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Neural activation during the processing of ambiguous fearful facial expressions: An ERP study in anxious and nonanxious individuals

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ABSTRACT

Event-related brain potentials (ERPs) were recorded from anxious and nonanxious participants during performance on a fear detection task. Sequential presentation of gradually increasing fear cues from neutral to fearful allowed an examination of anxiety-related differences in the neural activation patterns corresponding to participants' overt detection of fear in ambiguous stimuli as well as the activation patterns corresponding to stages of fear processing preceding overt fear detection. While centro-parietal Late Positive Potential (LPP) amplitude of nonanxious participants was significantly modulated by increases in stimulus fear intensity preceding overt fear detection, no such LPP sensitivity was detected in anxious participants. Additionally, anxiety group differences as well as emotion related modulation were found for earlier ERP components (P1, P2 and EPN). These findings reveal an anxiety-related dissociation between the early and late processing stages of threat processing. Implications are discussed in light of existing theories of cognitive biases in anxiety.

1. Introduction

Behavioral research has documented anxiety-related differences in the classification of ambiguous threat-related facial expressions (e.g., Richards et al., 2002). Based on such findings, biased processing of ambiguously threatening facial cues has been implicated as an etiologic and maintaining factor in anxiety (e.g., Mathews and Mackintosh, 2000; Mathews and MacLeod, 2002; Mathews et al., 2007; Wilson et al., 2006).

Here we examine the neural correlates of anxiety-related differences in the fear detection process. Specifically, event-related potentials (ERPs) were recorded during a fear detection task in which interpolated face stimuli were gradually unfolding from neutral, through mildly fearful, and up to moderately fearful expressions which eventually elicited an overt detection of fear. As such, the study design allowed neural activation to be examined both at the time of overt fear detection, and during the processing of fears' precursors in slightly less fearful stimuli not yet eliciting overt detection of fear.

Previous studies have employed a variety of emotional facial expressions as threat-related stimuli, for instance angry (e.g., Bar-Haim et al., 2005; Fox et al., 2002; Horley et al., 2003, 2004; Kolassa et al., 2009; Mogg et al., 2004; Mueller et al., 2009; Richards et al., 2002; Wilson and MacLeod, 2003), fearful (Fox, 2002; Holmes et al., 2008; Richards et al., 2002), disgust (Gilboa-Schechtman et al., 1999; Mansell et al., 1999). While some facial expressions are thought to be highly relevant for specific types of anxiety such as disgusted faces for socially anxious individuals (Amir et al., 2010; Cobb et al., 2005), or to elicit specific threat cues (e.g., an angry face in a frontal presentation), fearful faces are thought to signal the presence of a diffuse/unknown danger in the immediate environment thus, serving as a threatening stimulus that is generally effective across a wide range of contexts. Indeed, neuroimaging research indicates that fearful faces elicit the strongest fear-circuitry response (e.g., Dolan and Vuilleumier, 2003). Thus, here we examine anxiety-related differences in the fear detection process.

Threat detection in faces is comprised of several stages of information processing that can be grossly divided into early processes such as stimulus encoding and selective allocation of attention, and late strategic processes reflecting sustained motivated attention and stimulus interpretation. In attempt to provide further information on the time course and neural correlates of these, the present study focused on the examination of both early and late ERP components that are thought to differentially reflect these distinct cognitive processes. Specifically, early ERP components such as the attention-related P1 (e.g., Batty and Taylor, 2003; Eimer and Holmes, 2002, 2007; Holmes et al., 2003; Streit et al., 2003) and P2

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(e.g., Ashley et al., 2004), as well as the Early Posterior Negativity (EPN) (e.g., Junghofer et al., 2001; Sato et al., 2001; Schupp et al., 2003, 2004), are thought to reflect early selective visual processing of emotion stimuli. Late ERP components such as the Late Positive Potential (LPP) are taken to reflect more strategic high-level processes such as decision making, response criterion, and sustained elaborate analysis of emotional content (e.g., Ashley et al., 2004; Moser et al., 2006; Schupp et al., 2004), and are thought to be driven by motivational salience (Hajcak et al., 2010).

Previous research reveals anxiety-related differences in the above mentioned ERP components during the processing of threatening facial expressions. Relative to nonanxious participants, anxious participants exhibit larger P1 amplitudes in response to emotional facial expressions in general (e.g., Kolassa et al., 2007, 2009) and in response to fearful (Holmes et al., 2008), or angry faces (Mueller et al., 2009) in particular. The results concerning later ERP components are less consistent. For instance, some studies revealed threat related augmentation of P2 amplitudes (Bar-Haim et al., 2005), EPN (Muhlberger et al., 2009), and LPP amplitudes (Holmes et al., 2008; Moser et al., 2008) in anxious relative to nonanxious controls, whereas other studies found threat-related reductions in P2 amplitudes (Holmes et al., 2008), EPN (Holmes et al., 2008), and LPP amplitudes (Holmes et al., 2008; Muhlberger et al., 2009) in anxious relative to nonanxious controls thus warranting further research.

In the present study two sets of predictions were made. First, at the behavioral level, the intensity of fear expression in the face stimuli necessary to generate overt fear detection was expected to be smaller in anxious versus nonanxious participants. This prediction was based on previous studies associating anxiety with a negative interpretive bias of ambiguous stimuli (Mathews and Mackintosh, 2000; Mathews and MacLeod, 2002; Mathews et al., 2007; Richards et al., 2002; Wilson et al., 2006) and a more liberal criterion in the detection of threat (Becker and Rinck, 2004; Manguno-Mire et al., 2005; Windmann and Kruger, 1998; Winton et al., 1995).

