Pictures cueing threat: brain dynamics in viewing explicitly instructed danger cues

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Recent event-related brain potential studies revealed the selective processing of emotional and threatening pictures. Integrating the picture viewing and threat-of-shock paradigm, the present study examined the processing of emotional pictures while they were explicitly instructed to cue threat of real world danger (i.e. electric shocks). Toward this end, 60 pleasant, neutral and unpleasant IAPS-pictures were presented (1s) as a continuous random stream while high-density EEG and self-reported threat were assessed. In three experimental runs, each picture category was used once as a threat-cue, whereas in the other conditions the same category served as safety-cue. An additional passive viewing run served as a no-threat condition, thus, establishing a threat-safety continuum (threat-cue–safety-cue-no-threat) for each picture category. Threat-of-shock modulated P1, P2 and parieto-occipital LPP amplitudes. While the P1 component differentiated among threat- and no-threat conditions, the P2 and LPP effects were specific to pictures signaling threat-of-shock. Thus, stimulus processing progressively gained more accurate information about environmental threat conditions. Interestingly, the finding of increased EPN and centro-parietal LPP amplitudes to emotional pictures was independent from threat-of-shock manipulation. Accordingly, the results indicate distinct effects associated with the intrinsic significance of emotional pictures and explicitly instructed threat contingencies.

Keywords: ERP; emotion; attention; threat-of-shock

INTRODUCTION

A growing body of evidence supports the hypothesis that emotionally significant stimuli guide attentional processes. Specifically, research examining emotional picture processing as well as studies using the threat-of-shock paradigm revealed the preferential processing of emotional stimuli. Integrating these paradigms, the present study examined the perceptual processing of emotional pictures serving as explicitly instructed cues for threat of aversive events or safety.

Learning about threat contingencies is of high importance to prevent future harm and danger. Based on inherited or previously acquired knowledge, the encounter with threat-cues is associated with physiological response patterns which facilitate fast and accurate behavior (Öhman et al., 2000; Bradley, 2009). In humans, defensive response programs can be primed by merely verbal instructions about upcoming aversive events and danger cues. Recent studies used the threat-of-shock paradigm to investigate instructed fear effects. In this paradigm, participants are verbally instructed that they might receive an electric shock when a specific cue is presented (e.g. red light), whereas another cue signals a safety period in which participants know they will not receive a shock. It is a consistent finding that viewing instructed threat- as compared to safety-cues is associated with potentiated startle reflexes, enhanced electrodermal activity and heart rate deceleration (Grillon et al., 1991; Grillon and Davis, 1995; Funayama et al., 2001; Olsson and Phelps, 2004; Bradley et al., 2005). In addition, functional magnetic resonance imaging (fMRI) studies have revealed neural substrates involved in verbally mediated threat imminence. Threat as compared to safety cues were found to be associated with increased BOLD responses in the amygdala, insular and prefrontal cortices (Phelps et al., 2001; Dalton et al., 2005; Mechias et al., 2010). Further studies used event-related brain potentials (ERPs) indicating enhanced perceptual and evaluative processing of threat-cues. As defined by grating patterns varying in spatial frequency, threat- compared to safety-cues elicited ERP modulations over visual processing areas (60–100 ms poststimulus), proposed to reflect early sensory stimulus processing (Baas et al., 2002). Furthermore, threat-cues elicited an enhanced P2 amplitude over frontal leads (160–240 ms) and were associated with larger late positive potentials over parieto-occipital brain regions (300–400 ms; Baas et al., 2002; Böcker et al., 2004). Taken together, stimuli signaling danger are suggested to sensitize perceptual processing and increase selective attention according to explicitly instructed threat significance.
With regard to visual emotion processing, accumulating evidence supports the notion of motivationally guided selective attention to significant stimuli (Lang et al., 1997; Öhman et al., 2000). Viewing emotional scenes is accompanied by clear differences in autonomic, somatic and reflex activity varying as a function of the picture valence and arousal (Bradley, 2000; Lang and Davis, 2006). In addition, neuroimaging studies have shown the enhanced perceptual processing of emotional stimuli. For instance, fMRI studies revealed increased BOLD responses for emotionally arousing pictures in distributed cortical networks including occipital, parietal, and inferior temporal cortices (Bradley et al., 2003; Sabatinelli et al., 2005; Junghöfer et al., 2006). Furthermore, ERP research assessed the temporal dynamics of visual attention to emotional stimuli such as pictures of naturalistic scenes, faces, hand gestures and words. Consistently the early posterior negativity (EPN; ~150–300 ms) and late positive potential (LPP; ~300–700 ms) differentiate among emotional and neutral picture contents (Schupp et al., 2004, 2006; Kissler et al., 2007; Flaisch et al., 2009). In addition, both EPN and LPP components have been observed to occur spontaneously (i.e. while passive picture viewing), and even when attention is actively directed to non-emotional distractor tasks (Schupp et al., 2007a, 2008a). Overall, these findings suggest that stimulus perception and evaluation are in part directed by underlying motivational systems organizing avoidance and approach behavior (Lang et al., 1997).

