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Adapting effects of emotional expression in anxiety: evidence for an enhanced Late Positive Potential.

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ABSTRACT:

An adaptation paradigm was used to investigate the influence of a previously experienced visual context on the interpretation of ambiguous emotional expressions. Affective classification of fear-neutral ambiguous expressions was performed following repeated exposure to either fearful or neutral faces. There was a shift in the behavioural classification of morphs towards 'fear' following adaptation to neutral compared to adaptation to fear with a non-significant trend towards the high anxiety group compared to the low being more influenced by the context. The event-related potential (ERP) data revealed a more pronounced late positive potential (LPP), beginning at ~400 ms post-stimulus onset, in the high but not the low anxiety group following adaptation to neutral compared to fear. In addition, as the size of the behavioural adaptation increased there was a linear increase in the magnitude of the late-LPP. However, context-sensitivity effects are not restricted to trait anxiety, with similar effects observed with state anxiety and depression. These data support the proposal that negative moods are associated with increased sensitivity to visual contextual influences from top-down elaborative modulations, as reflected in an enhanced late positive potential deflection.

KEY WORDS: Adaptation, Anxiety, Depression, ERPs, LPP

1. INTRODUCTION:

Being sensitive to threatening information has an evolutionary advantage as it enables danger to be detected rapidly and appropriate behaviour to be initiated quickly. Emotional stimuli are prioritized for processing, and threat-related stimuli are processed efficiently (Eysenck & Calvo, 1992; Eysenck, Derakshan, Santos, & Calvo, 2007; Öhman, Lundqvist, & Esteves, 2001) and possibly without cognitive resources (Dolan & Vuillumier, 2003, but see Pessoa & Adolps, 2010). However, the threat signal is often weak or ambiguous – the moving shadow as you walk along a country path on a dark evening could be a predator or simply a tree swaying in the breeze, and we need to be able to differentiate one from another. A failure to detect a potential threat could be very costly but on the other hand, being overly sensitive to stimuli that turn out to be innocuous can be counterproductive and interfere with current goals.

Anxiety is associated with an enhanced tendency to detect negativity in ambiguous stimuli that may signify the presence of threat (e.g., Bar-Haim et al., 2007; Blanchette & Richards, 2010; Cisler & Koster, 2010; Huppert, Pasupuleti, Foa, & Mathews, 2007; Mathews & Mackintosh, 2000; Mathews & MacLeod, 2002; Simmons, Matthews, Paulus, & Stein, 2008; Richards, 2004; Richards et al., 2002; Sprengelmeyer, et al. 1997; Stopa & Clark, 2000), and there is some recent work to suggest that variations of the allele in the promotor area of the 5-HTTLPR serotonin transporter gene is related to emotional interpretation biases (Fox & Standage, 2012). Ambiguity resolution has typically been investigated independently from contextual influence, yet we rarely process information in a contextual vacuum. Whether context has an effect early (e.g., Marslen-Wilson, 1987) or late (e.g., Friederici, 2002) in processing, it is clear that environment in which an event occurs provides a valuable source of information (Gaskell & Marslen-Wilson, 2001) and in many circumstances contextually-consistent meanings take preference over context-incongruent

meanings (Aviezer et al., 2008; Barrett, Lindquist, & Gendron, 2007; Lucas, 1999). In evolutionary terms, using contextual cues to disambiguate potentially threatening situations should aid survival, as they can render a situation benign (a person running up behind you in a busy shopping mall) or dangerous (a person running up behind you in a dark alley). Although there is robust evidence to support the idea that anxiety is associated with a threat-related interpretative bias (e.g., Richards, 2004) there is evidence that contextual information overrules this bias (e.g., Blanchette & Richards, 2003).

Presenting ambiguous stimuli within different contexts allows mood-congruency and context-sensitivity to be examined. A mood-congruency hypothesis (e.g., Bower, 1981) proposes that ambiguity is resolved in line with the participant's mood with the context having no influence on the direction of the interpretation. In other words, an anxious person would interpret a threat/neutral ambiguous stimulus in the threatening manner whereas a non-anxious person would resolve this ambiguity in the neutral direction, irrespective of the context. On the other hand, the context-sensitivity hypothesis (Blanchette & Richards, 2003) predicts context congruent resolutions. This means that when the context is negative, the ambiguity in the ambiguous stimulus will be resolved in the *mood-congruent* direction, if current mood is also negative. However, when that same stimulus is resolved within a positive or neutral context, the resolution will be *mood-incongruent* in that it will be interpreted in the more positive/neutral manner. In earlier research, both anxious and non-anxious individuals were influenced by context, over and above mood, but the effect was significantly stronger in the former group (Blanchette & Richards, 2003; Blanchette & Richards, 2010; Blanchette, Richards, & Cross, 2007; Richards, Blanchette, & Munjiza, 2007). Such results are also consistent with Fiedler's (2000) view that compared to positive affect, negative affect is associated with increased bottom-up processing, where a wider range of information is used in order to make a decision. Although the earlier studies examined

state anxiety, one study (Blanchette et al., 2007) found that trait anxiety was associated with a mood-congruent rather than context-sensitivity effect. In line with the paucity of research into trait anxiety, to date, contextual sensitivity in depression has not been investigated in this way even though there is evidence of negative (i.e., mood-congruent) interpretative bias in depression (e.g., Hertel & El-Messidi, 2006; Miller & Norman, 1986; Wisco & Nolen-Hoeksema, 2010). Rossignol, Philippot, Crommelinck and Campanella (2008) argue that depression and anxiety should be investigated due to its importance in major clinical dimensions. In the current experiment we focus on trait anxiety but, in order to assess whether any effects may reflect negative mood more broadly, we also examine state anxiety and depression using ERPs in an adaptation paradigm.

Emotions are expressed dynamically in facial expressions, where the emotional signal changes from, for example, surprise to fear. The dynamic nature of facial expression has enabled emotionally ambiguous signals to be generated for use in ambiguity resolution research. Anxious individuals are more sensitive than non-anxious to fear cues present in emotionally ambiguous facial expressions (e.g., Richards et al., 2002; Sprengelmeyer et al., 1997) and this bias occurs fairly late on in processing (Richards & French, 2002; Calvo & Castillo, 2001a, 2001b; Calvo, Castillo, & Estevez, 1999), suggesting that it is a product of late elaborative processes as opposed to early automatic processes. Prolonged exposure to a facial expression biases the perception of a subsequent emotional expression along an emotional expression continuum away from the adapting expression. For example, a fear/happy target will be perceived as being more 'fearful' following repeated exposure to a happy compared to a fearful adapting stimulus (Webster, Kaping, Mizokami, & Dohamel, 2004; Webster, 2011). Previous research has presented contextual information simultaneously with the ambiguous stimulus (e.g., Blanchette & Richards, 2003; Richards, Blanchette, & Munjiza, 2007) but here we create a context using adaptation that is produced

by a *previous* visual experience (e.g., Butler, Oruc, Fox, & Barton, 2008; Furl, van Rijsbergen, Treves, & Dolan, 2007; Webster, Kaping, Mizokami, & Dohamelal, 2004). In earlier behavioural research, the context was presented simultaneously and therefore perhaps in competition with the ambiguous target. By using the adaptation technique, this competition has been removed thereby ensuring that all participants are fully exposed to the context prior to the presentation of the target. In previous behavioural research, no external demands were imposed on the participants to process the context, and therefore these earlier studies investigated how the context is used naturally. In other words, these studies examined whether the context was used or not to resolve the ambiguous stimulus. This contrasts with the present design, where we examine the influence of a created context then see how this influences ambiguity resolution. According to Furl et al. (2007; 2011) earlier visual and sensory experiences are used as a referent for visual perception. Visual stimuli are inherently ambiguous and the adaptation period prior to perception serves as a context for that perception. In the current research, we are examining relatively short-term contextual influences that contrast with the relatively long-term semantic representations accessed in the previous behavioural research.

Adaptation, sometimes referred to as repetition suppression, has been observed for low level stimulus properties such as colour and also for higher order dimensions such as faces and bodies (e.g., Taylor, Wiggett, & Downing, 2010). Explanations for adaptation aftereffects range from local, neural fatigue accounts to top-down modulations of one neural region by a higher-level neural region (Henson & Rugg, 2003; Friston, 2005). Both low- and high-level visual representations contribute to behavioural aftereffects. Face adaptation is partially position invariant (Afraz & Cavanagh, 2008; Kovács, Zimmer, Harza, & Vidnyánszky et al., 2007; Leopold, O'Toole, Vetter, & Blanz, 2001) and size invariant although the effect is twice as large if the adaptor and target are the same size compared to if they differ in size

(Zhao & Chubb, 2011). Adaptation aftereffects have been observed using neurophysiological techniques such as fMRI (e.g., Ewbank et al., 2011; Furl et al., 2011), ERPs (e.g., Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Kloth, Schweinberger, & Kovács, 2010) and MEG (Ewbank, Smith, Hancock, & Andrews, 2008; Furl et al., 2007).