Second, based on previous findings in non-selected populations revealing emotion-related modulation of the P1 (e.g., Batty and Taylor, 2003; Eger et al., 2003; Eimer and Holmes, 2002; Holmes et al., 2003; Pourtois et al., 2005; Streit et al., 2003), P2 (e.g., Ashley et al., 2004; Eimer and Holmes, 2007; Holmes et al., 2003), EPN (e.g., Junghofer et al., 2001; Sato et al., 2001; Schupp et al., 2004), and LPP components (e.g., Krolak-Salmon et al., 2001; Sato et al., 2001; Schupp et al., 2004), we expected to find enhanced P1, P2, and LPP positivity as well as enhanced EPN in response to increase in stimulus fear intensity in both anxious and nonanxious participants. More importantly, anxiety-related differences were expected to emerge in each of these components. Due to inconsistent findings thus far, exact predictions regarding the nature of these differences could not be drawn. Nevertheless, based on cognitive theories associating anxiety with a greater vigilance toward threat during early perceptual stages of stimulus processing, one could expect that relative to nonanxious participants, anxious participants would display enhanced P1, P2, and EPN components in response to fearful stimuli compared to neutral stimuli. And, in line with theories associating anxiety with avoidance of threatening stimuli during strategic stages of processing (Amir et al., 1998; Mogg et al., 1997; Williams et al., 1997), the LPP component, assumed to reflect sustained and elaborate stages of processing, may be expected to be attenuated in anxious versus nonanxious participants in response to fearful stimuli thus indicating inhibition of deep elaboration of threatening cues.

Finally, differences in elaborate processing stages may give rise to interaction effects such that gradual increases in stimulus fear intensity preceding overt fear detection would elicit greater LPP modulation in nonanxious relative to anxious individuals. Such findings would implicate more elaborate, complex, and finely tuned analysis in later stages of processing related to decision criterion in nonanxious relative to anxious individuals. Anxiety related differences of this kind may underlie findings reported by previous signal detection studies revealing a more stringent decision criterion toward threat cues in nonanxious participants versus a more liberal criterion in anxious participants (Becker and Rinck, 2004; Manguno-Mire et al., 2005; Windmann and Kruger, 1998; Winton et al., 1995).

2. Materials and methods

2.1. Participants

High and low trait anxious individuals were selected from a pool of 240 undergraduate psychology students based on response to Spielberger's State-Trait Anxiety Inventory (STAI) trait scale (Spielberger et al., 1983). Participants who scored in the top and bottom 10% of the sample's distribution were invited to participate and were allocated to the anxious and nonanxious groups, respectively. Six subjects from the anxious group and two subjects from the nonanxious group declined participation leaving the anxious group with 17 participants (14 females, Mean STAI-Trait score = 59.0, *SD* = 5.2), and the nonanxious group with 22 participants (16 females, Mean STAI-Trait score = 27.2, *SD* = 4.4). The groups did not differ in age, $F < 1$, *Mean Age* = 22.76, *SD* = 1.95, or gender distribution, Fisher's Exact Test = 0.70 (two-sided). The study was approved by the institutional review board, and all participants provided written informed consent.

2.2. Apparatus

The experiment was programmed using EPrime software adapted to EGI's Netstation version 4.2. Displays were generated by a Dell computer attached to a 17″ CRT monitor, using 1024 × 768 resolution graphics mode. Responses were collected via a button press response box. Participants were seated in a comfortable seat at a viewing distance of 80 cm from the monitor. The experiment was conducted in a dark room.

2.3. The fear detection task

Interpolated face stimuli were sequentially presented while gradually unfolding from neutral, through mildly fearful, and up to moderately fearful stimuli which eventually elicited overt detection of fear. Each trial consisted of one facial continuum depicting one individual, and each continuum was presented once. Additional trials consisting of neutral-disgust facial continua were randomly scattered throughout the experiment serving as "catch trials" to ensure valid detection of fear.

Instructions were read as follows: '*You will be presented with facial continua. The first face in each continuum will express a neutral expression. As the continuum progresses, the facial expression will change gradually from neutral to fearful. Each face will appear on the screen for 1 second. Your task is to look at the face carefully and decide whether or not you begin to detect fear in that face. Once the face has disappeared you must report your answer: if the face does not yet look fearful, press (1). If the face looks fearful, press (2). Pay attention! Not all continua develop into a fearful expression. A small number of continua do not develop into fear, and rather develop into another facial expression. In these cases, press "1" throughout the progression of the entire continuum – namely judging the face as "not yet fearful".*'

Fig. 1 presents the sequence of events in an experimental trial. Each trial consisted of one morphed facial continuum, presented in progressive order from neutral to emotion (fearful or disgust), increasing in increments of 5% emotion between successive images. As long as subjects pressed "1" namely not yet detecting fear in the face and judging the expression as "not yet fearful", the successive image from the same morphed continuum was presented. Once subjects pressed "2", namely detecting fear in the face and judging the expression as "fearful", the trial was terminated and a new facial continuum was presented. Thus, each trial began with the presentation of a neutral expression and was terminated once an overt detection of fear was elicited.

To avoid a set response pattern (i.e., a pattern in which subjects repeatedly report fear detection after the presentation of a set number of images), as well as possible confounds of order and predictability, the neutral face (0% emotion) was presented at the beginning of each trial between 1 and 4 times (i.e. the neutral face appeared either once, twice, three times, or four times). The number of repetitions of the neutral face was randomized across trials. Participants were not aware of this repetition and were required to judge these stimuli in the same manner as all other stimuli.