The present study investigated the mutual impact of implicit picture valence and explicitly instructed threat-of-shock on selective visual attention processes. Measuring response output parameter, a recent study by Bradley and colleagues (2005) examined physiological responding to pleasant and unpleasant pictures instructed as either threat-of-shock or safety cues. Results showed that viewing pleasant pictures serving as threat-cues prompted autonomic and somatic responses consistent with defense preparation (e.g. threat-potentiated eyeblink startle reflex). However, unpleasant pictures did not exhibit further threat-of-shock potentiated startle amplitudes. Thus, with regard to response output measures a defensive activation hypothesis is supported, according to which instructed threat-cues activate the defense system regardless of the a priori picture valence.

Using a similar study design (cf. Bradley et al., 2005), the present study examined perceptual and evaluative stimulus processing as measured by ERPs. With respect to the hypotheses, two methodological extensions are particularly noteworthy. First, in addition to emotional (pleasant and unpleasant) pictures, a neutral picture category was included. Thus, in three experimental runs each picture category served once as a threat-cue, whereas signaling safety in the other conditions. Based on previous findings (Baas et al., 2002; Böcker et al., 2004), it was assumed that neutral pictures serving as a signal for imminent threat increase P1, P2 and LPP components. Furthermore, it was examined whether threat-of-shock effects vary with the hedonic picture valence. Previous research suggested a negativity bias with stronger responding to negative cues as reflected by the P1 (Smith et al., 2003), P2 (Carretié et al., 2001; Correll et al., 2006) and LPP component (Ito et al., 1998). According to the negativity bias hypothesis, stimulus processing may be specifically facilitated when unpleasant images serve as threat-cues. Alternatively, relating to the arousal dimension of the picture content, threat imminence may specifically facilitate emotional picture processing reflected by the EPN and LPP component (Schupp et al., 2007b). Second, a further passive viewing run served as a no-threat condition establishing a threat-safety continuum in which the same pictures served either as threat-cue, as safety-cue within a threat context, or were seen in a no-threat context. The inclusion of a no-threat condition enables the detection of unspecific sensitization or hypervigilance effects as reflected by enhanced P1 amplitudes in phobic patients viewing their feared objects (Kolassa et al., 2007; Michalowski et al., 2009). Furthermore, the responsiveness of ERP components to threat imminence may vary across time. A recent study revealed that phobia-related effects became increasingly specific at later processing stages as indicated by the LPP component (Michalowski et al., 2009). Accordingly, reflecting unspecific vigilance towards potential threat, it was hypothesized that early processing stages (P1) may differentiate between experimental contexts (threat- vs no-threat). In contrast, later processing stages (P2, LPP) were assumed to become increasingly threat specific, i.e. discriminating between threat-cues and safety-cues presented in a threat context.

**METHODS**

**Participants**

Participants were 24 healthy students (12 females) between the ages of 19 and 33 years ($M = 22.4, s.d. = 3.2$) recruited from the University of Konstanz (BDI: $M = 4.3, s.d. = 2.9$; STAI-State: $M = 37.0, s.d. = 6.0$; STAI-Trait: $M = 36.5, s.d. = 5.1$). Before providing written informed consent, participants were fully informed about the study protocol, which was approved by the institutional ethics committee. Participants received 10 Euros for their participation.

