2008; Dimberg and Petterson, 2000b; Dimberg et al., 2000a, 2002), and is thought to be the result of increased tension in corrugator muscles at baseline due to anticipatory focus and attention towards an imminent visual stimulus presentation (van Boxtel and Jessurun, 1993; Van Boxtel et al., 1996).

Then, from 500 to 750 ms, spontaneous muscle activity emerged as a function of emotion category for both face and scene stimuli, seen via a significant main effect of emotion ($F(2, 44) = 9.39, p < .001, \eta^2 = .30$) that remained reliably significant across the next three time windows.[3]

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[2] We performed the ANOVA again using the 23 data sets plus the data for one participant who was excluded from the analysis due to having too few EEG trials. Results showed that the main effect of Stimulus appeared to strengthen (F (1, 23) = 6.62, $p = .017$, $\eta 2 = .22$).

[3] Statistical values for the main effect of Emotion at time intervals 1000, 1250, and 1500 ms are: At 1000 ms, $F(1.70, 37.41) = 7.08, p = .004, \eta^2 = .24$, with sphericity corrections $\chi^2 = 6.14, p = .046, \epsilon = .85$; at 1250 ms, $F(2, 44) = 5.82, p = .006, \eta^2 = .21$; at 1500 ms, $F(2, 44) = 4.30, p = .020, \eta^2 = .16$.

Table 2
Summary of significant factor main effects and/or significant factor interactions related to *zygomaticus major* EMG data.

EMG	Zygomaticus					
	0–250	250–500	500–750	750–1000	1000–1250	1250–1500
*Stimulus * Emotion*				P = .016	P = .003	P = .012
Stimulus Emotion * Task*			P = .049			

As seen in the bottom panel in Fig. 6, spontaneous activity tended to be greater for fearful and neutral faces and negative and neutral scenes, while happy faces and positive scenes led to greater relaxation of the CS muscles. Paired samples *t*-tests were again used to determine significant fluctuations in CS activity between emotional categories, done separately for faces and scenes at each time interval of interest i.e. intervals three to six (with a corrected significance threshold of .017). For faces, spontaneous emotion-related activity emerged only briefly at 500–750 ms as a trend (comparisons at all other intervals, $p > .07$). Here, fearful and neutral expressions evoked significantly ($p = .017$; $p = .061$ (only trend)) greater CS activity compared to happy expressions, respectively. Contrastingly, negative scenes evoked a stronger, more enduring spontaneous effect from 500–750 ms onwards, producing significantly greater activity relative to positive scenes across most of the epoch ($p = .017$, <.001, .091, .005, respectively for intervals 3-6). The generally stronger activity evoked by neutral compared to positive scenes reached significance only at the fourth interval between 750 and 1000 ms ($p = .638$, .014, .078, .186, respectively for intervals 3–6), and similar to the effects observed in ZM activity, negative and neutral scenes evoked very little difference in CS activity ($p = .043$, .161, .801, .048, respectively for intervals 3–6). See Table 3 summarising all statistically significant corrugator effects.

Skin conductance recordings

The ANOVA corresponding to the first 1000 ms post S1-onset showed a trend towards a significant main effect of Stimulus type ($F(1, 22) = 3.97$, $p = .059$, $\eta^2 = .15$), followed by a significant effect