The high temporal resolution associated with ERPs provides an excellent means of investigating the time course of differential processes involved in the perception and resolution of emotionally ambiguous material. Several event-related potential (ERP) components appear to be modulated by emotion and anxiety. A number of studies report evidence for an enhancement of the visual P1 component (maximal at ~120 ms) to negative compared with neutral facial expressions (e.g., Batty & Taylor, 2003; Holmes, Nielsen, & Green, 2008; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005). The Early Posterior Negativity (EPN) is another early emotion-modulated component (Junghöfer, Bradley, Elbert, & Lang, 2001), characterised by an enhanced negativity at temporo-occipital regions developing at around 150 ms and maximal at 260-280 ms post stimulus onset. It has been shown to be sensitive to emotional compared to neutral expressions (Balconi & Pozzoli, 2003; Eimer, Holmes, & McGlone, 2003; Schutter, de Haan, & van Honk, 2004). These early ERP effects are considered to reflect the early detection and attentional enhancement of emotional facial information (see, e.g., Eimer & Holmes, 2007; Schupp, Flaisch, Stockburger, & Junghöfer, 2006a).

Given the behavioural evidence that emotionally ambiguous stimulus resolution is modulated by anxiety at later rather than earlier stages of processing, the late positive potential (LPP) may be of particular relevance. This is a broadly distributed stimulus-locked sustained positive deflection developing around 200-300 ms post-stimulus onset and is maintained past 700 ms (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Eimer & Holmes, 2007; Schupp, Junghöfer, Weike, & Hamm, 2004; Weinberg, Hilgard, Bartholow, &

Hajcak, 2012). The LPP reflects post-perceptual processing of emotionally salient visual stimuli and is said to be more reflective of elaborative processing after the stimulus has been categorised (Ritter & Ruchkin, 1992; Schupp et al., 2006b; Weinberg & Hajcak, 2010). Holmes and colleagues (e.g., Eimer & Holmes, 2007; Holmes, Nielsen, & Tipper, 2009) suggest that the early-phase of the LPP (~200-400 ms) may be elicited via prefrontal mechanisms involved in the rapid detection of emotionally relevant stimuli in working memory. By contrast, the late-phase of the LPP (post 400 ms) may reflect the active maintenance of emotion representations in working memory, enhancing their accessibility to high order decision and response-related processes. Lee et al. (2010) obtained enhanced LPP deflections when a fearful face was reported having been seen in the absence of one being presented, suggesting that the LPP reflects cognitive processes that are independent of stimulus properties, and is therefore very useful for examining context and interpretation effects. Evidence for the sensitivity of LPPs to interpretation and appraisal comes from studies by Gootjes, Franken Ingmar and Van Strien (2011) and Moser, Hajcak, Bukay, & Simons (2006) who found that reappraising aversive images in a positive direction reduced the magnitude of the LPP.

It should be noted that the LPP is also referred to as a P3b (e.g., Schupp et al., 2006a), but it is unclear as to whether the LPP elicited by emotional faces reflects the same underlying processes as the P3b. The former typically has a fronto-central maximal distribution (Eimer & Holmes, 2007) whereas the latter has a centro-parietal maxima (Polich, 2007), indicating that despite the similarities in the time course and amplitude of these components, they are at least partially separable. A systematic account of the similarities and differences between the P3b and LPP has yet to emerge (Olofson, Nordin, Sequeira, & Polich, 2008).

The current experiment employs the adaptation paradigm where previous visual experience (i.e., context) influences the perception of current stimuli, to examine the resolution of ambiguity. Fear/neutral morph target stimuli will be classified by participants following adaptation to the fearful or the neutral exemplar that was used to create the morphs. On the basis of earlier behavioural research, we predict that anxiety-related effects will be apparent at later (mid- and late-phase LPPs) rather than earlier (P1 and EPN) ERP components. A mood-congruent model would predict a main effect of group, that is, an enhanced LPP following both neutral and fear adaptation for high compared to low anxiety participants, consistent with the fear/neutral morph being perceived as more fearful by high anxiety individuals. This mood-congruent effect would be apparent for target stimuli irrespective of context. The context-sensitivity hypothesis, on the other hand, would predict an interaction between group and adaptation: the previously experienced visual neutral context would be expected to enhance the perception of fear in the morph and therefore trigger an augmented LPP for high compared to low anxiety, whereas the fearful context should lessen the perception of fear in the morph and elicit an attenuated LPP for high compared to low anxiety participants. In other words, the nature of the context should influence the perception of the target in the opposite direction to the context. Although not predicted, an examination of the early components such as the P1 and EPN will determine whether anxiety modulates adaptation at early processing stages. Due to their fine temporal resolution, ERPs are the most suitable means of exploring whether any context effects have their influence at an early or late stage of processing. In addition, we will examine depression and state anxiety to determine whether any effects are restricted to trait anxiety or whether they are associated with negative mood more generally.

2. METHOD

2.1 Participants:

The participants were 44 healthy volunteers. Two participants were excluded because of excessive noise in the electroencephalography (EEG) data, so that 42 participants (21 male, 18 female; 18-45 years old; mean age: 25.38 years, SD = 6.38) remained in the sample. All participants had normal or corrected-to-normal vision, and the majority ($N = 33$) were right-handed. Participants completed the state and trait versions of the STAI (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and the Beck Depression Inventory (BDI-II: Beck, Steer, & Brown, 1996). Scores on the trait anxiety scale were ranked, and a median split performed (median = 38, range = 21-61). Allocation of participants to high and low-trait anxiety groups was made on the basis of scores falling above or below the median, excluding participants with scores that fell on the median ($N = 3$; see, e.g., Fox, Russo, Bowles, & Dutton, 2001; Holmes, Nielsen, & Green, 2008, for a similar approach). This resulted in the assignment of 21 participants to the low-trait anxiety group and 18 participants to the high-trait anxiety group. The two anxiety groups did not differ in defensiveness (means of 4.4 and 3.4 for low and high anxiety respectively; $t(37) = 1.5$, $p = .13$). Allocating participants to groups using this method resulted in some participants in the high-trait group with trait scores that fall outside the high-anxiety range as specified by Spielberger et al. (1983). We have adopted this approach in order to maintain consistency with previous research in the area. However, there were significant interactions between state and trait anxiety ($r = .60$), state anxiety and depression ($r = .61$) and between trait anxiety and depression ($r = .61$), suggesting a level of comorbidity between the measures. We performed supplementary linear mixed models analyses when anxiety has had a significant effect to examine the whole continuum of trait anxiety scores and to see whether the effects generalise to state anxiety and depression. Participants also completed the short-form Social Desirability Scale (SDS:

Strahan & Gerbasi, 1972), as defensiveness may confound anxiety and processing measures (Mogg, Garner, & Bradley, 2007). However, there were no differences in defensiveness between the groups ($t(37) = 1.5$, ns).

The experiment was performed in compliance with relevant institutional guidelines and was approved by the School ethics committee.

2.2 Stimuli:

Facial expressions were selected from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). A pilot study was performed in order to select appropriate stimuli. One male (M14) and one female (F11) identity was selected and each was morphed with their corresponding neutral expression to create a series of fear/neutral morphs using Sqrilz 1.2 landmark based morph software. All images were cropped to occlude hair, converted to grey scale, and matched for average luminance. For each of the two models, 10 morphs were selected from the fear/neutral continuum to be used as test faces; 5 from the neutral side of the categorical boundary and 5 from the fear side of the boundary. The percentages of fear in the fear/neutral morphs for the targets that were pre-classified as 'fearful' were 60% to 64% for both F11 and M14 models. The percentages of fear in the morphs pre-classified as 'neutral' were 46% to 50% (F11) and 40% to 44% (M14). The neutral exemplar expressions used for the adaptation period for both F11 and M14 contained 1% fear/99% neutral whereas the fear exemplar contained 99% fear/1% neutral. The happy expression for F11 and M14 was selected for use on dummy trials. Morphs from the two extremes (below 20% fear and above 80% fear) of the continua for F11 and M14 were used for the practice trials.