**Stimulus materials**

Sixty pictures were collected from the International Affective Picture System (IAPS; Lang et al., 2008) depicting people either in neutral, pleasant (e.g. erotica, sports) or unpleasant situations (e.g. mutilation, human threat).1 High arousing

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1IAPS identifying numbers for pleasant pictures: 4141, 4180, 4232, 4255, 4290, 4460, 4490, 4530, 4530, 4538, 4550, 4606, 4611, 4623, 4625, 4653, 4658, 4670, 4680, 4690, 4694; for neutral pictures: 2102, 2104, 2191, 2305, 2328, 2372, 2383, 2396, 2397, 2435, 2495, 2513, 2515, 2520, 2570, 2580, 2595, 2650, 3410, 7350 and for unpleasant pictures: 3010, 3015, 3061, 3063, 3064, 3071, 3102, 3110, 3120, 3130, 3500, 3530, 6250, 6313, 6375, 6390, 6510, 6550, 6560, 6570.
pleasant and unpleasant picture contents were selected, as these pictures elicit most pronounced modulations in ERP, fMRI, defensive reflex and autonomic measures (Bradley et al., 2001; Junghöfer et al., 2005; Schupp et al., 2006). IAPS pictures (640 x 480 pixels) were presented on a 22-inch computer screen with a refresh rate of 85 Hz using Presentation software (Neurobehavioral Systems). Distance between participants and screen was ~75 cm.

Electrical stimuli were administered using a constant current electro-stimulator applied through a stimulation electrode (1 mm in diameter) at the tip of the left index finger. Maximum intensity was 10 mA with a duration of 10 ms.

Procedure
Following the attachment of the EEG sensor net, a shock work-up procedure was carried out to ensure the plausibility of threat instructions (cf. Bradley et al., 2005; Bublatzky et al., 2010). Toward this end, the intensity of the electric shock was individually adjusted within up to 10 warned stimulus presentations. Shock intensity was gradually increased from very low intensity (~0.3 mA) until the participants reported the stimulation as ‘maximally unpleasant, but not yet painful’. Mean intensity of the maximum electric shock was 7.19 (s.d. = 2.6). Participants were told that the intensity of the electric shocks given during the experiment would correspond to the intensity experienced as highly aversive but not painful.

The main experiment consisted of four experimental runs in which pictures were presented (1 s) as a continuous stream in random order with respect to picture valence. In each run, the entire picture set was repeated 6 times amounting to a total of 360 trials. Three conditions included a threat-of-shock manipulation, in which each picture category served once as a threat-cue, while in the other conditions the same category indicated safety (Bradley et al., 2005). In the ‘pleasant threat-cue’ condition, for example, participants were verbally instructed that electric shocks might be administered while viewing pleasant pictures, whereas no shocks will occur during the presentation of neutral and unpleasant pictures (safety-cues). A further run without threat-of-shock instructions served as no-threat condition. The order of the four experimental runs was counterbalanced across participants. Breaks in between served to instruct participants about the following assignment of picture categories as threat- and safety-cues. During the experimental runs no electric shocks were administered. After each experimental run participants were asked to rate how threatening they perceived threat- and safety-cues, respectively no-threat cues, using a visual analog scale ranging from 1 (not at all) to 8 (very threatening). Furthermore, at the end of the experiment, IAPS pictures were rated on dimensions of valence and arousal (SAM; Bradley and Lang, 1994).

ERP data collection
Electrocortical activity was recorded using a 256-channel system (EGI; Electrical Geodesics, Inc., Eugene, Oregon). Electrode impedance was kept below 30 kΩ, a suitable impedance level for this type of EEG system. EEG data were collected continuously with the vertex sensor as reference electrode. Netstation software and EGI amplifiers served to assess EEG with a sampling rate of 250 Hz, online band-pass filtered from 0.1 to 100 Hz. Data editing, artifact rejection and correction was done as described by Junghöfer and colleagues (2000). On average, 13.3% of the trials were excluded due to artifacts. Data were baseline corrected and converted to an average reference. Stimulus synchronized epochs were extracted lasting from 100 ms before to 800 ms after stimulus onset. Grand means were calculated for each picture category (pleasant, neutral, unpleasant) when serving either as an instructed threat-cue (predictive for threat-of-shock), safety-cue (predictive for safety) or during the no-threat condition (no threat-of-shock).

