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The role of trait anxiety in attention and memory-related biases to threat: An event-related potential study

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ABSTRACT

Threat-related information strongly competes for attentional selection, and can subsequently be more strongly represented within visual working memory. This is particularly the case for individuals reporting high trait anxious personality. The present study examined the role of anxiety in both attention and memory-related interactions with threat. We employed a hybrid working memory / visual search task, with participants pre-selected for low and high anxious personality traits. They selected and memorized an emotional face (angry or happy) appearing together with a neutral face in encode displays. Following a delay period, they matched the identity of the memorized face to a probe display item. Event-related markers of attentional selection (N2pc components) and memory maintenance during the delay period (i.e., CDA) were measured. Selection biases towards angry faces were observed within both encode and probe displays, evidenced by earlier and larger N2pcs. A similar threat-related bias was also found during working memory maintenance, with larger CDA components when angry faces were stored. High anxious individuals showed large selection biases for angry faces at encoding. For low anxious individuals, this bias was smaller but still significant. In contrast, only high anxious individuals showed larger CDA components for angry faces. These results suggest that threat biases in attentional selection is modulated by trait anxiety, and that threat biases within working memory may only be present for high anxious individuals. These findings highlight the key role of individual differences in trait anxiety on threat-related biases in visual processing, especially at the level of working memory maintenance.

Keywords: Anxiety, Threat, Visual Search, Visual Working Memory, Anger Superiority Effect; Event-related Potentials
INTRODUCTION

Stimuli within our visual environment compete for attention via both top-down and bottom-up processes. Top-down attention guides selection towards information that matches a particular current goal or motivation, whereas bottom-up processing biases attention towards salient objects such as abruptly appearing or flickering information. Some kinds of stimuli, however, are able to rapidly bias our attention even when they are neither physically salient nor task-relevant. A prime example of this is emotion-laden and particularly threat-related content. Such information, including images of emotional facial expressions or charged words, are typically detected more rapidly during visual search (e.g., Öhman, Flykt, & Esteves, 2001). Moreover, when irrelevant to a current task, such stimuli produce costs to search performance indicative of distractibility (e.g., Algom, Chajut, Lev, 2004).

Much evidence for the role of threat-related content in biasing attention has come from the classic “face-in-the-crowd task”. Here, participants search an array of face images for a target displaying a discrepant emotional expression, usually either an angry face among happy non-target faces or vice versa. Reaction times to detect discrepant angry faces are typically much faster than for happy target faces, suggesting an ‘anger superiority effect’ that is assumed to result from a bias in attentional allocation towards threat-related stimuli (e.g., Hansen & Hansen, 1988). This facilitation can also be observed using event-related markers of attentional selection. When presented with visual search displays containing an angry target face, an earlier and larger contralateral negativity over posterior electrode sites (N2pc component) is observed in response to these objects compared to happy face targets (Feldmann-Wüstefeld, Schmidt-Daffy, & Schubö, 2011). A similar N2pc component can be observed even when emotional faces are task-irrelevant within visual search displays, both for angry and fearful faces (Burra, Barras, Coll, & Kerzel, 2016; Eimer & Kiss, 2007). The N2pc occurs approximately 200 ms post-stimulus onset, is assumed to be generated within extrastriate visual cortex (Hopf et al., 2000), and is believed to reflect the enhancement of neural response to objects at specific
locations during their attentional selection (e.g., Luck & Hillyard, 1994; Eimer, 1996). The presence of N2pcs to task-irrelevant angry/fearful faces, and of larger and earlier N2pcs for angry target faces, suggests that attention is more readily biased to threat-related information in the visual environment. Importantly, it has been suggested that this advantage for threat may be modulated by individual personality types; individuals characterized by high trait anxious personality or by anxiety-related clinical disorders typically show larger behavioral anger superiority effects in face-in-the-crowd tasks (e.g., Ashwin, Holas, Broadhurst, Kokoszka, Georgiou, & Fox, 2012; Byrne & Eysenck, 1995; Gilboa-Schectman, Foa, & Amir, 1999; Juth, Lundqvist, Karlsson, & Öhman, 2005). There is also evidence that threat biases in attention are generally more pronounced among highly anxious individuals, and may in fact be unreliable for low or non-anxious individuals (see Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007).