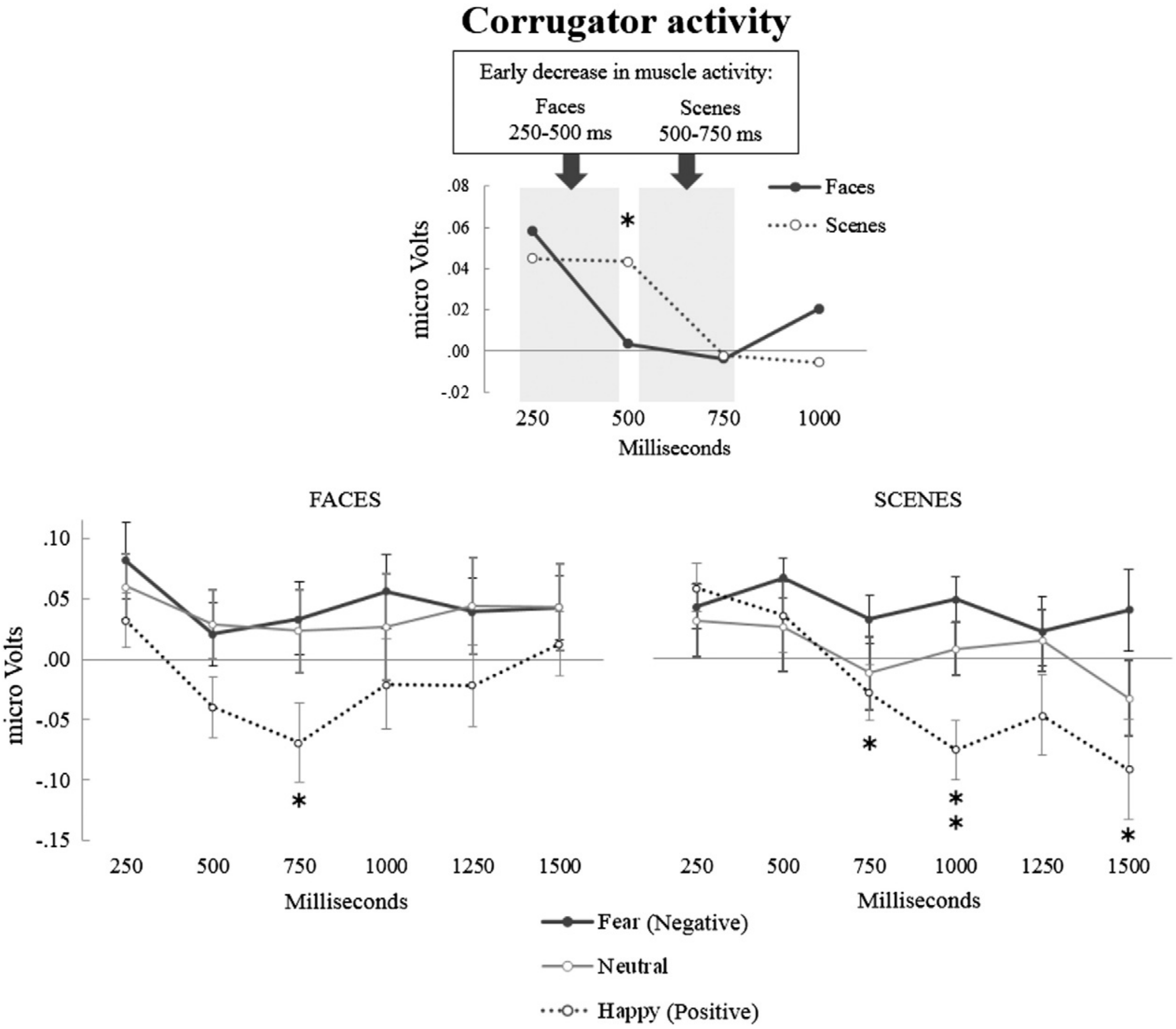

Fig. 6. Mean corrugator muscle EMG amplitudes (μV) and error bars for 1 standard error, time-locked to the onset of the passively viewed Stimulus 1 (onset = 0 ms). The top graph illustrates the mean amplitudes evoked by emotional faces compared with scenes after collapsing across emotion and task categories in order to highlight early latency differences involving corrugator muscle relaxation between the stimuli, presumably reflecting differences in the speed of early attentional orienting. The bottom graphs illustrate the different patterns of spontaneous corrugator activity elicited by emotional faces and scenes. Note that amplitude values differ across the scales in the top and bottom panel graphs. * = The differences are significant after Bonferroni corrections.

Table 3
Summary of significant factor main effects and/or significant factor interactions related to *corrugator supercilii* EMG data.