A central fixation cross (500 ms) was presented prior to each centrally presented facial image (1000 ms). Once the face was removed a blank screen appeared with a small "?" in its' center prompting participants to judge whether or not the image appeared fearful. Participants were tested in one session consisting of 77 trials presented in random order (70 experimental trials consisting of 70 neutral-fearful face

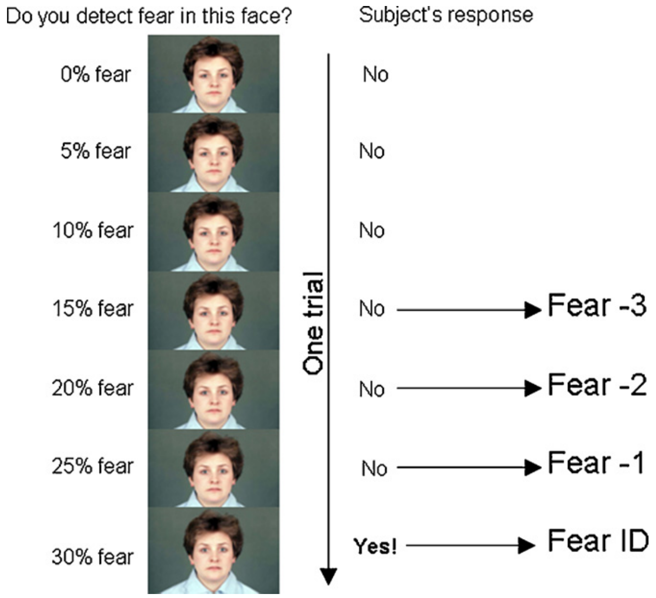

Fig. 1. An example of one trial in the fear detection task.

continua and 7 "catch" trials consisting of 7 neutral-disgust face continua). The experiment was divided into three blocks allowing for two short intermissions.

2.4. Stimuli

Pictures of Caucasian faces were selected from a pool of chromatic face photographs gathered from 4 different databases: the Japanese and Caucasian Facial Expressions of Emotion (JACFEE, Matsumoto and Ekman, 1988), the NimStim Set of Facial Expressions (Tottenham et al., 2009), the Karolinska Directed Emotional Faces (Lundqvist et al., 1998), and The Israeli Database of Emotional Facial Expressions (Frenkel and Bar-Haim, 2006). Seventy pairs of pictures from 70 individual actors, one with a fearful expression and one with a neutral expression, were selected for creation of the experimental stimuli. Seven additional pairs of pictures, from seven different actors, one with an expression of disgust and one with a neutral expression, were selected for the creation of stimuli for 7 catch trials. We selected disgust to serve as catch stimuli based on models of facial expression classification (Russell, 1980; Woodworth and Schlosberg, 1954), indicating that fear and disgust are equally unpleasant facial expressions of emotion, which are not highly confusable. Thus, while the catch stimuli are discriminable from the experimental stimuli they do not change the overall affective tone of the experiment. The selected photos were standardized via Adobe Photoshop CS2 to yield equiluminant images with equal resolution, centered faces of similar size, and identical background colors.

Selection of the fearful and neutral face pairs was based on a pilot study in which 40 undergraduate psychology students (20 female) were asked to rate the neutral and fearful faces on a scale ranging from 1 to 7 in terms of how fearful they appeared. The selected face pairs were those for which the neutral photograph was rated 1 and the fearful photograph was rated 5, 6, or 7. All faces were selected with at least 70% inter-rater agreement.

Interpolated (or "morphed") face stimuli were created using Morpheus Photo Compressor software by combining the prototypical emotional expression (fearful or disgust) with the neutral expression of the same individual. Morphed faces included images ranging from 0% to 100% of the prototypical emotional face (fear or disgust) with 5% increments between consecutive images. Seventy neutral-fear and seven neutral-disgust facial continua were created, totaling in 1617 different stimuli depicting 77 different individuals with 21 levels of emotion expression within each continuum. Each facial image subtended 600 × 900 pixels and appeared against a gray background.

2.5. EEG recordings and ERP derivation

Electrophysiological data were recorded while participants performed the fear detection task. Continuous EEG was recorded using a Geodesic Sensor Net (V2.0 – Electrical Geodesics, Inc., Eugene, OR), consisting of 64 electrodes evenly distributed across the scalp. During collection EEG data were referenced to the vertex and was then re-referenced offline to average reference. The EEG signal was recorded with a 0.1–100 Hz band-pass filter and digitized at a 500 Hz sampling rate. Continuous EEG data were processed offline using NetStation 4.0.1 (Electrical Geodesics Inc., Eugene, OR), and segmented into stimuli synchronized epochs which were extracted from 100 ms before until 1000 ms after face picture onset. EEG comprising artifacts (EEG Max–Min > 200 μV) were automatically removed from further analysis. Eye blinks that appeared in the EOG signal were removed based on a criterion of Max–Min > 140 μV in windows of 640 ms. Trials containing horizontal eye movements were also removed from further analysis. Before derivation of the ERPs, the EEG signal was subjected to a low-pass digital filtering of 40 Hz.

Based on previous reports in the literature and a review of the grand mean ERPs of the different experimental conditions of interest, time windows of P1, P2, EPN, and LPP components were pre-selected for analysis. EEG epochs in which participants detected fear, were averaged into the "Fear ID" ERP waveform. EEG epochs from face stimuli preceding fear detection were averaged into the "Fear 1" (5% less fear than Fear ID), "Fear 2" (10% less fear than Fear ID), and "Fear 3" (15% less fear than Fear ID) ERP waveforms, each representing a decrease of 5% stimulus fear intensity relative to the "Fear ID" ERP. In addition, subjects' response to the initial neutral face stimulus was examined. P1, P2, EPN, and LPP components were extracted for each participant for each condition.