Self-report data analysis
Threat, valence and arousal ratings were analyzed with repeated measures analyses of variances (ANOVA) including the factors Threat Imminence (threat-cue vs safety-cue vs no-threat) and Picture Category (pleasant vs neutral vs unpleasant).

ERP data analysis
A two-way procedure was used to identify relevant ERP components followed by conventional ERP analyses based on area scores, i.e. mean activity in selected sensor regions and time windows. In a first step, visual inspection and single sensor waveform analysis were used in concert to
identify relevant ERP components. To replicate previous emotion effects, single sensor waveform analyses were calculated for each sensor and time point separately including the factor Picture Category (pleasant vs neutral vs unpleasant). Similarly, to reveal effects associated with the threat-of-shock manipulation, further analyses contained the factor Threat Imminence (threat-cue vs safety-cue vs no-threat). To correct for multiple testing, effects were only considered meaningful, when the effects were observed for at least eight continuous data points (20 ms) and two neighboring sensors (Sabbagh and Taylor, 2000). Visual inspection assured that no effects relevant for the main hypothesis regarding the interaction of Threat Imminence and Picture Category were missed.

In a second step, the mean activity across selected sensor sites and time bins was calculated to score ERP components (Figure 1). The P1 component was assessed in a parieto-occipital cluster for a time window ranging from 92 to 112 ms. The P2 component was scored over central sites in a time window from 188 to 208 ms. The EPN was assessed in a time window from 200 to 300 ms over occipito-temporal leads. With regard to the LPP, threat imminence and picture category effects showed different topographical distributions and temporal dynamics and were accordingly assessed in two separate sensor clusters and time windows. Specifically, the LPP component was scored over centro-parietal and parieto-occipital regions in the time windows from 400 to 600 ms and 496 to 724 ms, respectively.

A multivariate ANOVA including the factors ERP Component (P1 vs P2 vs EPN vs centro-parietal LPP vs parieto-occipital LPP), Threat Imminence (threat-cue vs safety-cue vs no-threat), Picture Category (pleasant vs neutral vs unpleasant), and Laterality (left vs right hemisphere) was calculated. Using Wilks statistics, significant main effects of ERP Component, \( F(4,20) = 33.97, P < 0.001 \), Threat Imminence \( F(2,22) = 5.97, P < 0.01 \) and Picture Category, \( F(2,22) = 5.90, P < 0.01 \), were qualified by significant interactions of Component by Threat Imminence, \( F(8,16) = 4.23, P < 0.01 \), and Component by Picture Category, \( F(8,16) = 20.43, P < 0.001 \). Directly testing the interaction of the three threat-sensitive ERP components (P1, P2, parieto-occipital LPP) and Threat Imminence did not reach significance, \( F(4,20) = 1.79, P = 0.17 \). However, acknowledging notable differences in the result patterns for threat-sensitive ERP components, exploratory follow-up tests were conducted. Interestingly, when comparing P1 and parieto-occipital LPP components a significant interaction was revealed, \( F(2,22) = 3.70, P < 0.05 \). In contrast, comparing the P2 with either the P1 or the LPP, no significant interaction of Component by Threat Imminence was observed, \( F(2,22) = 1.22 \) and \( 2.17, P's = 0.32 \) and 0.14, respectively. Contrasting emotion-sensitive EPN and centro-parietal LPP components revealed a significant interaction of Component by Picture Category, \( F(2,22) = 83.07, P < 0.001 \). In further analyses, ERP components were submitted to separate repeated measures ANOVAs including the factors Threat Imminence and Picture Category. The factor Laterality was dropped from these analyses as there were no interactions with either Threat Imminence or Picture Category for any of the components.

For effects involving repeated measures, the Greenhouse–Geisser procedure was used to correct for violations of sphericity. To control for Type I error, Bonferroni correction was applied for post hoc t-tests.