2.3 Design:

There were two baseline blocks of trials at the beginning of the experiment in which each of the 20 fear/neutral morphs was presented 3 times for classification. This was to

ensure that classification without contextual influence was the same for the two anxiety groups. Each baseline trial began with a fixation cross for between 2200 and 2500 ms, and was followed by the fear/neutral morph for 300 ms. When the face stimulus disappeared, participants were required to classify the morph as being fearful, neutral or happy by pressing the appropriate key on the keyboard using the index finger of their dominant hand. After participants had made their decision, the next trial began (see Fig. 1).

The experimental block comprised 12 adaptation blocks. Six blocks were fear adaptation blocks and 6 were neutral adaptation (the male model was used for half of the blocks and the female model for the other half of the blocks). Each of the 12 adaptation blocks comprised a total of 78 trials, 35 of which were adapting trials in which the adapting stimulus (either the fear or neutral exemplar) was followed by 33 test trials. The adapting trials did not require a response from the participant whereas each of the 33 test trials required the face to be classified. Of the 33 test trials, 20 trials were critical (fear/neutral morphs), 5 were top-up trials (exemplar re-presented), and 8 were dummy trials (happy exemplars). The design of the current experiment was based on that of Furl et al. (2007). The 12 adapting blocks were presented in random order.

2.3.1 Adaption Trials. A fixation cross appeared for 400 ms and was immediately replaced by the adapting stimulus for 1000 ms. A fixation cross then appeared for 50 ms before the next trial (ITI of 450 ms).

2.3.2 Test Trials. The fixation cross appeared for between 2200 and 2500 ms and was immediately followed by either a critical face stimulus (fear/neutral morph) for 300 ms, a top-up stimulus (adapting face) for 2200 ms, or a dummy stimulus (happy expression) for 300 ms. Participants were required to classify each face as fearful, neutral or happy. The dummy trials were presented for the same duration as the critical trials and were included in

order for the participants to use the three classification options. There were a total of 936 trials in the experimental block, of which 240 were critical. Participants completed 2 practice blocks prior to the experimental blocks. The first practice block comprised 20 trials (10 adaptation, 8 critical face, 2 top-up) with a slow presentation in order for the participants to become familiar with the procedure. The second practice block was the same as the first, but presentation of the trials was at the same speed as that for the experimental blocks.

Participants completed the STAI, BDI and SDS questionnaires.

3 DATA PREPARATION

3.1 EEG recording and data analysis:

EEG data were DC recorded (low-pass filter at 40 Hz, linked-earlobe reference) and digitized at a sampling rate of 500 Hz using a SynAmps amplifier (Neuroscan). Signals were recorded from 23 electrodes FP1, FP2, F3, Fz, F4, F7, F8, FC1, FCz, FC2, FC5, FC6, C3, Cz, C4, CP5, CP6, P3, P4, P7, P8, O1, O2 (according to the 10-20 system). Horizontal eye-movements (HEOG) were measured from two electrodes placed at the outer canthi of both eyes, and impedances for electrodes were kept below 5 K Ω . Following EEG recording, the EEG was epoched relative to a 100 ms pre-stimulus baseline. Trials with lateral eye movements (HEOG exceeding $\pm 30 \mu\text{V}$), as well as trials with vertical eye movements, eye blinks (FP1/FP2 exceeding $\pm 60 \mu\text{V}$), or other artefacts (a voltage exceeding $\pm 60 \mu\text{V}$ at any electrode) measured after stimulus onset were excluded from analysis. ERP mean amplitudes were obtained for specific sets of electrodes within predefined measurement intervals. One set of electrodes (FC1, FCz, FC2, C3, Cz, C4) was defined as a cluster representing frontocentral effects. Regional activity was analyzed at this cluster of electrodes within successive post-stimulus intervals of 160-220 ms (early positivity), 220-400 ms (early-phase LPP), 400-600 ms (mid-phase LPP), and 600-800 ms (late-phase LPP). Activity was also analyzed at occipital electrodes (O1, O2) within a time range of 100-140 ms in order to

examine the P1, and across occipito-parietal electrodes (P7, P8, O1, O2) within a time window of 260-380 ms in order to examine EPN component effects. These electrode sites and time windows were determined on the basis of visual inspection of individual and grand averaged waveforms and of topographical maps showing the distribution of ERP effects across the scalp (see Fig. 3 and 4). The electrode sites were determined also on the basis of previous reports and overlap primarily with channels selected by Holmes et al. (2009). The time windows were also based on previous reports, which have similarly discriminated between an early positivity (160-220 ms) and early LPP (220-400 ms) (Holmes et al., 2008). The selection of time windows for the later phases of the LPP was informed by previous studies which have shown that differences in emotion processing may be reflected in earlier and later windows of the LPP (e.g., Foti & Hajcak, 2008; Weinberger et al., 2012). The time windows of 400-600 ms and 600-800 ms were based specifically on those selected by Weinberger, Hilgard, Bartholow, & Hajcak, 2012).

3.2 Treatment of EEG data:

Separate averages were computed across all conditions for each participant and ERP measure. For the early positivity and the early, mid, and late phases of the LPP, mean amplitudes were entered into a 2 x 2 x 2 mixed analysis of variance (ANOVA) with within-subjects factors of adaptation (neutral, fear), sex of expression (female, male) and a between-subjects factor of anxiety (high, low). For the P1 and EPN, mean amplitudes were entered into mixed ANOVAs with the same factors as outlined above but with an additional within-subjects factor of electrode position (P1:O1, O2; EPN: P7, P8, O1, O2). Further comparisons were carried out for low- and high-trait anxiety groups separately whenever significant emotional expression ERP main or interaction effects were produced from the omnibus ANOVA results. For all analyses, Greenhouse-Geisser adjustments to the degrees of freedom were performed. When effects involving adaptation were significant, we performed more

powerful linear mixed effects analyses to see if trait anxiety, state anxiety and depression were important.

4. RESULTS

4.1 Behavioural Measures:

The proportion of fearful responses made to targets was calculated. A 3 (adaptation: fearful, baseline, neutral) x 2 (identity: male, female) x 2 (anxiety group: low, high) ANOVA was performed on the proportion of fearful responses in the baseline block and the two adaptation blocks. There was a main effect of adaptation ($F(2, 74) = 153.29, p < .001, \eta_p^2 = .81$). More fear responses were made following neutral than in the baseline condition (mean proportions of .87 and .63, respectively, $t(38) = 7.06, p < .001, CI_{95} 0.17, 0.30$) and fewer following fear adaptation than in the baseline condition (mean proportions following fear adaptation of .31, $t(37) = -9.15, p < .001, CI_{95} -.40, -.26$). In addition, there was an interaction between adaptation and identity ($F(2,72) = 8.03, p < .001, \eta_p^2 = .18$; see Fig. 2). There was a difference in the proportion of fearful classification for the male and female identity in the baseline condition ($t(38) = 2.15, ns, CI_{95} = 0.01, .18$) and following neutral adaptation ($t(38) = 2.33, p < .05, CI_{95} = .02, .33$) and fewer fearful classifications for females than males following fearful adaptation ($t(38) = 2.43, p < .05, CI_{95} = 0.01, 0.11$). The proportion of fearful faces for male and females expressions was not different following fearful adaptation ($t(30) = 1.88, ns$). The high anxious group were slightly more influenced by the context than the low anxious group but this interaction was non-significance ($F(2,72) = 2.31, p = .106, \eta_p^2 = .06$).

4.2 Event-related potential measures:

Fig. 3 shows ERPs at frontocentral and occipito-parietal electrodes in response to target fearful faces following adaptation to fearful faces (black lines) or neutral faces (red lines), separately for low-trait anxious (top panel) and high-trait anxious (bottom panel) participants.

LPP at frontocentral locations (early-phase: 220-400 ms post-stimulus measurement window). There were no significant main effects or interactions (all F s < 3.12, all p s > .09).

LPP at frontocentral locations (mid-phase: 400-600 ms post-stimulus measurement window). There was a significant main effect of adaptation, $F(1, 37) = 4.14, p < .05, \eta_p^2 = .10$, as the LPP was enhanced for ambiguous morphed expressions following adaptation to neutral ($M = 2.65 \mu\text{V}, SD = 1.69$) relative to fearful ($M = 2.25 \mu\text{V}, SD = 1.69$) faces. There were no other significant main effects or interactions (all F s < 1). Planned analyses revealed an enhanced LPP following neutral compared to fearful adaptation for the high anxious group (means of $3.00 \mu\text{V}$ and $2.42 \mu\text{V}$, respectively; $F(1,17) = 6.84, p < .05, \eta_p^2 = .29$) but not for the low-trait anxious group (means of $2.32 \mu\text{V}$ and $2.10 \mu\text{V}$, respectively; $F < 1$).