EMG	Corrugator					
	0–250	250–500	500–750	750–1000	1000–1250	1250–1500
Stimulus		P = .027				
Emotion			P < .001	P = .004	P = .006	P = .020
Stimulus Emotion * Task*						

between 1000 and 2000 ms ($F(1, 22) = 5.22, p = .032, \eta^2 = .19$), which then diminished from 2000 ms onwards ($p > .3$). As seen in Fig. 7, skin conductance levels were greater overall at an early post-stimulus stage and tended to decrease over the three second presentation, with face stimuli evoking slightly greater activity during the early stage. That the effect occurred at such an early stage relative to a typical skin conductance response which emerges more slowly at around 2 s post stimulus, suggests that differences between faces and scenes were a residual effect related to the S2 active response stage of preceding trials. Nevertheless, the significant effect indicates that faces and scenes evoked different arousal-related activity which was independent of emotional content. See Table 4 summarising all statistically significant skin conductance effects.

Discussion

The aim of the current study was to determine the differences in emotional face and scene processing at neural and behavioural (i.e. spontaneous facial activity) levels. Using EEG to measure neural activity we found that the early visually-evoked P1 component peaked earlier for faces than for scenes, and that the type of task differently modulated the depth of this visual-related processing for faces and scenes. For faces the N170 was sensitive to the emotional content of the stimuli whereas the N100 for scenes was not. The EPN was sensitive to the emotional content of both faces and scenes, but differently so. For faces, the EPN was enhanced by fearful expressions as was the N170, while for scenes, positive content elicited enhanced EPN amplitudes, more prominent over the right hemisphere. Using fEMG we found that positive scenes but not happy faces elicited enhanced spontaneous zygomatic activity, whereas both fearful faces and negative scenes elicited enhanced spontaneous corrugator activity, but again this emotion effect was more enduring for scenes. Furthermore, prior to the influence of emotion, corrugator activity was marked by a rapid orienting response that occurred faster for faces than for scenes, which was akin to early P1 effects. Finally, skin conductance responses revealed slightly greater arousal levels when viewing faces than when viewing scenes. That the effect occurred at an early stage relative to a typical skin conductance response which emerges more slowly at around 2 s post stimulus, suggests that differences between faces and scenes were a residual effect related to the S2 active response stage of preceding trials. Nevertheless, the significant effect indicates that faces and scenes evoked different arousal-related activity which was independent of emotional content.

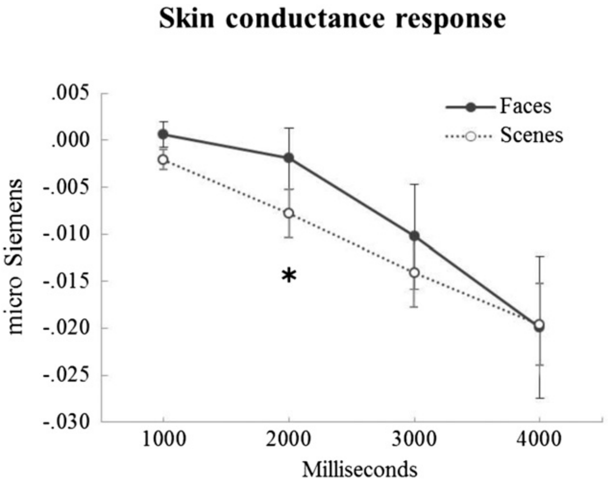

Fig. 7. Mean skin conductance amplitudes (μS) and error bars for 1 standard error evoked by emotional faces and scenes time-locked to the onset of the passively viewed Stimulus 1 (onset = 0 ms). Means were calculated by collapsing across emotion and task categories. * = The differences are significant after Bonferroni corrections.

Early neural processing of emotional faces and scenes

P1 component

Neural activity at the early visually evoked P1 component showed that stimulus-specific features of faces and scenes evoked different degrees of rapid attentional processing irrespective of emotional content. Scenes generated greater visually-evoked cortical activity compared to faces, most likely because of their greater degree of complexity (Bradley et al., 2007). Bradley et al. also found that picture complexity influences the magnitude of evoked potentials proceeding the P1, which would explain the large differences in visually evoked potentials between stimulus groups in the current study. The Pic–Pic task also differently influenced the depth of P1-related visual processing of scenes and faces in a manner that was proportional to the complexity of the stimuli. In other words, processing of scene stimuli, which were more complex, was considerably enhanced, whereas processing of face stimuli, which were less complex, was only slightly enhanced.