The P1 and P2 amplitudes were scored as the adaptive mean amplitude (in microvolts) in the time interval from 80 to 126 ms and 190 to 248 ms following face onset, respectively. Based on the sensor locations used by Kolassa et al. (2009), and Holmes et al. (2008) these components were examined over posterior and occipital electrode sites collapsing across Electrical Geodesic Sensors 30, 44, (corresponding to T5 and T6 in the 10-20 system), 32, 43, and 35, 37, 39 (corresponding to O1, Oz, and O2 in the 10-20 system). EPN amplitude was scored as the adaptive mean amplitude (in microvolts) in the time interval from 224 to 360 ms following face onset. Based on the sensor locations used by Schupp et al. (2004), the EPN component was examined over temporo-occipital sites collapsing across Electrical Geodesic Sensors 24, 29, 30, 32, and 35 on the left hemisphere, and 39, 43, 44, 47, and 52 on the right hemisphere. Finally, LPP amplitude was scored as mean amplitude (in microvolts) in the time interval from 400 to 800 ms following faces onset. Based on the sensors used by Schupp et al. (2004), the LPP component was examined over centro-parietal sites collapsing across Electrical Geodesic Sensor 21, 26, 27, 28 (P3 in the 10-20 system), 31, and 33 on the left hemisphere and 38, 40, 41, 42 (P4 in the 10-20 system), 45, and 46 on the right hemisphere. Fig. 2 depicts the relevant sensor locations from which EEG data were used for derivation of the different ERP waveforms.

2.6. Data analysis

Independent samples *t*-tests were used to assess differences between groups in the intensity of stimulus fear needed to elicit conscious fear detection. Anxiety-related modulations in ERP mean amplitudes were examined using four separate analyses of variance (ANOVAs) for the P1, P2, EPN, and LPP components. Group (anxious, nonanxious) served as a between-subjects factor, Stimulus Fear Intensity (Neutral, Fear 3, Fear 2, Fear 1, Fear ID), and Laterality (left hemisphere, right hemisphere) served as a within-subject factors. Significant main effects of Stimulus Fear Intensity were clarified using post hoc contrasts. Significant interaction effects were followed by one way ANOVAs within each group.

Secondary analyses examining anxiety-related differences between the neural response to the neutral face and the Fear-ID condition were conducted to control for potential confounds of certainty/confidence. This was achieved via separate ANOVAs for each of the pre-specified ERP components using only the Neutral and Fear ID conditions yielding a within-subject Emotion-Intensity factor. ERPs of neutral stimuli were those elicited in response to the first face stimulus in the stimulus train (stimuli which participants knew for certain were neutral). This analysis was chosen based on the assumption that subjects were similarly certain/confident both in judging the first presented neutral face as "not yet fearful" and in judging the Fear-ID face as "fearful". Additionally, independent samples *t*-tests were employed to assess between-group differences in baseline ERPs elicited by the initial neutral stimuli.

Whenever assumptions of sphericity in repeated measures analyses were violated (assessed by Mauchly, 1940 test of sphericity), the Greenhouse–Geisser statistic (Greenhouse and Geisser, 1959) was used to adjust the degrees of freedom. The application of the Greenhouse–Geisser correction is indicated by the epsilon value (ε) reported in the results. The degrees of freedom indicated in the text are those before the Greenhouse–Geisser correction. Finally, effect sizes (Cohen's *d* for comparisons between two means, or Partial Eta Squared for ANOVAS) were computed for significant effects.

3. Results

3.1. Behavioral data

As expected anxious participants needed significantly less stimulus fear intensity for conscious fear detection ($M = 32.44\%$, $SE = 2.03$) than did nonanxious participants ($M = 38.59\%$, $SE = 1.92$), $t(32) = 2.15$, $p < 0.05$, Cohen's $d = 0.69$. The data also indicate that the disgust (catch) sequences were processed differently than the fear sequences confirming that participants were selectively looking for fear. Specifically, fear was detected in 98.47% of the fear trials, and in only 26.73% of the disgust trials, Chi-Square = 1711.96, $p < 0.0001$. Finally, to control for the possibility that anxious and nonanxious participants adopted different strategies in completing

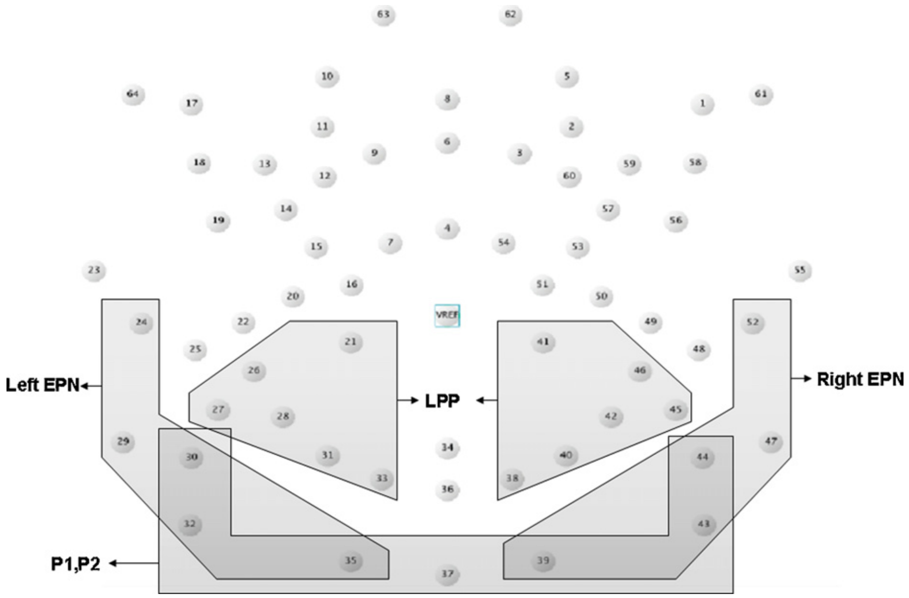

Fig. 2. The relevant sensor locations from which EEG data were used for derivation of the different ERP waveforms.

the fear detection task, Hit and False Alarm rates were calculated for fearful and disgust trials and contrasted between the groups. No group differences were found, all $ps > 0.50$.