Attentional biases towards threat-related content may not only influence the initial selection of visual objects, but also their subsequent maintenance within visual working memory. If this was the case, it should also give rise to a threat advantage in event-related markers of visual working memory. The encoding and storage of visual objects in working memory maintenance is reflected by a sustained contralateral negativity, which often follows the N2pc in a variety of tasks. This negativity is referred to as a sustained posterior contralateral negativity (SPCN; typically in search tasks) or contralateral delay activity (CDA; typically in memory tasks), which presumably reflect the same underlying process (e.g., Jolicœur, Brisson, & Robitaille, 2008; Mazza, Turatto, Umiltà, & Eimer, 2007; Vogel & Machizawa, 2004). Within face-in-the-crowd tasks, larger SPCN components have been observed for angry face targets, demonstrating prioritized encoding within working memory (Feldmann-Wüstefeld et al., 2011). Larger CDA amplitudes have also been observed during the maintenance of fearful versus neutral face images within working memory for an upcoming memory test probe (Sessa, Luria, Gotler, Jolicœur, & Dell’Acqua, 2011). Once again, this phenomenon may also be modulated by individual differences in
anxious personality. High anxious individuals have been found to show larger CDA components for disgusted relative to neutral faces (Judah, Grant, & Carlisle, 2016). These individuals also have greater difficulty filtering out task-irrelevant threat images from working memory (Stout, Shackman, & Larson, 2013; Berggren, Curtis, & Derakshan, 2017; see also Berggren, 2020). It is particularly worth noting that while low anxious individuals do seem to show some advantages in detecting threat-related objects during visual search (e.g., Ashwin et al., 2012; Stout et al., 2013), evidence of heightened distractibility by threat and threat-related enhancements in working memory may only be observed among high anxious individuals (e.g., Judah et al., 2016). This could suggest that while threat may carry some advantage in its ability to compete for attentional selection for all observers, biases to task-irrelevant threat within visual working memory may be specific to anxious personality types.

Overall, threat-related information enjoys privileged access both in its competition for attentional selection and in its representation in visual working memory, and both of these biases may be strongly influenced by individual differences in trait vulnerability to anxiety. To date, threat-related biases during attentional selection and during working memory maintenance and the effects of trait anxiety on these biases have typically been investigated separately, with different procedures. The goal of the present study was to investigate both of these biases, and the role of trait anxious personality differences, within a single experimental setting. To do this, we used a simplified variation of the face-in-the-crowd test, while also adding a memory component. Participants viewed two face images at the start of each experimental trial. In these memory encoding displays, one showed an emotional expression (either happy or angry) and the other a neutral expression. The task was to memorize the identity of the emotional face and, after a short delay period, match this face to an emotional face image in a subsequent probe display. The probe image always showed the same expression as the memorized face, but could either be the same face (match) or the face of a different individual (mismatch). To measure threat-related biases on attentional selection and working memory processing,
we recorded electrophysiological data during the task. This allowed us to measure N2pc components elicited by both angry and happy faces, separately for the encoding and probe displays, as markers of attentional selection. In addition, we also measured CDA components elicited during the delay period between the encoding and probe displays, when participants maintained the selected angry or happy face in working memory. Any general bias towards threat-related information during attentional selection and subsequent working memory storage should be reflected by larger and possibly also earlier N2pc components as well as by larger CDA amplitudes on trials with angry as compared to happy target faces.

To assess the impact of individual differences in anxiety on these biases, we tested two groups of participants with either low or high levels of trait anxiety. Given previous behavioral evidence for stronger anger superiority effects during visual search among high anxious individuals (e.g., Ashwin et al., 2012), we predicted that differences in the onset and amplitude of N2pc components to angry as compared to happy faces should be more pronounced in the high anxious group, both in response to encoding and probe displays. As anger superiority effects have previously also been found for low anxious individuals, albeit to a lesser degree (e.g., Ashwin et al., 2012), we also predicted some benefit for angry faces at the level of the N2pc for the low anxious group. If individual differences in trait anxiety also modulate threat-related biases in working memory, this should be reflected by corresponding differences between the high and low anxious group for CDA components elicited during the maintenance of angry as compared to happy faces during the delay period between encode and probe displays. High anxious individuals should show a stronger bias towards threat, as indicated by larger CDA amplitude differences between trials with angry versus happy faces as compared to low anxious individuals. Given previous evidence that threat-related biases in working memory might only occur for high anxious individuals (Judah et al., 2016), we assessed the possibility that, in contrast to N2pc
components elicited during attentional selection, any CDA differences between angry and happy faces might only be found for the high anxious group and be entirely absent for low anxious individuals.

METHOD

Participants

Forty-five participants took part in the experiment, recruited via advertisement in our local Psychology subject pool database. Of these, six participants were excluded from analysis due to a high number of trials excluded due to EEG artifact rejection within encode or probe displays (> 70 % data loss). Participants were pre-screened on the basis of scores on the trait portion of the State-Trait Anxiety Inventory, a well-validated and widely-used questionnaire measuring trait vulnerability to anxiety in the general population which shows a high test re-test reliability (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983). The participant inclusion criterion was a trait score of ≤ 35 for the low anxious group and ≥ 45 for the high anxious group, consistent with previous studies (e.g., Fox et al., 2008). Participants completed the pre-screen questionnaire no more than 3 weeks prior to attending the experimental sessions. The final sample was 19 participants within the low anxious group (M age = 28 years, SD = 6; 12 male; 2 left-handed) and 20 within the high anxious group (M age = 27 years, SD = 6; 1 male; 2 left-handed). We note that our a priori desired sample size was 24 participants within each group but, due to restrictions caused by the COVID-19 pandemic, data collection ceased and data analysis was conducted. Informed consent was obtained from all participants, and all methods were approved by the local institution ethics committee.
Stimuli and Procedures