It is important to mention that even though we can rule out that both luminance and spatial frequency (see method section) explain later task- and emotion-specific effects it is theoretically possible that those physical features explain category-specific effects like the ones described above.

Beyond this stage, other early processes involved in face and object perception, i.e. the N100/N170 and EPN components, were not differently modulated by faces and scenes as a function of the recognition tasks.

N100/N170 component

A critical finding at the neural level was that affective information in faces influenced neural activity earlier than affective information in scenes, as reflected by the enhanced activity of the N100/N170 for fearful faces, but not for emotional compared to neutral scenes. Recently, Thom et al. (2014) also compared neural activity generated by emotional faces and scenes in a single experimental paradigm, and found that neural processes underlying the N100/N170 component were sensitive to affective information for scenes. These differences between Thom et al.'s and our findings may be explained by methodological differences including that, in their study, some emotional scene stimuli contained faces (fear, joy and angry stimuli, but not neutral, which were all inanimate objects), while we specifically did not include scenes

Table 4
Summary of significant factor main effects and/or significant factor interactions related to SC data.

SC				
	0–1000	1000–2000	2000–3000	3000–4000
Stimulus	P = .059	P = .032		

with forward-facing faces. Also, their participants were all males whereas in the current study participants were a mixture of males and females. The latter distinction is important because males have been shown to generate enhanced N100/N170 amplitudes compared to females (Proverbio et al., 2009), and it has been shown that natural scenes with and without human faces can evoke significantly different activity in the N100/N170 time window (Ferri et al., 2012; Proverbio et al., 2009). It is possible that these factors, particularly when combined, led to selective enhancement of amplitudes in the N100/N170 time window during their emotional scene presentations.

The negativity bias of fearful facial expressions relative to neutral and other emotional expressions has received a variety of interpretations in the literature. Some have suggested that the early discrimination of fearful from neutral faces is due to crude threat or signs of danger which rapidly activate neural circuits specialised for detecting danger (e.g. Esteves et al., 1994; Hansen and Hansen, 1988; LeDoux, 2003; Öhman, 2005; Öhman and Mineka, 2001). However, this theory likely does not explain our results, as we would have expected negative scenes, which included fearful components such as snakes and spiders to evoke such activity as well, particularly considering that detecting negative scenes is highly survival-relevant, and that negative scenes in this study were rated as more unpleasant and more arousing than fearful faces.

Vuilleumier and Pourtois (2007) instead reason that the anatomical regions involved in facial expression recognition may be spatially organised according to emotion categories, in that sub-regions associated with encoding facial features more unique to one expression are spatially segregated from sub-regions associated with encoding those that are more unique to another expression. Hence, emotion category-specific modulation of the N170 component may be reflecting these regional variations rather than motivational emotional significance of the stimuli (Vuilleumier and Pourtois, 2007). In support of this theory, they argue that activity in the N170 time window has been found to be differently sensitive to a range of facial expressions in addition to fear such as surprise and disgust. Along this line, faces with more similar expressions such as anger and fear (both negative and with overlapping facial muscle contraction) evoke more similar modulatory activity than when compared with happy faces (Thom et al., 2014). On this basis, and when considering that emotional content is identified faster for faces compared to scenes (Britton et al., 2006; Dimberg et al., 2002; Eisenbarth et al., 2011), the current data could be reflecting faster extraction of low level semantic affective information from faces than from scenes, but not necessarily faster identification of motivational emotional significance.