In order to increase statistical power we performed a mixed effects analysis using R statistics software (<http://www.r-project.org/>) with adaptation and trait anxiety entered as fixed effects and subjects entered as a random effect. This analysis revealed a small but significant interaction between trait anxiety and adaptation ($\beta = .034, t = 2.5, p = .02$). A second analysis with state anxiety revealed a non-significant interaction between adaptation and state anxiety, but a final analysis revealed effects with the BDI that mirror those obtained with trait anxiety ($\beta = .089, t = 4.43, p < .001$). The first of these mixed effects analyses confirms the anova, showing that as trait anxiety increases there is a corresponding increase in amplitude for morphed expression following neutral compared to fearful adaptation.

However, additional analyses revealed that the effect is not restricted to anxiety as depression also significantly interacted with valence.

To test whether the behavioural response correlated with the neural response, two difference indices were calculated and then correlated with each other. The first index represented the difference in the proportion of fear classifications for targets following fear and neutral adaptation and the second represented the difference in the magnitude of the LPP for the targets following the two adaptation conditions. There was no correlation between the two indices ($r=.13$).

LPP at frontocentral locations (late-phase: 600-800 ms post-stimulus measurement window). There was a significant main effect of adaptation, $F(1, 37) = 5.97, p < .05, \eta_p^2 = .14$, and a significant adaptation x anxiety interaction, $F(1, 37) = 4.38, p < .05, \eta_p^2 = .11^3$. Further comparisons again showed that there was an enhanced LPP for the high anxious group following neutral adaptation compared to fearful adaptation (means of 4.18 μV and 3.27 μV , respectively; $F(1,17) = 11.00, p < .001, \eta_p^2 = .39$), but no effect for the low anxious group (means of 3.2 μV and 3.1 μV , respectively, $F < 1$; see Fig. 4 for topographical maps showing scalp distributions).

A mixed effects analysis with adaptation and trait anxiety entered as fixed effects and subjects entered as a random effect. This analysis revealed an interaction between trait anxiety and adaptation ($\beta=.064, t = 4.40, p < .001$). A comparable analysis with state anxiety entered revealed a significant interaction between adaptation and state anxiety ($\beta=.047, t = 2.69, p = .012$). A second analysis with depression and adaptation revealed a significant

³ When electrode position (FC1, FCz, FC2, C3, Cz, C4) was included as a factor within the LPP analyses, none of the adaptation main effects or adaptation x anxiety interactions were found to be significantly modified by this factor (all F s < 1.7, all p s > 1.5).

interaction in line with the effects observed for state and trait anxiety ($\beta=.10$, $t = 5.05$, $p < .001$). This finding confirms the anova showing that as anxiety increases there is an increase in mean amplitude following neutral compared to fearful adaptation. However, we find a similar effect for trait and state anxiety and for depression.

In order to examine the relationship between the behavioural and neural responses, the same two indices as outlined above were calculated and correlated. This analysis was significant, showing that as the proportion of fear classifications for targets following neutral compared to fear adaptation increased, there was a corresponding increase in the magnitude of the LPP ($r=.38$, $p=.013$).

P1 at posterior locations (100-140 ms post-stimulus measurement window). There were no significant main effects or interactions involving adaptation (all F s < 1.16 , all p s $> .28$) or any other factor (all F s < 3.61 , all p s $> .06$).

EPN at posterior locations (260-380 ms post-stimulus measurement window). There was a significant main effect of electrode position, $F(3,111) = 58.44$, $p < .001$, $\eta_p^2 = .61$, but no other significant main or interaction effects (all F s < 2.6 , all p s $> .10$).

5 DISCUSSION:

We explored the modulatory effects of a previously experienced visual context and of mood on the resolution of ambiguity using behavioural and electrophysiological methods in an adaptation paradigm. Adaptation provides an excellent means to test the mood-congruent and context-sensitivity hypotheses, as the target stimuli are invariant across conditions enabling physical differences in target stimuli to be ruled out as explanations for any effects. The behavioural data revealed that adaptation was successfully induced with classifications following neutral adaptation being significantly more fearful than following fearful adaptation. The sex of the identity was also influential, with a greater proportion of the

female expressions being classified as fearful following neutral adaptation compared to fearful adaptation. When the expressions were classified at baseline, more of the female faces were classified as being fearful than male faces, and the same effect was apparent following neutral adaptation. It must be noted, however, that the baseline condition was performed before the two adaptation conditions (the order of the two adaptation conditions was counterbalanced across participants). The use of only two identities limits conclusions regarding anxiety effects on adaptation to abstract or higher-level structural representations of facial emotion. A greater range of identities needs to be presented to disentangle sex from identity. There was a trend in the behavioural data for anxiety group to interact in the adaptation. This suggests that the failure to find significant anxiety-related modulations at a behavioural level may reflect a lack of power. However, anxiety had significant modulatory effects in the electrophysiological analyses. Although there were no *significant* modulations of the adaptation in the behavioural data, there was evidence that those individuals showing the greatest behavioural adaptation were also the ones showing the greatest neural response. As the proportion of fear classifications increased following neutral compared to fearful adaptation, there was a corresponding significant increase in the LPP for neutral compared to fearful adaptation at the later-phase of the LPP.

The ERP data, which may be more sensitive than behavioural data, revealed that previously experienced visual context effects were modulated by anxiety at later stage. There were no early differences in ERP waveforms, with no general context effects or anxiety-related effects for the P1 or EPN. These findings support earlier research by Rossignol, Philippot, Douilliez, Crommelinck and Campanella (2005) who, when using a visual oddball paradigm failed to show any modulatory effects of anxiety of perceptual or attentional ERP components, such as the P1, N170 and N2b although later effects (P3b) were observed. The early-phase of the LPP also showed no adaptation effects and equivalent waveforms for the

two anxiety groups. However, effects began to emerge at the mid-phase LPP, with an enhanced positive deflection for fear-neutral morphed expressions following neutral adaptation compared to fear adaptation. When the effects were examined with respect to anxiety group the context effect was apparent for the high anxiety but not the low anxiety group and the mixed effects analyses confirmed the anxiety-related effect with the entire group. Additional analyses showed that this pattern extended to depression. The effect was maintained at the late-phase of the LPP, where the median-split ANOVA showed that there was an overall more positive deflection for the neutral than fearful adapting condition that was modulated by anxiety. Once again, the high anxiety group showed enhanced LPP effects for fear-neutral expressions following neutral compared to fearful expression repetition whereas there was no difference for the low-anxiety group. This later phase of the LPP may reflect the fearful representation of the target being actively maintained in working memory making it more readily available for high order decision making processes and response outputs. These effects were not restricted to trait anxiety, with state anxiety being involved at the late phase and depression important at both mid- and late-phases of the LPP. We therefore have to conclude that context-sensitivity is related to negative effect in general and not specifically to anxiety. There is co-morbidity between anxiety and depression measures in general and these may have been exacerbated in the present study by our choice of questionnaires. The Spielberger State Trait Anxiety Inventory (STAI) was selected primarily because it is one of the most commonly used instruments for assessing anxiety. There are criticisms of the Spielberger scale (e.g., Caci, Baylé, Dossios, Robert, & Boyer, 2003) but it has been found to be as effective a measure as a number of other anxiety scales (Fountoulakis et al., 2007), and also retains the advantages of validity, reliability, and a history of extensive use in psychological and health research. One possibility is that anxiety and depression are separate constructs but with overlap, particularly at later stages (Eizenman et al., 2003; Mogg

& Bradley, 2005). An alternative view is that anxiety and depression, with their high comorbidity, are the same construct (Barlow, 2002; Brown, 2007; Wilamowska, 2010). Clearly, further research is needed.

Despite the current research offering no support for an early effect of adaptation at a local, stimulus-led level (e.g., Grill-Spector, Henson, & Martin, 2006), there is evidence from previous research showing that adaptation occurs across the visual hierarchy, with other researchers showing high-level adaptation aftereffects (e.g., Kovács, Zimmer, Harza, & Vidnyánszky, 2007). Previous research from single cell studies and to a lesser extent, fMRI studies, has shown adaptation effects in regions such as the Occipital Face Area (OFA), Fusiform face Area (FFA) and the Superior Temporal Sulcus (STS), and it is therefore likely that aftereffects are the product of effects at a number of stages (e.g., Clifford & Rhodes, 2005). The current findings indicate that the adaptation effects can occur late on but do not deny the existence of adaptation effects at earlier stages. These findings are consistent with the results of Furl, van Rijsbergen, Treves and Dolan (2007) who used an adaptation paradigm in an MEG experiment. Although Furl et al. (2007) found M170 sensitivity to expression, sensitivity to ambiguous expression adaptation did not emerge until 300-400 ms post-stimulus onset. They suggest that these late effects are consistent with a view that there are backward connections that mediate predictive codes, and argued that their findings are problematic for feedforward or recurrent models of adaptation. The ventromedial frontal cortex has been shown to have a role in top-down modulation of other neural regions and is therefore suggested by Furl et al. as a possible source of the predictive feedback.