RESULTS

Self-report data

Picture category ratings

Pleasure and arousal ratings differed significantly for picture content, \( F(2,46) = 117.7 \) and 63.9, \( e's = 0.82 \) and 0.86, \( P's < 0.001 \). Pleasant pictures (\( M = 6.7 \), s.d. = 1.13) were rated more pleasant than neutral (\( M = 5.53 \), s.d. = 0.58)

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**Table 1** Mean ERP amplitudes in microvolt (s.d.) for pleasant, neutral, and unpleasant pictures varying as a function of instructed Threat Imminence (threat-cue, safety-cue, no-threat)

<table>
<thead>
<tr>
<th></th>
<th>Pleasant</th>
<th>Neutral</th>
<th>Unpleasant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Threat-cue</td>
<td>Safety-cue</td>
<td>No-threat</td>
</tr>
<tr>
<td>P1 (parieto-occipital)</td>
<td>1.56 (0.98)</td>
<td>1.42 (1.03)</td>
<td>1.25 (1.08)</td>
</tr>
<tr>
<td>P2 (central)</td>
<td>1.18 (0.70)</td>
<td>0.90 (0.85)</td>
<td>1.08 (0.84)</td>
</tr>
<tr>
<td>EPN (occipito-temporal)</td>
<td>1.10 (1.42)</td>
<td>1.10 (1.05)</td>
<td>1.14 (1.34)</td>
</tr>
<tr>
<td>LPP (centro-parietal)</td>
<td>0.25 (0.56)</td>
<td>0.11 (0.67)</td>
<td>0.19 (0.62)</td>
</tr>
<tr>
<td>LPP (parieto-occipital)</td>
<td>1.16 (0.64)</td>
<td>0.88 (0.83)</td>
<td>1.08 (0.79)</td>
</tr>
<tr>
<td>Threat ratings</td>
<td>4 (2.6)</td>
<td>1.53 (0.85)</td>
<td>1.46 (0.74)</td>
</tr>
</tbody>
</table>

For each of the ERP components, amplitudes were averaged over left and right hemisphere sites. Last rows specify mean threat ratings (s.d.) for pleasant, neutral, and unpleasant pictures varying as a function of instructed Threat Imminence (threat-cue, safety-cue and no-threat).
and unpleasant pictures ($M = 2.51$, s.d. = 0.88), $P's < 0.001$, and neutral as more pleasant than unpleasant pictures, $P < 0.001$. Arousal ratings for both pleasant ($M = 4.16$, s.d. = 1.91) and unpleasant ($M = 5.35$, s.d. = 1.85) pictures were higher than for neutral ($M = 1.75$, s.d. = 0.77), $P's < 0.001$, and unpleasant images were rated as more arousing than pleasant pictures, $P < 0.01$.

**Threat ratings**

After each experimental run, picture categories were rated regarding their perceived threat-value. As shown in Table 1, threat ratings differed significantly between picture categories, $F(2,46) = 92.24$, $P < 0.001$, $\varepsilon = 0.76$. Overall, unpleasant pictures were rated as more threatening than pictures depicting pleasant and neutral contents, $P's < 0.001$. Pleasant pictures did not differ from neutral materials, $P = 0.99$.

As expected, the interaction of Threat Imminence and Picture Category was significant, $F(4,92) = 4.78$, $P < 0.01$, $\varepsilon = 0.59$. To follow up the differential impact of threat-cue, safety-cue and no-threat condition, picture categories were tested separately. For pleasant pictures, threat ratings varied as a function of instructed Threat Imminence, $F(2,64) = 25.13$, $P < 0.001$, $\varepsilon = 0.57$. Post hoc tests revealed that pleasant pictures serving as threat-cues were perceived as more threatening than the same pictures instructed as safety-cues or during no-threat condition, $P's < 0.001$. Ratings for pleasant no-threat and safety-cues did not differ, $P = 1.0$. Neutral picture ratings differed as a function of threat-of-shock instruction, $F(2,46) = 34.66$, $P < 0.001$, $\varepsilon = 0.53$, whereas neutral threat-cues were perceived as more threatening than neutral no-threat and safety-cues, $P's < 0.001$, neutral no-threat and safety-cues did not differ, $P = 1.0$. Similarly, threat ratings for unpleasant pictures varied by threat-of-shock condition, $F(2,64) = 17.86$, $P < 0.001$, $\varepsilon = 0.99$. Whereas unpleasant pictures serving as threat-cues were more threatening compared to no-threat and safety-cue conditions, $P's < 0.001$, no-threat and safety-cues did not differ, $P = 0.17$.