EPN time window

An EPN emerged at a similar latency for emotional faces and scenes, occurring immediately following the offset of the N100/N170 components. For faces, the EPN was pronounced only for fearful expressions, while for scenes, the EPN was pronounced only for positive content. When considered separately, these selective modulations of the EPN are in line with past research showing enhanced negativity for fearful faces in the EPN time window compared to neutral (Leppänen et al., 2008; Stekelenburg and de Gelder, 2004) and happy expressions (Herbert et al., 2013b; Mühlberger et al., 2009; Schupp et al., 2004b), and enhanced EPN negativity for positive scenes compared to negative and neutral scenes (Bublatzky and Schupp, 2011; Franken et al., 2008; Schupp et al., 2004a, 2006b, 2007b, 2013b; Weinberg and Hajcak, 2010). Further research also supports our observation that neural activity during the EPN time-frame was generally more negative over the left hemisphere compared with the right (Schupp et al., 2004b; Smith et al., 2013), while stronger emotion-specific modulation occurred over the right hemisphere, and seemed to be an exclusive effect of scene stimuli (Junghöfer et al., 2001; Schupp et al., 2007b). These findings suggest that EPN activity includes a commonality between processing of fearful facial expressions and positive scenes.

Still, there seems to be no clear explanation in the literature addressing why emotional faces and scenes evoke such different category-specific responses in the EPN time window. Speculation has centred on the motivational significance of affective cues, particularly in that erotica are highly arousing stimuli. In the present study, stimuli with low or moderate arousal were chosen which could have facilitated an arousal-driven processing bias for positive scenes due to the erotica content. However skin conductance recordings during these presentations do not support this interpretation, and instead, suggest that all face stimuli evoked enhanced arousal levels compared to scenes. Findings from Thom et al.'s study of faces and scenes (2014) also showed that despite positive scenes (including erotica) being rated as more arousing than all other emotional scene categories, these stimuli did not produce enhanced EPN activity. Thus it seems that other factors are more likely.

Experiments involving EPN analyses have inevitably become more elaborate, and there is now some evidence linking EPN activity to modulations of self-reference or task relevance (e.g. Herbert et al., 2013a,b; Stekelenburg and de Gelder, 2004), which could also be extended to explain the differential effects of face and scene stimuli seen in the current study. Evidence from several studies suggest that as stimuli become more salient with respect to the complexity of required processing, typically as a result of task demands, so too does the degree of EPN modulation during the associated stimulus presentations, suggesting that EPN activity could be a precursor to more conscious levels of stimulus evaluation (Herbert et al., 2013a; Stekelenburg and de Gelder, 2004).

For example, in a study requiring participants to categorise fearful and neutral faces as either upright or inverted, upright fearful faces predictably evoked increased EPN activity compared to upright neutral faces. When faces were inverted however, the EPN was enhanced for both fearful and neutral faces compared to when the same faces were shown in the upright position (Stekelenburg and de Gelder, 2004). This suggests that the EPN is sensitive to task-induced changes in stimulus complexity.

These effects extend even to self-referential emotion processing whereby emotional faces preceded by matched self-relevant word cues such as ‘my fear’ or ‘my happiness’ evoked enhanced EPN activity compared to when the preceding cues were meaningless letter strings (Herbert et al., 2013b), supporting the view that the self-reference of affective stimuli facilitates motivated attention capture to emotional stimuli as reflected by the EPN component. In another study, participants were asked to use specific cue words (e.g. cues like ‘no fear’, ‘no panic’ etc.) to intentionally regulate their feelings evoked by fearful and happy faces. Using these cue words that attenuated the emotion described in the picture (e.g. no fear paired with a fearful face) attenuated ERP amplitudes to fearful faces as early as in the EPN time window (Herbert et al., 2013a).