The findings here are in line with higher-level, top-down explanations of adaptation aftereffects (Ewbank et al., 2011; Henson & Rugg, 2003; Friston, 2005; Furl, van Rijsbergen, Treves & Dolan, 2007). The failure to find effects at early levels of processing is partially consistent with the early behavioural work on anxiety-related emotional ambiguity

experiments, in that the resolution takes place as a result of later, strategic, top-down effects (e.g., Richards & French, 1992; Calvo & Castillo, 2001a, 2001b; Calvo, Castillo, & Estevez, 1999). However, these earlier studies were supportive of a mood-congruency explanation, with anxiety being associated with resolving ambiguity in the mood congruent direction (i.e., threat-related). The current findings do not support a mood-congruency explanation, as the high-anxiety group did not make more fearful classifications overall compared to the low-anxiety group and the associated LPP was not of a larger magnitude compared to the low-anxiety group. For the high-anxiety participants, this amounts to *mood-incongruent* processing of emotional expressions following fear adaptation (i.e., neutral context but negative mood) but *mood-congruent* processing following neutral adaptation. In other words, these findings provide support for the context-sensitivity hypothesis.

Previous behavioural research (Blanchette & Richards, 2003; Blanchette & Richards, 2010; Blanchette, Richards, & Cross, 2007; Richards, Blanchette, & Munjiza, 2007) found state related context-sensitivity effects but mood-congruent trait-anxiety effects, although this latter effect was observed in just one study. The current findings provide the first demonstration of an association between the context-sensitivity effect and trait anxiety. This association, however, was also found for depression, as well as state and trait anxiety. These results indicate therefore that enhanced contextual influences are more generally related to negative mood as opposed to being specific to anxiety. Fiedler (2000) proposes that negative compared to positive affect increases the reliance on a wide range of information in order for a decision to be made. In the current experiment, the target stimulus is ambiguous and therefore additional information may be sought in order to resolve the ambiguity. Participants in negative moods appear to rely more heavily on previously experienced contextual cues. In evolutionary terms it is adaptive in uncertain situations to make greater use of additional, disambiguating information. The processing bias for threat that has been observed in previous

behavioural (Eysenck, Mogg, May, Richards, & Mathews, 1991; Mathews, Richards, & Eysenck, 1989; Richards et al., 2002), electrophysiological (Holmes, Nielsen, & Tipper, 2009; Williams, Palmer, Liddell, Song, & Gordon, 2006) and haemodynamic (Bishop, 2007; Simmons, Matthews, Paulus, & Stein, 2008) studies may be overridden when the target is ambiguous and there is relevant external contextual information. It would be predicted that when resolving ambiguity in the absence of external contextual cues, participants would rely on internal mechanisms resulting in mood-congruent processing. However, such mood congruent effects would be supplanted by relevant contextual cues, and negative mood would be more influenced by the context than the neutral mood even when the context dictates a resolution in the opposite direction to that of the mood.

To sum, anxiety was associated with non-significantly different performance at a behavioural level with equivalent levels of fearful classifications for the adaptation condition and following fearful and neutral adaptation. The adaptation paradigm successfully biased responding at a behavioural level but anxiety was not significantly influential. However, the ERP data showed context effects were modulated by state and trait anxiety and depression, with enhanced LPP amplitudes apparent participants in a negative mood following neutral compared to fearful adaptation. In addition, there was a relationship between the magnitude of the late-LPP and the size of behavioural adaptation, showing that individuals who had the largest adaptation effect displayed the largest neural response. This study highlights the advantages of using ERPs to examine the temporal aspects of ambiguity resolution in emotional moods.

6. REFERENCES

Afraz, S. R., & Cavanagh, P. (2008). Retinotopy of the face aftereffect. *Vision Research*, 48, 42-54.

- Aviezer, H., Hassin, R. R., Ryan, J., Grady, C., Susskind, J., Anderson, A., et al. (2008). Angry, disgust, or afraid? Studies on the malleability of emotion perception. *Psychological Science, 19*, 724-732.
- Baloni, M., & Pozzoli, U. (2003). ERPs (Event-Related Potentials), semantic attribution, and facial expression of emotion. *Consciousness and Emotion, 4*, 63-80.
- Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychological Bulletin, 133*, 1-24.
- Barlow, D. H. (2002). *Anxiety and its disorders: The nature and treatment of anxiety and panic*. 2nd Ed. New York: Guilford Press.
- Barrett, L. F., Lindquist, K. A., & Gendron, M. (2007). Language as a context for the perception of emotion. *Trends in Cognitive Sciences, 11*, 327-332.
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research, 17*, 613-620.
- Beck, A. T., Steer, R. A., & Brown, G. K. (1996b). *Manual for the Beck Depression Inventory-II*. San Antonio, TX: Psychological Corporation.
- Bishop, S. J. (2007). Neurocognitive mechanisms of anxiety: an integrative account. *Trends in Cognitive Sciences, 7*, 307-316.
- Blanchette, I., & Richards, A. (2003). Anxiety and the interpretation of ambiguous information: Beyond the emotion-congruent effect. *Journal of Experimental Psychology: General, 132*, 294-309.
- Blanchette, I., & Richards, A. (2010). The influence of affect on higher level cognition: A review of research on interpretation, judgment, decision making and reasoning, Invited Review, *Cognition and Emotion, 24*, 561-595.

- Blanchette, I., Richards, A., & Cross, A. (2007). Anxiety and the interpretation of ambiguous facial expressions: The influence of contextual cues. *Quarterly Journal of Experimental Psychology*, *60*, 1011-1116.
- Bower, G.H. (1981). Mood and memory. *American Psychologist*, *36*, 129-148.
- Brown, T.A. (2007). Temporal course and structural relationships among dimensions of temperament and DSM-IV anxiety and mood disorder constructs. *Journal of Abnormal Psychology*, *116*(2), 313-328.
- Butler, A., Oruc, I., Fox, C. J., & Barton, J. J. S. (2008). Factors contributing to the adaptation aftereffects of facial expression. *Brain Research*, *1191*, 116-126.
- Caci, H., Baylé, F.J., Dossios, C., Robert, P., & Boyer, P. (2003). The Spielberger Trait Anxiety Inventory measures more than anxiety. *European Psychiatry*, *18*, 394-400.
- Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. *Neuropsychologia*, *47*, 639-643.
- Calvo, M. G., & Castillo, M. D. (2001a). Bias in predictive inferences during reading. *Discourse Processes*, *32*, 43-71.
- Calvo, M. G., & Castillo, M. D. (2001b). Selective interpretation in anxiety: Uncertainty for threatening events. *Cognition & Emotion*, *15*, 299-320.
- Calvo, M. G., Castillo, M. D., & Estevez, A. (1999). On-line predictive inferences in reading: Processing time during versus after the priming context. *Memory & Cognition*, *27*, 834-843.
- Cisler, J. M., & Koster, E. H. W. (2010). Mechanisms of attentional bias towards threat in anxiety disorders: An integrative review. *Clinical Psychology Review*, *30*, 203-216.
- Clifford, C. W. G., Rhodes, G. (Eds) (2005). *Fitting the mind to the world: Adaptation and after-effects in high level vision*. Oxford: Oxford University Press.

- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N. & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology*, *52*, 95-111.
- Dolan, R. J., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. In P. Shinnick-Gallagher, A. Pitkänen, A. Shekhar, L. Cahill (Eds.), *The amygdala in brain function: Basic and clinical approaches* (Annals of the New York Academy of Sciences, Vol. 985, pp. 348-355). New York: New York Academy of Sciences.
- Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, *45*, 15-31.
- Eimer, M., Holmes, A., & McGlone F. P. (2003). The role of spatial attention in the processing of facial expression: An ERP study of rapid brain response to six basic emotions. *Cognitive, Affective, and Behavioural Neurosciences*, *3*, 97-110.
- Eizenman, M., Yu, L. H., Grupp, L., Eizenman, E., Ellenbogen, M., Gemar, M., et al. (2003). A naturalistic visual scanning approach to assess selective attention in major depressive disorder. *Psychiatry Research*, *118*, 117-128.
- Ewbank, M. P., Smith, W. A., Hancock, E. R., & Andrews, T. J. (2008). The M170 reflects a viewpoint-dependant representation of inanimate objects and places in human visual cortex, *NeuroImage*, *28*, 268-279.
- Ewbank, M. P., Lawson, R. P., Henson, R. N., Rowe, J. B., Passamonti, L., & Calder, A. J., (2011). Changes in “top-down” connectivity underlie repetition suppression in the ventral visual pathway. *The Journal of Neuroscience*, *31*, 5635-5642.
- Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: The processing efficiency theory. *Emotion*, *7*, 336-353.
- Eysenck, M., Mogg, K., May, J., Richards, A., & Mathews, A. (1991). Bias in interpretation of ambiguous sentences related to threat in anxiety. *Journal of Abnormal Psychology*, *100*, 144-150.