**ERPs**

The main finding is that threat-of-shock instructions modulated early and later picture processing as indicated by enhanced P1, P2 and parieto-occipital LPP amplitudes.
Importantly, these threat modulations occurred regardless of the a priori picture valence. Furthermore, emotional differentiation as indicated by the EPN and centro-parietal LPP was replicated in the no-threat condition and were similarly present during safety-cue and threat-cue conditions (Figures 4 and 5).

**P1 component**

Replicating previous findings, the P1 amplitude increased as a function of Threat Imminence, $F(2,46) = 7.58$, $P < 0.01$, $\epsilon = 0.84$. Follow-up tests revealed significant differences between threat-cue and safety-cue as opposed to no-threat condition, $P's < 0.05$, whereas threat-cue and safety-cue conditions were not significantly different, $P = 0.59$.

Furthermore, hedonic picture valence modulated the P1 amplitude, $F(2,46) = 10.07$, $P = 0.001$, $\epsilon = 0.83$. Follow-up tests revealed that the P1 amplitude for unpleasant pictures was larger compared to neutral, $P < 0.05$ and pleasant picture contents, $P < 0.01$, whereas pleasant and neutral pictures did not differ, $P = 1.0$.

**P2 component**

The P2 peak over central sensor sites was sensitive to Threat Imminence, $F(2,46) = 8.25$, $P < 0.01$, $\epsilon = 0.68$. P2 amplitude was significantly larger for threat-cue as compared to safety-cue, $P < 0.01$ and no-threat conditions, $P < 0.01$, whereas differences between safety-cue and no-threat conditions did not reach significance, $P = 0.25$.

Furthermore, the P2 amplitude was modulated by Picture Category, $F(2,46) = 15.54$, $P < 0.001$, $\epsilon = 0.93$. Follow-up analyses revealed that pleasant and unpleasant images elicited larger P2 amplitudes as compared to neutral pictures, $P's < 0.01$. Pleasant and unpleasant pictures were not significantly different, $P = 0.23$.

**Early posterior negativity**

Replicating previous findings, the EPN amplitude varied as a function of Picture Category, $F(2,46) = 118.71$, $P < 0.001$, $\epsilon = 0.75$. Pleasant and unpleasant picture processing was associated with enlarged EPN amplitudes as compared to
neutral stimuli, \( P < 0.001 \). As reported in previous research, the EPN for pleasant pictures was more pronounced than for unpleasant images, \( P < 0.001 \). The main effect of Threat Imminence was not significant, \( F(2,46) = 0.14, P = 0.81, \varepsilon = 0.76 \).

**Centro-parietal late positive potential**

Similar to previous studies, the centro-parietal LPP was modulated by Picture Category, \( F(2,46) = 66.95, P < 0.001, \varepsilon = 0.89 \). Pleasant and unpleasant pictures elicited larger LPPs compared to neutral materials, \( P < 0.001 \), whereas the LPP was more pronounced for pleasant than for unpleasant pictures, \( P < 0.01 \).

Over centro-parietal brain regions, the main effect of Threat Imminence approached significance, \( F(2,46) = 2.77, P = 0.08, \varepsilon = 0.91 \). Exploratory follow-up analyses revealed significant differences between threat-cue and safety-cue conditions, \( P < 0.05 \), but not for threat-cue and safety-cue conditions as compared to no-threat condition, \( P > 0.65 \).

**Parieto-occipital late positive potential**

Replicating previous findings, the parieto-occipital LPP varied as a function of Threat Imminence, \( F(2,46) = 8.10, P = 0.001, \varepsilon = 0.97 \). Follow-up tests revealed a pronounced positive potential for threat-cue as opposed to the safety-cue, \( P < 0.01 \) and no-threat conditions, \( P < 0.05 \). Safety-cue and no-threat conditions did not significantly differ, \( P = 1.0 \).

Furthermore, the parieto-occipital LPP varied as a function of Picture Category, \( F(2,46) = 17.08, P < 0.001, \varepsilon = 0.89 \). Pleasant and unpleasant pictures elicited larger LPP amplitudes as compared to neutral cues, \( P < 0.01 \), whereas differences between pleasant and unpleasant pictures were not significant, \( P = 0.19 \).