In the frame of active versus passive tasks, similar effects have also been documented during the EPN time interval. For example, Schupp et al. (2007b) compared the effect of passively viewing emotional scenes versus the effect of actively counting the number of times a specifically valanced scene was presented. They found typical EPN modulation during the passive viewing task, whereby erotica (pleasant stimuli) elicited enhanced EPN activity compared to mutilation (unpleasant) and neutral stimuli, but when participants were required to count the number of presentations occurring for each emotion category, EPN activity was significantly modulated relative to when the same category of emotional stimuli were passively viewed (Schupp et al., 2007b). More recently, a study by Schupp et al. (2013a) comparing passive viewing to active semantic categorisation also suggested a link between EPN activity and higher cognitive evaluations. Here, emotional scenes were overlayed with simple pictures of either animals or other non-animal scenes and objects. In the active categorisation task, participants were required to judge whether the foreground picture was either an animal or not, while no response was required during passive viewing. Again, in the passive viewing task, stimuli with pleasant scenes as the background image evoked stronger EPN activity than did stimuli with unpleasant or neutral background scenes. However, active categorisation led to the diminishment of emotion-specific modulation, and instead, EPN activity was enhanced overall relative to the passive viewing task regardless of the emotional background. Moreover, EPN activity was significantly enhanced for foreground pictures of animals compared to non-animals, suggesting that task difficulty and stimulus salience can override emotional significance in the EPN time window.

In the current experiment, where the task was to passively view the S1 stimuli, but also to implicitly identify its emotional content, stimulus salience, and thus EPN activity, should have been driven, at least partially, by emotion recognition difficulty. Fearful facial expressions and positive scenes, which evoked enhanced EPN activity, may have been more difficult to recognise relative to other sub-categories, resulting in a call for more sophisticated cognitive processing to accurately identify and categorise these stimuli. This is exactly what past research predicts. Recio et al. (2014) twice demonstrated that recognising fearful faces as expressing fear was more difficult than recognising happiness from smiling faces and neutrality from neutral faces, and found that negative expressions (i.e., anger, disgust, fear, sadness and surprise) were most often confused, whereas happy faces enjoy a recognition advantage in the EPN time window (Calvo and Beltran, 2013). As would be predicted by these findings, other research further shows that happy faces are identified and responded to faster than angry faces (Sonnby-Borgström, 2002; see also Leppänen and Hietanen, 2004; Calvo and Lundqvist, 2008) supporting the view that happy faces are attention grabbing due to their salience (i.e. the biologically determined social relevance of a happy face for both interaction partners including the perceiver and the receiver (Becker and Srinivasan, 2014)).

Speculatively, this could also explain why positive scenes evoked enhanced EPN activity relative to other emotional scene categories. The negative, mainly fearful (e.g. spiders and snakes) and neutral (e.g. a computer, a chair) scene stimuli used in the current study were generally rather obvious and intuitive to categorise. However, the content of positive scene stimuli was more varied (e.g. extreme sports, nature scenes, appetising foods and erotica), thereby providing less-intuitive cues directly linked to 'happiness'. Hence, emotion-category specific modulation of the EPN may have been related to differences in recognition difficulty, resulting in a call for more sophisticated cognitive processing to accurately categorise emotional stimuli which lacked intuitive cues, thereby causing fearful facial expressions and positive scenes to become more salient with respect to EPN-related brain activity.

Spontaneous facial reactions to emotional faces and scenes

Emotion-related spontaneous activity of both the zygomatic and corrugator muscles emerged between 500 and 1000 ms post stimulus, which is consistent with other fEMG studies of emotional faces (Dimberg, 1982, 1997b; Moody et al., 2007) and scenes (Dimberg et al., 1998). It suggests that faces and scenes trigger the same neural affective processes, or processes with similar latencies leading to spontaneous facial reactions. This is also consistent with the observation that emotional significance was detected in neural activity at a similar latency for face and scene stimuli.

One difference between faces and scenes however, was that spontaneous zygomatic activity was evoked by positive scenes but not by happy faces. Künecke et al. (2014) also found no effect of happy faces on spontaneous zygomatic activity, while fearful facial expressions evoked reliably enhanced corrugator activity. Moreover, their experiment was also conducted in the frame of an emotion recognition task which, similar to the current study, required a delayed rather than immediate recognition judgement. As has been discussed above, one possible explanation for why positive scenes but not happy faces evoked spontaneous reactions is that, in the frame of an emotion recognition task, smiling faces may simply be easy to recognise and semantically categorise, whereas semantically categorising positive scenes requires more effortful mental processing. If this is the case, we want to speculate on these findings and point to two possible ideas: firstly, emotion-related spontaneous facial activity is linked to emotion recognition processes. Secondly, the mechanisms are triggered only when emotional information is ambiguous, as has been suggested by others (Winkielman et al., 2009). Moreover, basic motor-mimicry is not necessary for social-emotion recognition, as has been demonstrated by others (Grèzes et al., 2013; Magnée et al., 2007; Moody et al., 2007). The latter interpretation is particularly supported by the observation that happy faces did not seem to evoke any substantial change in zygomatic activity relative to baseline.