- Eysenck, M. W., & Calvo, M. G. (1992). Anxiety and performance: The processing efficiency theory. *Cognition & Emotion*, *6*, 409–434.
- Fiedler, K. (2000). Toward an integrative account of affect and cognition phenomena using the BIAS computer algorithm. In J. P. Forgas (Ed.), *Feeling and Thinking. The Role of Affect in Social Cognition* (pp. 223-252). Cambridge: Cambridge University Press.
- Foti, D., & Hajcak, G., (2008). Deconstructing reappraisal: descriptions preceding arousing pictures modulate the subsequent neural response. *Journal of Cognitive Neuroscience*, *20*, 977–988.
- Fox, C.J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research*, *1127*, 80-89.
- Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, *130*, 681-700.
- Fox, E., & Standage, H. (2012). Variation on the serotonin transporter gene and bias in the interpretation of ambiguity. *Journal of Cognitive Psychology*, *24*, 106-114.
- Fountoulakis, K. N., Vieta, E., Siamouli, M., Valenti, M., Magiria, S., Oral, T., Fresno, D., Giannakopoulos, P., Kaprinis, G. S. (2007). Treatment of bipolar disorder: A complex treatment for a multi-faceted disorder. *Annals of General Psychiatry*, *9*, 6-27.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*(2), 78–84.
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B; Biological Transactions*, *360*, 1273-1302.
- Furl, N., van Rijsbergen, N. J., Treves, A., & Dolan, R. J. (2007). Face adaptation aftereffects reveal anterior medial temporal cortex role in high level category representation. *NeuroImage*, *37*, 300-310.

- Furl, N., Kumar, S., Alter, K., Durrant, S., Shawe-Taylor, J., & Griffiths, R. D. (2011). Neural prediction of higher-order auditory sequence statistics. *NeuroImage*, *54*, 2267-2277.
- Gaskell, M. G., & Marslen-Wilson, W. D. (2001). Lexical ambiguity resolution and spoken word recognition: Bridging the gap. *Journal of Memory and Language*, *44*, 325-349.
- Gootjes, L., Franken Ingmar, H. A., & Van Strien, J. W. (2011). Cognitive emotion regulation in yoga meditative practitioners sustained modulation of electrical brain potentials. *Journal of Psychophysiology*, *25*, 87-94.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Science*, *10*, 14-23.
- Henson, R. N., & Rugg, M. D. (2003). Neural response suppression, haemodynamic repetition and behavioural priming. *Neuropsychologia*, *41*, 263-270.
- Hertel, P. T., & El-Messidi, L. (2006). Am I blue? Depressed mood and the consequences of self-focus for the interpretation and recall of ambiguous words. *Behavior Therapy*, *37*, 259-268.
- Holmes, A., Nielsen, M. K., & Green, S. (2008). Effects of anxiety on the processing of fearful and happy faces: An event-related potential study. *Biological Psychology*, *77*, 159-173.
- Holmes, A., Nielsen, M. K., & Tipper, S. (2009). An electrophysiological investigation into the automaticity of emotional face processing in high versus low trait anxious individuals. *Cognitive, Affective, and Behavioral Neuroscience*, *9*, 323-334.
- Huppert, J. D., Pasupuleti, R. V., Foa, E. B., & Mathews, A. (2007). Interpretation biases in social anxiety: Response generation, response selection, and self-appraisals. *Behaviour Research and Therapy*, *45*, 1505-1515.
- Junghöfer, M., Bradley, M. M., Elbert, T. R., & Lang, P. J. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, *38*, Special Report, 175-178

- Kloth, N., Schweinberger, S. R., & Kovács, G. (2010). Neural correlates of generic versus gender-specific face adaptation. *Journal of Cognitive Neuroscience*, *22*, 2345-2356.
- Kovács, G., Zimmer, M., Harza, I., & Vidnyánszky, Z. (2007). Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research*, *47*, 3141-3149.
- Lee, K-Y., Lee, T-H., Yoon, S-J., Cho, Y. S., Choi, J-S., & Kim, H. T. (2010). Neural correlates of top-down processing in emotion perception: An ERP study of emotional faces in white noise versus noise-alone stimuli. *Brain Research*, *1337*, 56-63.
- Leopold, D., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototyped-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89-94.
- Lucas, M. (1999). Context effects in lexical access: A meta-analysis. *Memory & Cognition*, *27*, 385-398.
- Lundqvist, D., Flykt, A., & Ohman, A. (1998) The Karolinska Directed Emotional Faces – KDEF, CD ROM from Department of Clinical Neuroscience, Psychology section, Karolinska Institutet, ISBN 91-6307-164-9.
- Marslen-Wilson, W.D. (1987). Functional parallelism in spoken word-recognition. *Cognition*, *25*, 71-102.
- Mathews, A., & Mackintosh, B. (2000). Induced emotional interpretation bias and anxiety. *Journal of Abnormal Psychology*, *109*, 602-615.
- Mathews, A., & MacLeod, C. (2002). Induced processing biases have causal effects on anxiety. *Cognition & Emotion*, *16*, 331-354.
- Mathews, A., Richards, A., & Eysenck, M. W. (1989). The interpretation of homophones related to threat in anxiety states. *Journal of Abnormal Psychology*, *98*, 31-34.
- Miller, I. W., & Norman, W. H. (1986). Persistence of depressive cognitions within a subgroup of depressed inpatients. *Cognitive Therapy and Research*, *10*, 211-224
- Mogg, K., & Bradley, B. P. (2005). Attentional bias in generalised anxiety disorder versus depressive disorder. *Cognitive Therapy & Research*, *29*, 29-45.

- Mogg, K., Garner, M., & Bradley, B. P. (2007). Anxiety and orienting of gaze to angry and fearful faces. *Biological Psychology*, *76*, 163-169.
- Moser, J. S., Hajcak, G., Bukay, E., & Simons, R. F. (2006). Intentional modulation of emotional responding to unpleasant pictures: an ERP study. *Psychophysiology*, *43*, 292-296.
- Öhman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology*, *80*, 381–396.
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, *77*, 247-265.
- Pell P. J., & Richards A. (2011). Cross-emotion facial expression aftereffects. *Vision Research*, *51*, 1889–1896.
- Pell, P. J., & Richards, A. (2013). Cross-emotion facial expression aftereffects are identity-dependent. *Vision Research*, *79*, 1-7.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773-783.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128-2148.
- Pourtois, G., Dan, E. S., Grandjean, D., Sander, D., & Vuilleumier, P. (2005). Enhanced extrastriate visual response to bandpass spatial frequency filtered fearful faces: time course and topographic evoked-potentials mapping. *Human Brain Mapping*, *26*, 65–79.
- Richards, A. (2004). The resolution of ambiguity and anxiety. In J. Yiend (Ed.) *Cognition, Emotion and Psychopathology: Theoretical, empirical and clinical directions*. Cambridge: Cambridge University Press.
- Richards, A., Blanchette, I., & Munjiza, J. (2007). Contextual influences in the resolution of ambiguity in anxiety. *Cognition and Emotion*, *21*, 879-890.

- Richards, A., & French, C. C. (1992). An anxiety-related bias in semantic activation when processing threat/neutral homographs. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, 45A, 503-525.
- Richards, A., French, C. C., Calder, A. J., Webb, B., Fox, R., & Young, A. W. (2002). Anxiety-related bias in the classification of emotionally ambiguous facial expressions. *Emotion*, 2, 273-287.
- Ritter, W., & Ruchkin, D. S. (1992). A review of event-related potential components discovered in the context of studying P3. *Annals of the New York Academy of Sciences*, 658, 1-32.
- Rossignol, M., Philippot, P., Douilliez, M., Crommelinck, M., & Campanella, S. (2005). The perception of fearful and happy facial expression is modulated by anxiety: an event-related potential study. *Neuroscience Letters*, 377, 115–120.
- Rossignol, M., Philippot, P., Crommelinck, M., & Campanella, S. (2008). Visual processing of emotional expressions in mixed anxious-depressed subclinical state: an event-related potential study on a female sample. *Neurophysiologie Clinique*, 38, 267–275.
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: an ERP analysis. *Psychophysiology*, 41, 441-449.
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006a). Emotion and attention: event-related brain potential studies. *Understanding Emotions: Progress in Brain Research*, 156, 31-51.
- Schupp, H. T., Stockberger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2006b). Stimulus novelty and emotion perception: the near absence of habituation in the visual cortex. *NeuroReport*, 17, 365-369.
- Schutter, D. J. L. G., de Haan, E. H. F., & van Honk, J. (2004). Functionally dissociated aspects in anterior and posterior electrocortical processing of facial threat. *International Journal of Psychophysiology*, 53, 29-36.