**DISCUSSION**

The present study investigated the temporal dynamics of visual attention to pleasant, neutral and unpleasant pictures explicitly instructed to signal threat of electric shocks. Providing a millisecond time resolution of electrocortical activity, ERP measures revealed processing differences for
picture cues as a function of their verbally mediated threat contingencies. Specifically, the manipulation of stimulus significance along a threat-safety continuum (threat-cue > safety-cue > no-threat condition) was associated with modulations of the P1, P2 and parieto-occipital LPP components. Of particular interest, threat-of-shock effects occurred regardless of the a priori picture valence and revealed a partly distinct neural signature as compared to indices of visual emotion processing (e.g., EPN and centro-parietal LPP). These results support a threat-sensitization hypothesis according to which a processing advantage for visual signals of danger is suggested. A further finding regards the tuning of distinct ERP components to threat-predictive picture cues. Specifically, threat imminence effects were observed initially as being threat unspecific (P1), whereas later in time accurate extraction of the explicitly instructed picture significance was observed (P2 and LPP). These findings may provide another instance of the notion that the fear system is organized according to the principle of ‘in dubio pro defensio’ (Öhman and Mineka, 2001; Weike et al., 2008).

Threat-of-shock modulations were differently pronounced across the processing stream. The first ERP component sensitive to threat imminence was the P1 component, which was enlarged to both threat- and safety-cues as compared to the no-threat condition. Thus, previous findings of a non-specific enhanced P1 component in anxiety patients (Kolassa et al., 2006, 2007; Michalowski et al., 2009) were replicated in healthy participants undergoing aversive anticipation. Considering research using spatial orienting tasks (Heinze et al., 1994; Hillyard and Anllo-Vento, 1998; Pourtois et al., 2004), this early P1 effect may reflect an increased allocation of attentional resources to potentially threat-related stimuli. The relationship to instructed threat contingencies became more refined at the level of the P2 component. Similar to the P1, the P2 was increased for threat-cues as compared to the no-threat condition. However, P2 amplitudes to safety cues were smaller as compared to threat cues and not significantly different from the no-threat condition. Thus, rather than reflecting unspecific vigilance effects, the P2 appears as a transitory processing stage at which differences in instructed threat imminence...
Explicit attention research revealed that a fronto-central P2 is usually elicited by stimuli containing target features (Luck and Hillyard, 1994). Furthermore, the P2 target effect is more reliable when targets are defined by simple rather than complex stimulus features. In this respect, natural pictures from the IAPS set are processed fast and with efficiency as information regarding emotion category is extracted in <200 ms (Codispoti et al., 2006; Schupp et al., 2007b). Accordingly, the threat-related enhancement of the P2 may reflect an affective counterpart to explicitly defined stimulus relevance (Baas et al., 2002). With regard to later stimulus processing, late positive potentials varied as a function of threat imminence. Specifically, threat-cues prompted larger late positive potentials over parieto-occipital brain areas compared to the safety-cue in a threatening context and the no-threat passive viewing condition. Thus, the LPP revealed specific threat processing effects, selectively responding to the instructed threat-of-shock cue. The notion that the LPP reflects the allocation of attentional resources suggests that threat-cues capture attentional resources (Johnson, 1988). Overall, as reflected by P1 and LPP amplitudes, the present findings suggest that the sensitivity to the instructed threat cue became increasingly specific across the processing stream. Manipulating the level of threat by means of verbal instructions may be used in future studies to explore the temporal details of unspecific and specific threat effects.

These findings may be considered from the perspective of the predator imminence model (Fanselow, 1994; Lang et al., 1997). According to this model, defensive behavior varies along different stages depending on the proximity of potential threats. Pre-emptive behavior and vigilance is suggested to be engaged during a pre-encounter stage. Analogously, when fleetingly confronted with potential threat-cues, the need of fast stimulus identification may engage a state of non-specific vigilance to all visual stimuli. This initial facilitation of perceptual processing is presumably reflected by the enhanced P1 component (Michalowski et al., 2009). Once the stimulus meaning is accessible (P2, LPP), attentional resources may be directed to specific picture categories (flexibly updated by instructed threat contingencies) in order to organize post-encounter defense behavior (Löw et al., 2008).
Time dependent changes in differential threat-of-shock effects may further reflect successive processing stages ranging from large-capacity sensory encoding to capacity-limited higher order elaboration (Öhman, 1986; Schupp et al., 2006, 2008b). Overall, gaining progressively more detailed information about environmental conditions, perceptual and evaluative processing may guide motor response stages according to threat imminence (Lang et al., 1997; Öhman et al., 2000).