In addition to effects related to the content of the images, motivational factors also seemed to contribute to the differential spontaneous reactions to faces and scenes. Emotional scenes not only elicited spontaneous activity in the emotion-appropriate muscles, but did so quite strongly compared to faces. The disparity is particularly evident in the observed corrugator activity in that fearful (and neutral[4]) faces evoked only a momentarily enhanced response, whereas negative scenes evoked a strong stable response which seemed to become even stronger at the same time that the effect of fearful faces diminished. Alpers et al. (2011) also reported stronger orbicularis oculi (ring muscle around the eyes) activity (an index of the Duchene smile) to pleasant scenes than to smiling faces, and more broadly, demonstrated greater activation of other behavioural indexes of motivation by emotional scenes compared to faces including decreased heart rate acceleration, greater startle reflex modulation and increased skin conductance levels, findings that were also replicated by Wangelin et al. (2012).[5] Indeed, stimulus arousal ratings in both our study and Alpers' study also point to motivational influences in that emotional scenes were rated as more arousing than emotional faces. It should also be considered that in such a task-primed context with little 'real-world' social-motivational relevance, the veracity of motivational influences of facial expressions on behaviour diminish, or perhaps strong stable behavioural–emotional responses are not necessary during social interactions, and instead could hinder one's ability to keep up with the naturally dynamic exchange of affective signals in social–emotional interactions. Contrastingly, emotionally evocative scenes more often involve an immediate approach/avoidance overt physical response, and thus even at such an automated stage of behaviour, it is logical to expect these stimuli will evoke more stable and enduring motivational reactions.

Consistencies between neural activity and spontaneous facial reactions

Stronger emotional responses to scenes

Consistent with the observation that emotional scenes evoked stronger and more stable spontaneous behavioural activations compared to faces, neural processes related to the EPN were also more strongly and stably activated by scenes than by faces. These effects also emerged in

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[4] Interestingly, neutral stimuli also tended to evoke enhanced corrugator activity, particularly neutral facial expressions. That both fearful and neutral stimuli evoked enhanced activity relative to baseline (remembering that corrugator muscles are typically tensed at baseline), suggests that neutral stimuli were perceived as being more negative rather than fearful stimuli being perceived as more neutral. This is in line with recent findings that neutral scenes evoke more negative rather than positive-related patterns of facial activity (Wu et al., 2012), and that neutral faces tend to be perceived in a negative context rather than simply representing an emotionally void canvas (Adams et al., 2012; Blasi et al., 2009; Hess et al., 2009; Lange et al., 2012).

[5] We suspect that differences in skin conductance activity between faces and scenes in the current experiment were a residual product of factors relating to the S2 stimuli of each trial preceding the S1 stimulus presentations, particularly when considering that the emotion recognition tasks were probably easier for face-matching trials, and that increased task difficulty reduces the skin conductance response (Pecchinenda, 1996). However, this remains speculative given that skin conductance responses would have also been affected by other experimental factors such as unforced response errors, for which the current analysis was not designed to cover.

Thom et al.'s comparison of faces and scenes (2014), where they discussed this effect in terms of scenes activating stronger motivationally relevant activity, particularly with respect to theories pointing to increased amygdala activations as a contributing source of EPN activity. Thom and colleagues interpretation is further supported by functional MRI data showing that biologically relevant stimuli do activate stronger functional connectivity between visual areas and the amygdala than do socially relevant stimuli (Sakaki et al., 2012). Hence motivational factors may influence how long evoked affective responses persist, rather than or in addition to the strength of the response. Such a distinction may have gone unnoticed in past facial EMG research, given that many studies focus on an averaged amplitude for a block of time (some up to six seconds), rather than shorter sequential averages.