- Simmons, A., Matthews, S. C., Paulus, M. P., & Stein, M. B. (2008). Intolerance of uncertainty correlates with insula activation during affective ambiguity. *Neuroscience Letters*, *430*, 92-97.
- Spielberger, C. C., Gorsuch, R. L., Lushene, R., Vagg, P. R., & Jacobs, G. A. (1983). *Manual for the State-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.
- Sprenklemeier, R., Young, A. W., Sprenklemeier, A., Calder, A. J., Rowland, D., Perrett, D., et al. (1997). Recognition of facial expressions: Selective impairment of specific emotions in Huntington's disease. *Cognitive Neuropsychology*, *14*, 839-879.
- Sqirlz 1.2 Landmark multi-morphing freeware, <http://www.xiberpix.net/SqirlzMorph.html>
- Stopa, L., & Clark, D. M. (2000). Social phobia and interpretation of social events. *Behaviour Research and Therapy*, *38*, 273-283.
- Strahan, R., & Gerbasi, K. C. (1972). Short homogenous versions of the Marlowe-Crowne Social Desirability Scale. *Journal of Clinical Psychology*, *28*, 191-193.
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2010). fMRI-adaptation studies of viewpoint tuning in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, *103*, 1467-1477.
- Webster, M.A. (2011). Adaptation and visual coding. *Journal of Vision*, *11(5)3*, 1-23.
- Webster, M.A., Kaping, D., Mizokami, Y., & Dohamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*, 557-561.
- Weinberg, A., & Hajcak, G. (2010). The Late Positive Potential Predicts Subsequent Interference with Target Processing. *Journal of Cognitive Neuroscience*, *23*, 2994-3007.
- Weinberg, A., Hilgard, J., Bartholow, B. D., & Hajcak, G. (2012). Emotional targets: Evaluative categorization as a function of context and content. *International Journal of Psychophysiology*, *84*, 149-154.

- Wilamowska, Z. A., Thompson-Hollands, J., Fairholme, C. P., Ellard, K. K., Farchione, T. J. & Barlow, D. H. (2010). Conceptual background, development, and preliminary data from the unified protocol for transdiagnostic treatment of emotional disorders. *Depression & Anxiety, 27*, 882–890.
- Williams, L. M., Palmer, D., Liddell, B. J., Song, L., & Gordon, E. (2006). The ‘when’ and ‘where’ of perceiving signals of threat versus non-threat. *NeuroImage, 31*, 458-467.
- Wisco, B., & Nolen-Hoeksema, A. (2010). Interpretation bias and depressive symptoms: The role of self-relevance. *Behaviour Research and Therapy, 48*, 1113–1122.
- Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research, 41*, 2979–2994.

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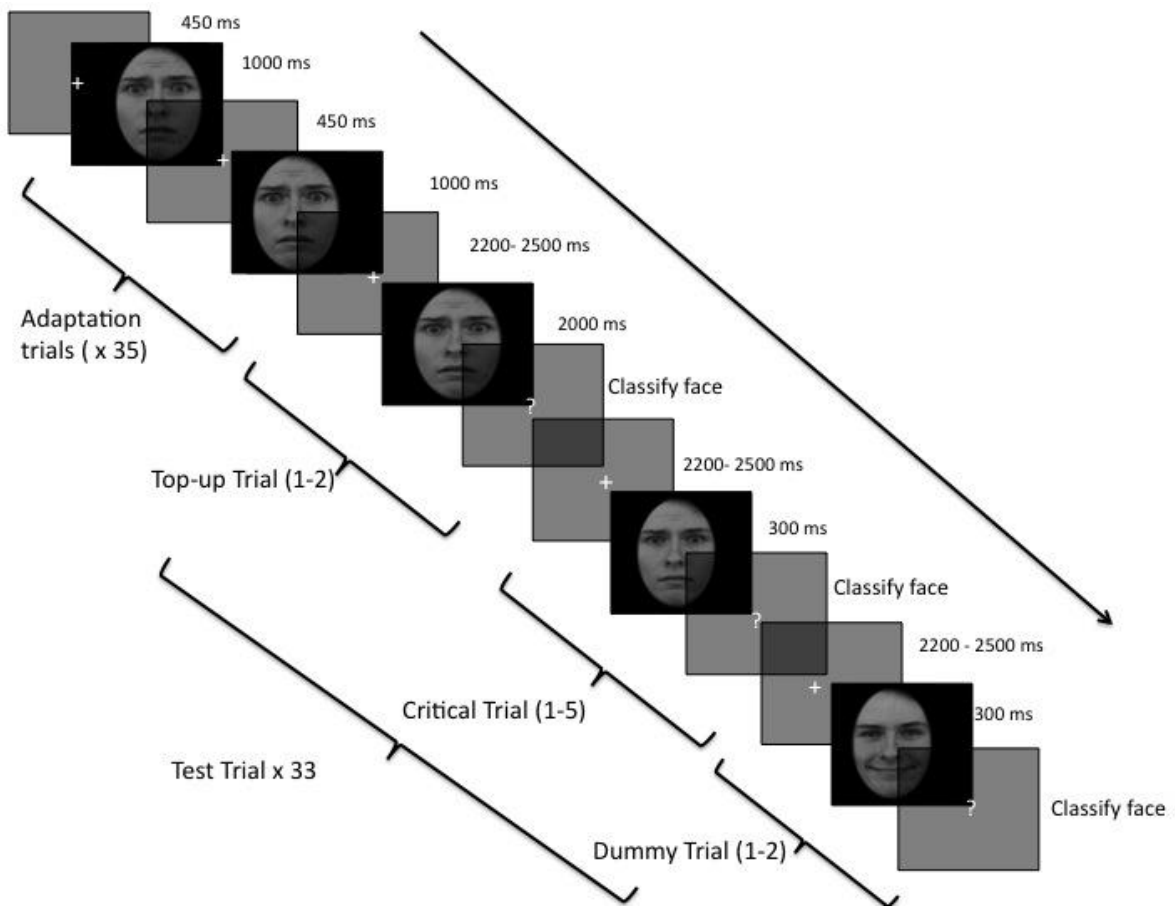
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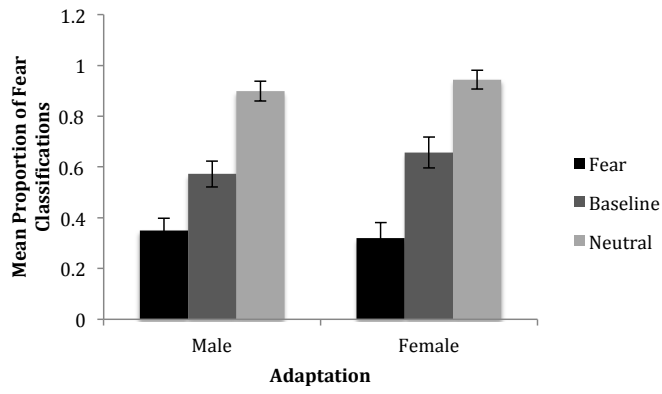
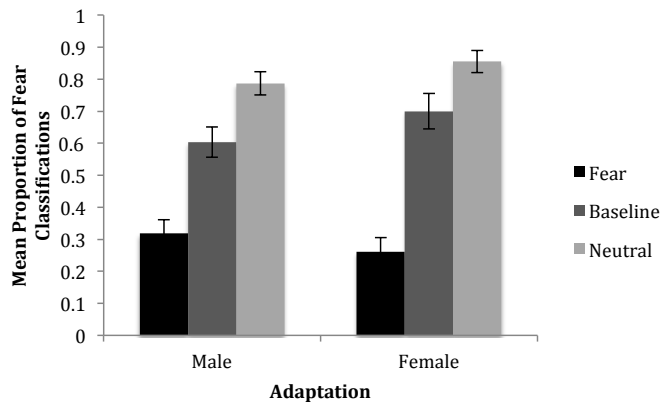
Fig. 1. An example of one block of trials comprising 35 adaptation and 33 test (20 critical, 8 dummy and 5 top-up) trials.