3.2. ERPs

3.2.1. P1 (80–126 ms post face stimulus onset)

A main effect of group was found such that relative to nonanxious participants ($M = 3.60$, $SD = 1.47$), anxious participants showed attenuated P1 amplitudes ($M = 2.53$, $SD = 1.48$), $F(1,36) = 4.90$, $p < 0.05$, $d = -0.73$. A main effect of stimulus fear intensity was also found, $F(4,36) = 5.82$, $\varepsilon = 0.67$, $p < 0.005$, $\eta_p^2 = 0.14$ (Fig. 3). Follow-up contrasts indicated that P1 amplitude peaked at Fear 1 (one image before overt fear detection), following a significant P1 increase in the transition from Fear 2 to Fear 1, $t(38) = 3.60$, $p < 0.001$, $d = 0.58$. P1 amplitude decreased in the transition from Fear 1 to overt fear detection (Fear ID), $t(38) = -2.18$, $p < 0.05$, $d = -0.35$. The interaction effect between Group and Fear Intensity was not significant. Secondary analyses indicate a null Emotion-Intensity effect such that the P1 amplitudes of the neutral and the Fear ID conditions did not differ, $F(1,36) = 1.34$, $p > 0.25$, as well as a null Group effect indicated by no anxiety-related differences in the change between the Neutral and the Fear ID conditions, $F(1,36) = 0.32$, $p > 0.57$.

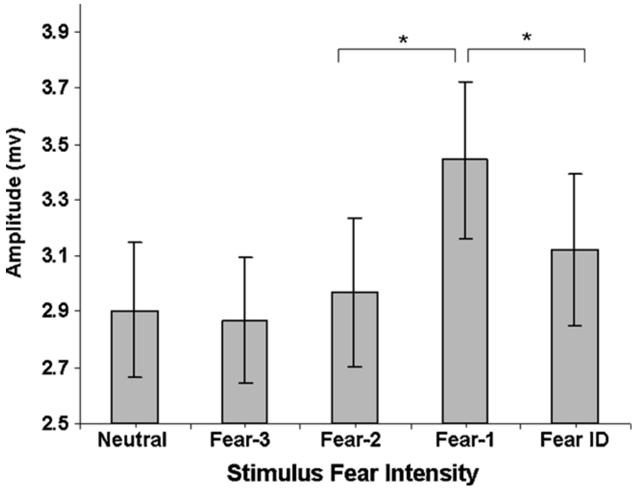

Fig. 3. Emotion-related modulation of the P1 component across participants. P1 amplitude increased and peaked in the transition from Fear-2 and Fear-1 (one image before overt detection), and decreased in the transition to overt fear detection (Fear ID) *significance $p < 0.05$.

3.2.2. P2 (190–248 ms post face stimulus onset)

A main effect of group revealed that anxious participants showed attenuated P2 amplitudes ($M = 2.62$, $SD = 1.57$), relative to nonanxious participants ($M = 3.87$, $SD = 1.57$), $F(1,35) = 5.70$, $p < 0.05$, $d = -0.79$. A nonsignificant trend of a stimulus fear intensity effect was found, $F(4,35) = 2.38$, $\varepsilon = 0.72$, $p = 0.07$. Follow-up contrasts indicated that this trend was driven by a significant decrease in P2 positivity in the transition from Fear 1 to Fear ID (overt detection of fear), $t(38) = -2.17$, $p < 0.05$, $d = -0.35$. Thus, while P2 amplitude was modulated by conscious detection of fear, it was not modulated by increases in stimulus fear intensity preceding conscious fear detection. Secondary analyses showed a non-significant Emotion-Intensity effect indicated by a nonsignificant difference between the neutral and the Fear ID conditions $F(1,35) = 0.82$, $p > 0.37$, as well as a null Group effect as no anxiety-related differences were found in the delta between the Neutral and the Fear ID conditions, $F(1,35) = 2.53$, $p > 0.10$.

3.2.3. EPN (224–360 ms post face stimulus onset)

As illustrated in Fig. 4, a significant main effect of Group was found such that relative to nonanxious participants ($M = 0.61$, $SD = 1.77$), anxious participants ($M = -0.70$, $SD = 1.77$) showed greater EPN over temporo-occipital sites, $F(1,37) = 5.23$, $p < 0.05$, $d = 0.74$. None of the interaction effects involving anxiety group reached statistical significance, all $ps > 0.20$. No laterality effect emerged, $p > 0.80$.

Replicating previous findings of emotion-related EPN modulation, a main effect for Stimulus Fear Intensity was found such that across the full sample, EPN increased as stimulus fear intensity increased, $F(4,37) = 5.33$, $\varepsilon = 0.68$, $p < 0.005$, $\eta_p^2 = 0.13$. This effect was driven by EPN increase in the transition from Fear 1 to Fear ID, $t(38) = 4.60$, $p < 0.0001$, $d = 0.74$ with non-significant changes between the other intensity levels. Thus, while EPN was modulated by overt detection of fear, it was not modulated by increases in stimulus fear intensity preceding overt detection. Secondary analy-