The findings therefore draw on two similarities between EPN activity and spontaneous facial reactions including stimulus salience, which is largely a product of task demands, and the persistence of motivational responses, which begs the question of whether EPN activity may be a precursor to motivated behaviour. To test this theory, responses to positive scenes were analysed (chosen because this stimuli evoked the strongest EPN activity as well as reliably strong zygomatic activity, and thus would be of greatest interest and least implicated by floor/ceiling effects) via a post hoc correlation of right hemispheric EPN activity, and spontaneous zygomatic activity averaged over the time frame of strongest emotional responding (750–1500 ms). If stronger EPN activity is related to stronger spontaneous zygomatic responses, then we would at least expect to see a negative linear correlation between these physiological outputs indicating that the stronger the negative shift in EPN-evoked potentials, the greater the amplitude of zygomatic muscle contractions. Even without attention to potential outliers, the analysis of the 23 data sets revealed a modest correlation in the predicted direction ($r = -.29$) which was trending towards significance ($p = .091$), while after removing one outlier, the correlation strengthened considerably ($r = -.47$, $p = .014$). Of course, this correlation may represent a consistency in the absolute levels of neural and behavioural activity within individuals. Therefore, further research is necessary to determine the meaning of this relationship between EPN activity and behavioural responses. In addition, it would also be interesting to investigate the modulation of late ERP potentials such as the LPP. The LPP has been shown to be influenced by emotional and cognitive factors. In contrast to early ERP potentials such as the EPN, however, the LPP is thought to reflect top-down controlled affective processing (Hajcak and Nieuwenhuis, 2006; for review see Olofsson et al., 2008; Korb et al., 2012).

Faster attentional orienting to faces

Of course it would also be interesting to explore the relationship between fEMG activity and LPP modulation. However, as argued above such a correlation would not reveal if cortical or facial changes occurred first. In the present study we show that EPN modulation is correlated with changes in fEMG activity, which suggests that facilitated early cortical processing of emotional scenes is a prerequisite for changes in facial muscle activity.

Early neural activity and behavioural responses to faces and scenes suggests that viewing emotional faces engages attention processes faster than when viewing emotionally evocative scenes. This was reflected in the earlier onset latency of the P1 component and the faster release of tension in the corrugator eyebrow muscles when viewing faces. Such differences can also be seen in evoked potentials in other studies of emotional faces and scenes (Kujawa et al., 2012; Thom et al., 2014). These findings could assist in explaining why the valence of emotional faces is identified faster than the valence of emotional scenes when measured via button press (Britton et al., 2006) and voluntary mimicry latencies (Dimberg et al., 2002; Eisenbarth et al., 2011), and may be a factor underlying why attention disengagement from socially-relevant stimuli to a secondary target is faster than from biologically-relevant stimuli (Sakaki et al., 2012).

Conclusions

The findings in this study point to two key differences between emotional face and scene stimuli during early visual processing, including rapid attentional capture mechanisms and motivated response mechanisms. Broadly, there was a logical chronology of stages of perception that could be seen in both neural activity and behavioural output in that selective attention determined what was attended to, which manifested into affectively-driven selective emotional responses. However, not all stimulus percepts affecting neural activity were apparent in behavioural activity. The picture- versus word-primed recognition tasks elicited different neural activity at the P1 and N100/N170 components, which broadly, reflects variations in basic object recognition processes. However, the recognition tasks did not influence the nature of spontaneous behavioural responses. This suggests that fast motivated emotional behaviour, including spontaneous facial reactions, is relatively robust to variations in basic object and face recognition pathways such as variations in semantic-priming, and logically corroborates with the idea that behavioural responses to emotional stimuli are grounded in motivational emotional significance.

Further research investigating consistencies between neural activity and behavioural responses is needed to replicate and extend the current research. Critically though, this will require careful sequential temporal analyses, as opposed to amplitude-only analyses, particularly at very early time frames of less than one second, which is quite rare in the facial EMG literature. However, the fact that EMG techniques offer excellent temporal resolution matching that of EEG means that such studies are viable and will be very valuable.

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