Fig. 2. Mean proportion of fearful classifications for the initial baseline session and following fearful and neutral adaptation for male and female faces (SEs represented by error bars). *Top*: Low trait anxiety group. *Bottom*: High trait anxiety group.

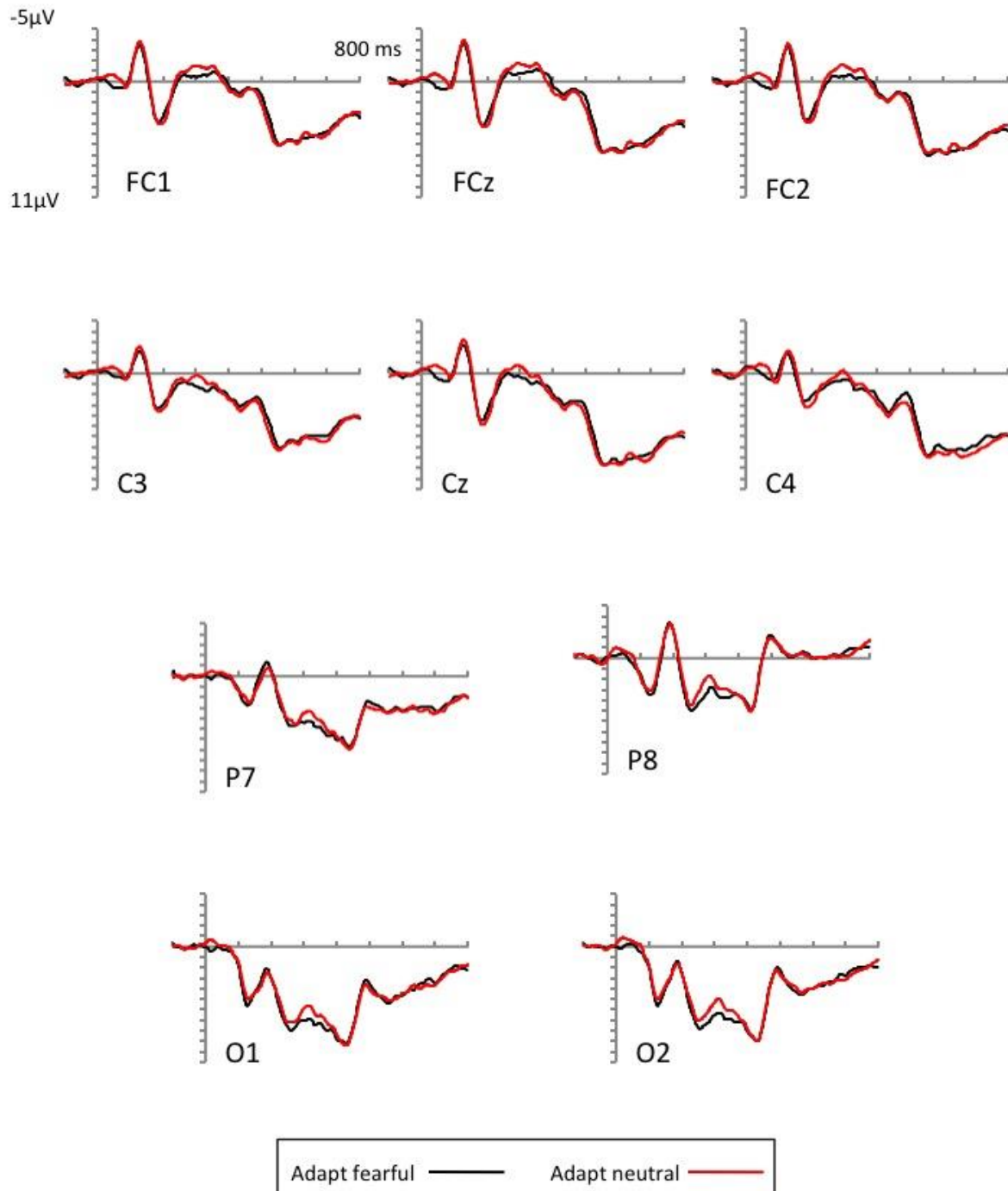
Fig. 3. Grand average ERPs elicited to target trials following fearful (black line) and neutral (red line) adaptation. *Top*: ERPs elicited for low trait anxiety group. *Bottom*: ERPs elicited for the high trait anxiety group with shaded areas indicate example LPP areas of interest.)

Fig. 4. Topographical maps showing scalp distributions of ERP differences following neutral adaptation compared to fearful adaptation (difference waveforms obtained by subtracting fearful adaptation ERPs from neutral adaptation ERPs) at two successive post-stimulus latencies. Red hues indicate an enhanced positivity for neutral relative to fearful adaptation conditions.

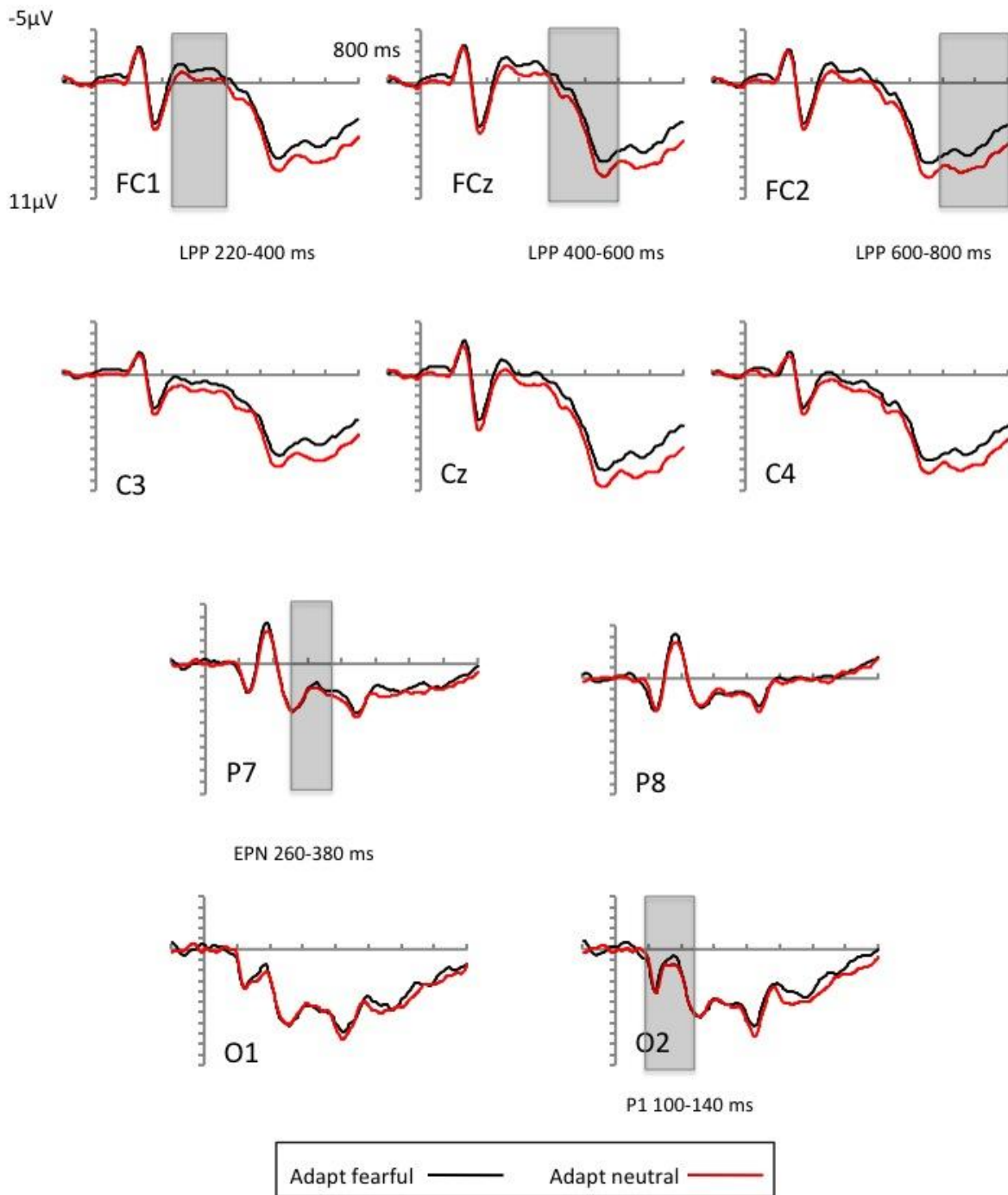




Low Trait Anxiety Group



High Trait Anxiety Group



Low trait anxiety

High trait anxiety