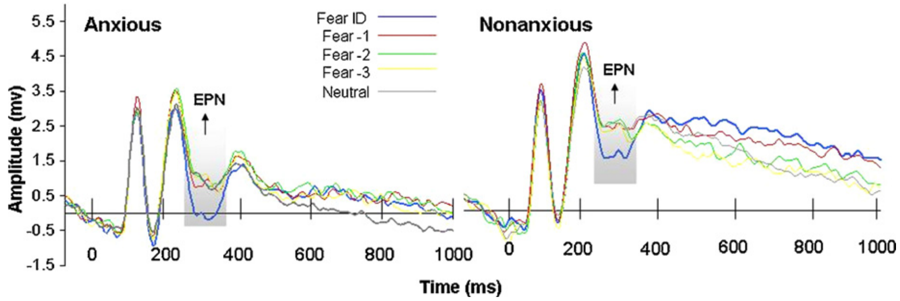

Fig. 4. Grand averaged Early Posterior Negativity (EPN) by anxiety group and fear intensity level; recorded over left- and right-posterior-temporal sensors (30 and 44). Fear ID (blue) – the face in which fear was consciously detected; Fear-1 (red) – the face which immediately preceded the Fear ID image consisting of 5% less fear; Fear-2 (green) – immediately preceded the Fear-1 image consisting of 10% less fear than the Fear ID image; and Fear-3 (yellow) – immediately preceded the Fear-2 image consisting of 15% less fear than the Fear-2 image; neutral face (gray). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

sis revealed a significant Emotion-Intensity effect with greater EPN in response to the overtly detected fearful stimulus (Fear ID) relative to the neutral stimulus, $F(1,37)=9.42$, $p<0.005$, $d=0.49$. No anxiety-related differences were found in this secondary analysis.

3.2.4. Late Positive Potential (LPP, 400–800 ms post face stimulus onset)

As illustrated in Fig. 5, a significant main effect of Stimulus Fear Intensity was observed over centro-parietal sites such that LPP positivity increased as a function of increase in stimulus fear intensity, $F(4,36)=10.62$, $p<0.0001$, $\eta_p^2=0.23$. This main effect was qualified by a significant interaction effect between Stimulus Fear Intensity and Anxiety Group, $F(4,36)=2.86$, $p<0.05$, $\eta_p^2=0.07$. Examination of this interaction effect in each group separately revealed that while LPP amplitude increased as a function of stimulus fear intensity in the nonanxious group, $F(4,80)=12.90$, $p<0.0001$, $\eta_p^2=0.39$, LPP amplitude did not change significantly as a function of stimulus fear intensity in the anxious group, $F(4,64)=1.51$, $p>0.20$. Separate contrasts between fear intensity levels within the nonanxious group, revealed significant LPP increases both in the transition between Fear 3 and Fear 2, $t(21)=2.43$, $p<0.05$, $d=0.52$, and in the transition between Fear 1 and Fear ID, $t(21)=3.97$, $p<0.001$, $d=0.85$.

Secondary analyses contrasting the neutral and the Fear ID conditions revealed a significant Emotion-Intensity effect with higher LPP amplitude in response to the fearful stimulus relative to the neutral stimulus, $F(1,36)=25.40$, $p<0.0001$, $d=0.82$. A significant interaction effect of Emotion-Intensity by Anxiety group was also found, $F(1,36)=8.14$, $p<0.01$, $\eta_p^2=0.18$. Nonanxious participants displayed a larger increase in LPP amplitude in response to the fearful relative to the neutral stimulus, $t(20)=5.24$, $p<0.0001$, $d=1.14$, than did the anxious participants, $t(16)=1.81$, $p=0.09$, $d=0.45$.

3.2.5. ERPs in response to baseline neutral stimuli

As illustrated in Fig. 6, relative to nonanxious participants, anxious participants displayed significantly lower P1 and EPN amplitudes in response to the initial neutral stimuli (first face presented in a sequence), $ts(36, 37)=2.02$ and 2.15, respectively, $ps<0.05$, $d=0.46$. A similar but nonsignificant numerical trend toward lower P2 amplitude in the anxious versus nonanxious participants may also be noted, $t(35)=1.61$, $p=0.12$. No group differences were found in LPP amplitudes, $t(36)=-0.28$, $p=0.78$.

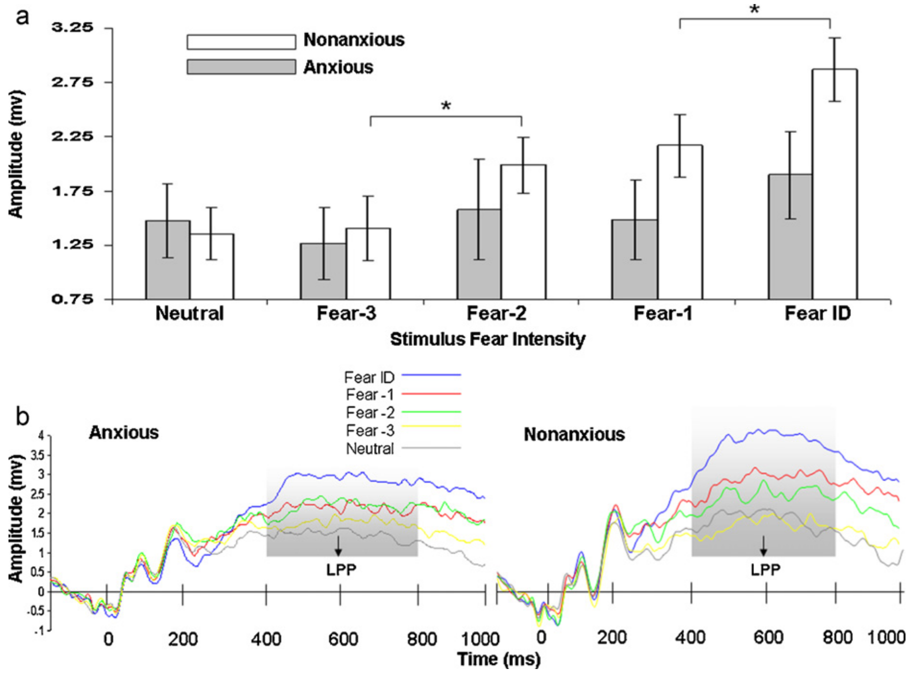

Fig. 5. Late Positive Potentials (LPPs) over centro-parietal sites by anxiety group and fear intensity level. (a) Mean LPP amplitudes, standard error bars, and significant post hoc contrasts; (b) grand averaged ERP waveforms. *Significance p < 0.05.