A noteworthy aspect of the present ERP findings refers to the independent effects of instructed threat-of-shock and emotional picture content. The critical comparison for the interaction of threat imminence and picture category was based on the processing of the same stimuli differently instructed in threat-predictive significance. In contrast to recent studies in which pictures were irrelevant to concurrently presented threat-signals (Bublatzky et al., 2010; submitted for publication), picture content was predictive for threat-of-shock or safety. However, the present findings provided little evidence that threat-of-shock enhanced the processing of either unpleasant or pleasant pictures. Thus, in the instructed fear paradigm, the present data support neither the hypothesis of a negativity bias nor an emotional arousal explanation. One interpretation of these findings is that facilitated stimulus processing due to threat imminence and emotional picture valence reflects differences in neural structures controlling perceptual processing. It has been suggested that the amygdala plays an important role in the enhanced visual processing of emotional stimuli (Vuilleumier, 2005), whereas evidence regarding amygdala activation in the instructed fear paradigm is mixed (Olsson and Phelps, 2007; Mechias et al., 2010). Furthermore, the more elaborate processing of instructed threat-cues may be guided by the activation of anterior prefrontal cortical structures (Mechias et al., 2010). Future studies using hemodynamic measures may reveal differences and similarities in the neural structures controlling perceptual processing as a function of verbally mediated threat and intrinsic stimulus significance.

The passive viewing condition (no-threat context) replicated previous findings of enlarged EPN and LPP components to emotional (pleasant and unpleasant) as compared to neutral stimuli (Schupp et al., 2006). Furthermore, emotional ERP modulations were similarly observed in experimental runs involving threat-of-shock regarding both threat- and safety-cues. This finding contrasts with research investigating the processing of feared stimulus materials in small animal phobia which observed increased EPN and centro-parietal LPP amplitudes to the feared stimulus materials (Kopp and Altmann, 2005; Michalowski et al., 2009). Similarly, Wieser and colleagues (2010) observed increased EPN amplitudes to angry compared to happy and neutral face pictures in participants anticipating public speaking. However, variant findings may reflect differences in methodology (e.g. within vs. between subject design), learning history (e.g. short vs long term), or learning mechanism (e.g. fear and avoidance learning in phobic people vs. verbal instructions about threat contingencies in healthy participants).

In the present study, late positive potentials were scored in separate clusters and time windows differentially sensitive to threat imminence and emotional picture category. While showing some overlap with regard to sensor regions and time, threat imminence and picture category effects revealed differences necessitating this approach. Emotional picture LPP modulation showed a much stronger effect size and evinced a much broader regional distribution extending from frontal to central to parietal sensor regions as compared to the threat-of-shock LPP. Furthermore, the emotional picture effect was most pronounced over centro-parietal sensor regions whereas a parieto-occipital focus was seen for the threat imminence effect (Figures 5 and 6). Interestingly, topographical differences correspond to previous findings. Specifically, in instructed fear paradigms, larger LPPs to threat stimuli were observed over parieto-occipital regions (Baas et al., 2002; Böcker et al., 2004) whereas the effect of larger LPPs to emotional pictures is usually most pronounced over centro-parietal regions (Schupp et al., 2006). While awaiting future replication, the observed difference in LPP topography supports the notion of partly distinct neural substrates involved in the processing of real-world threat cues and rather symbolic picture media (Bublatzky et al., 2010; submitted for publication; Funayama et al., 2001).

In summary, ERPs revealed processing differences for emotional and neutral pictures varying in predictive value for threat of aversive electric shocks. Of particular interest, verbally instructed threat-contingencies modulated picture processing irrespective of the hedonic picture valence. Depending on the predictive picture value and elapsed processing time, result patterns shifted from early non-specific vigilance effects to increasingly accurate extraction of picture meaning. Thus, the present findings support the notion of different perceptual processing stages gaining progressively elaborated information about environmental conditions.

Conflict of Interest
None declared.

REFERENCES