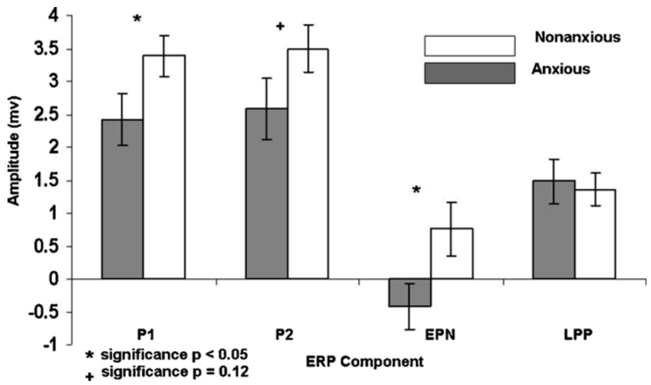

Fig. 6. Amplitudes of the P1, P2, EPN, and LPP ERP components in response to initial neutral stimuli by anxiety group.

4. Discussion

The present study examined whether progressively increasing fearful stimuli elicit differential ERP modulation both at the time of overt fear detection and prior to overt fear detection in anxious versus nonanxious participants. Analyses focused on the examination of both early (P1, P2, EPN) and late (LPP) ERP components which are thought to reflect differential stages in cognitive processing. A significant Stimulus Fear Intensity by Anxiety Group interaction effect immerged for the LPP over centro-parietal scalp locations. While LPP amplitude increased as a function of stimulus fear intensity in the nonanxious group, LPP amplitude was not significantly modulated by stimulus fear intensity in the anxious group. More specifically, nonanxious participants displayed both a larger overall increase in LPP amplitude in response to the fearful relative to the neutral stimulus, as well as significant gradual LPP increases in response to subtle changes in stimulus fear intensity prior to overt fear detection. Such gradual increases were not found in the anxious group. This anxiety-related insensitivity of the LPP to progressive increases in stimulus fear intensity prior to overt fear detection might compromise in-depth threat evaluation in anxious individuals. Such evaluation is necessary for effective decision making and criterion related processes in social circumstances such as allowing one to determine ambiguous cues as benign, thus inhibiting and down-regulating the initial fear response. Without such elaboration, anxious individuals may be prone to ongoing fear responses in the face of very subtle threat cues (Bar-Haim et al., 2007). Additionally, the subtle LPP enhancement preceding overt fear detection in nonanxious individuals may be viewed as a type of early sub-conscious warning mechanism allowing for preparation and adaptation in the face of potentially evolving threats. Anxious individuals may lack this graded underlying neural process and therefore might face threats with no prior warning signal – further contributing to their already heightened anxiety level and perhaps associated with their enhanced baseline threat vigilance (e.g., Mogg and Bradley, 1998; Mogg et al., 2004; Williams et al., 1997).

At the behavioral level, anxious participants needed significantly less stimulus fear intensity to elicit conscious fear detection. This finding rhymes well with previous reports that relative to their nonanxious counterparts, anxious individuals tend to employ a liberal criterion in threat detection, more readily judging stimuli as threat regardless of the stimulus presented to them (e.g., Frenkel et al., 2009; Manguno-Mire et al., 2005). Based on the premise that LPP reflects processing stages related to decision-criterion (Schupp et al., 2004), the LPP pattern displayed by anxious participants in the current study, not differentiating between small nuances of stimulus threat intensity, suggests that these participants engage less processing resources in higher-order decision making, perhaps underlying a relatively liberal criterion to report the presence of threat. Alternatively, the generic anxiety-related attenuation in synchronous neural activity displayed during earlier stages of processing (P1, P2, and EPN) may have compiled into the later stages of more in depth processing indexed by the non-modulated LPP pattern observed in anxious participants.

In contrast with the LPP, albeit generally attenuated neural activity in the anxious group, the present findings reveal that the overall ERP pattern of early cognitive processes indexed by the P1, P2, and EPN is highly equivalent in both groups and does not differ qualitatively as a function of anxiety level. That is, both groups showed a similar early ERP waveform pattern which was distinct during overt fear detection relative to pre-detection stages.

The anxiety-related attenuation of the early P1, P2, and EPN components was not specific to fearful stimuli and was elicited in response to neutral stimuli as well. This generic attenuation related to early stages of processing is in line with a previous signal detection study in which lower levels of sensitivity were displayed by anxious relative to nonanxious participants in response to both neutral and fearful stimuli (Frenkel et al., 2009). Perhaps the use of an explicit rather than implicit fear recognition task served to bias the mental set of participants to look for fearful stimuli (e.g., anxious participants were prepared to detect fearful faces), resulting in reduced stimulus-driven effects in these participants. This could potentially explain why the earlier ERP components were already reduced in anxious, relative to non-anxious participants regardless of stimulus emotion (fear/neutral). Further research including additional facial expressions of emotion (e.g., neutral to happy) is needed to determine whether the emotion effects revealed in the present study are specific to fear or rather generalize to other emotions as well.

Interpretation of the present findings should be viewed in light of some limitations. First, the present study used morphed facial stimuli gradually changing from neutral to fearful. In everyday social situations people rarely encounter a “snapshot” of an emotional expression, but rather view dynamic expressions which undergo change during social interaction. The use of morphed stimuli was thought to increase ecological validity, reflecting ambiguous expressions elicited during the dynamic change from one expression (neutral) toward another (fearful). Nevertheless, one may in fact question whether the blending of end expressions truly reflects an intermediate emotion. Thus, future studies may wish to employ short movies presenting gradual change from neutral to emotional facial expressions rather than morphed images. Second, expectation that fear is soon to appear, may have affected the processing strategy employed in the fear detection task causing participants to employ more liberal criteria in judging the faces as fearful (i.e., detecting fear more readily). This expectation effect could theoretically operate differently in anxious and nonanxious individuals offering an alternative interpretation to the between-group differences that emerged at the behavioral level. That is, anxious participants may be more sensitive to this type of effect, thus causing them to shift their decision criterion in the face of fear stimuli. This concern is alleviated to some degree by the fact that previous studies employing strict psychophysics techniques not susceptible to this potential confound produced similar results (e.g., Frenkel et al., 2009; Manguno-Mire et al., 2005).

In addition, the use of stimulus-trains to increase the independent variable (i.e., fear intensity) in a linear manner brings into play other variables that may confound ERP results. Importantly though, the primary focus of this study is anxiety-related individual differences, and these potentially confounding effects are equally valid for both the high and low anxious groups. Thus, Group effects and Group by Intensity interaction effects remain just as valuable despite these potential confounds. Nevertheless, the fact that the Fear ID stimulus always terminates the stimulus train may give rise to confounds related to "context-closure" meaning that rather than reflecting processes related to fear detection, late ERP positivity may reflect the updating of expectancies evoked by events that are awaited when subjects deal with repetitive, highly structured tasks (Verleger, 1988). Similarly, the fact that a deviant response is required when judging the Fear ID stimulus as "fearful" may give rise to confounds related to "context updating" meaning that late ERP positivity may in fact reflect activity occurring whenever one's model of the environment is revised (Donchin and Coles, 1988). Such potential confounds were considered in the experimental design and an attempt was made to bring these to a minimum. For instance, in order to address possible confounds regarding order and expectancy effects, or effects of stimulus response frequency, ERPs were locked to stimulus presentation and not to stimulus response. In this manner, although Fear ID stimuli always terminated the stimulus train, trial termination was determined in retrospect only after stimulus response. Thus participants in fact did not know prior to stimulus presentation that the upcoming stimulus would definitely terminate the trial. Similarly, although the Fear ID response was both less frequent and different than the "not yet fearful" response, ERP effects were in fact locked to neural activity prior to this deviant response. In the same vein attempts were made to minimize potential confounds related to the neutral stimuli as well. Specifically, neutral face stimuli were presented at the beginning of each trial between 1 and 4 times in a randomly determined manner without subjects being aware of this repetition. In this manner the neutral stimulus was in fact not systematically only the first stimulus in the train and participants could not always predict prior to stimulus presentation that it was going to be a neutral stimulus.

Certainty effects may also be reflected in the ERPs which rather than revealing fear detection or response criteria, may additionally be reflecting a continuum of uncertainty, from uncertain (Fear 3, Fear 2, Fear 1) to certain (Fear ID). The secondary analyses in the present study control for such certainty influences to an extent via the comparison between ERPs elicited in response to Fear ID stimuli and ERPs elicited in response to the first face presented in the stimulus train (i.e., neutral stimuli). One would expect Fear ID and the first presented neutral stimuli to elicit a similar sense of certainty (participants are 'certain' that neutral faces are not fearful, especially in light of the experimental directions clearly stating that the first face in each continuum will always contain a neutral expression, and certain the Fear ID stimuli are fearful). Based on this rationale, fear detection effects, as opposed to uncertainty effects, should be reflected by reduced ERP amplitudes to neutral faces compared with Fear ID faces. Indeed, both EPN and LPP positivity were significantly augmented in response to Fear ID stimuli versus neutral stimuli thus implying fear detection effects. This significant difference between the neutral and Fear ID stimuli displayed by nonanxious controls in both the EPN and the LPP components, is in line with previous studies reporting augmented EPN and LPP positivity triggered by emotional relative to neutral stimuli in normative samples (e.g., Ashley et al., 2004; Carretie and Iglesias, 1995; Eimer and Holmes, 2002, 2007; Schupp et al., 2004) Furthermore, in the LPP component significant group differences emerged revealing that nonanxious participants displayed a larger increase in LPP amplitude in response to the fearful relative to the neutral stimulus, than did the anxious participants. Certainty effects would apply to both anxiety groups whereas the present findings reveal group differences, further supporting the notion of fear detection effects. Nevertheless, interpretation of individual differences should be cautious and are not fully conclusive at this stage. Future studies may wish to control for possible certainty influences via the employment of an implicit task with a random rather than sequential presentation design.

Finally, the experimental design employed in this study allowed for the examination of neural processing at the time of overt fear detection as well as during the stages preceding detection. While the ERPs of both groups reflect comparable subjective experiences (i.e., the subjective detection of fear in the stimulus and the three stimuli preceding this experience reflecting fixed increments of 5% less fear each), ERPs for the anxious and nonanxious groups reflect different objective stimuli. Specifically, on average anxious participants needed ∼4% less stimulus fear intensity for overt fear detection than did nonanxious participants. Thus, while the Fear ID condition was locked to stimuli around the 30% fear, in the anxious group, it was locked to stimuli around the 35% fear in the nonanxious group. One may argue that this difference is responsible for the general attenuation found in the early ERPs of the anxious group. Nevertheless, this still does not explain the difference in amplitude found in response to the initial neutral stimulus nor does it explain the interaction between stimulus fear intensity and anxiety group found in the LPP component. We anchored our research in the subjective experience of overt fear detection and thus were able to evaluate its preceding sub-conscious neurocognitive processes.

To conclude, the novel approach of the present study differs from most studies on cognitive biases in anxiety that focus on differential processing of predetermined stimuli. While differences in design challenge the direct comparison to more conventional studies on the one hand, they serve to provide a novel perspective on the other. The present study raises valuable questions regarding the nature of the complex interplay between early automatic stages of processing and later sustained and more elaborate stages of processing in anxious and nonanxious individuals. Future studies may wish to employ this design with additional types of anxiety groups and emotional stimuli to further shed light on the present findings.

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