The experiment was programmed and executed using E-Prime 2.0 software (Psychology Software Tools, Inc.). All stimuli were presented on a 24-inch BenQ monitor (100 Hz; 1920 x 1080 screen resolution) attached to a SilverStone PC, at a viewing distance of approximately 90 cm. Manual responses were registered via standard keyboard button presses. All stimuli were presented on a black background, with a grey fixation dot (0.1 x 0.1 degrees of visual angle) presented constantly throughout each block. Face stimuli used in the experiment were eight facial identities, six from the NimStim database (Tottenham et al., 2009) and two from the Ekman database (Ekman & Friesen, 1976). Faces showed either neutral, happy, or angry expressions, and were cropped and ovalled to reduce the appearance of background and hair. All images were also converted to greyscale, matched for eye-level within oval images and controlled for luminance using the SHINE toolbox (Willenbockel, Sadr, Fiset, Horne, Gosselin, & Tanaka, 2010).

An example experimental trial is shown in Figure 1. Participants initially saw two face images in each memory encode display for 200 ms (1.53 x 2.42°), presented either side of fixation at an eccentricity of 0.95° (measured from the center of the face image to fixation). One of these faces was emotional, either happy or angry, and the other was neutral and always a different identity. Participants were asked to memorize the emotional face. Following a 600 ms blank screen retention interval, two new faces were presented within probe displays of larger size (2.74 x 4.33°) and at a greater eccentricity of 3.44°. The difference in face image sizes within probe displays followed formulae for cortical magnification as the average magnification factor for information in nasal and temporal visual fields (Rovamo & Virsu, 1979; Virsu & Rovamo, 1979). Probe displays again contained an emotional and neutral face image, and the emotional image always showed the same expression to the memorized item but could match or mismatch the identity. It appeared randomly and with equal probability on the same side or on the opposite side as the emotional face in the encode display. The identity of the
neutral face in the probe displays always differed from the identity of the neutral face in the preceding encode display. Participants were asked to respond by pressing the ‘1’ or ‘2’ key on the numeric keypad with their right index or middle finger for match or mismatch judgements, respectively. Probe displays appeared for 150 ms, followed by a 1350 ms blank screen interval, and so participants had up to 1500 ms to respond before the onset of the next trial. Speed and accuracy were equally emphasized in the task. Participants were reminded that the identity of the emotional face within encode displays was the important attribute to be compared to the probe face, rather than the emotion which would always match. Following practice, participants completed eight experimental blocks each containing 64 trials. Every four blocks ran through a counterbalanced list controlling for the encode face’s emotion, identity, location, as well as the probe emotional face’s match status and location relative to the encoded item.

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Insert Figure 1 about here

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**EEG Data Recording and Statistical Analysis**

EEG was DC-recorded with a BrainAmps DC amplifier at 27 scalp electrodes, mounted on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, PO7, PO8, PO9, PO10, and Oz. A 500-Hz sampling rate was employed with a 40 Hz low-pass filter. No other filters were applied offline. An electrode placed on the left earlobe acted as an online reference, with the average signal from both earlobes used for re-referencing offline. No other filters were applied. Trials with eye blinks (exceeding ±60 µV at Fpz), horizontal eye-movements (exceeding ±30 µV deflection between the left and right HEOG channels), and muscle movement artifacts (exceeding ±80 µV at all other channels) were removed from analyses, as were incorrect-response trials for probe display analysis. All remaining trials were segmented into epochs. Encode display epochs spanned from 100 ms
before to 800 ms after encode display onset, separately for trials where the to-be-encoded item was an angry or happy face and presented in the left or right visual field. Probe display epochs spanned from 100 ms before to 500 ms after probe display onset, split as for encode displays as well as for when the probe display’s emotional face matched or mismatched the encoded face’s identity. N2pc components were quantified within both encode and probe displays based on ERP mean amplitude obtained at lateral posterior electrode sites PO7/PO8 250-350 ms post-stimulus onset. CDA components were quantified within encode display epochs at the same electrode sites 400-800 ms post-stimulus onset. N2pc and CDA amplitude analyses included the factor Laterality (electrode PO7/PO8 contralateral versus ipsilateral to the side where the emotional face image appeared), as well as Expression and Group within mixed Analyses of Variance (ANOVA). Effect sizes are reported as partial eta square for F-tests, with Cohen’s d and dz scores used for between- and within-subject t-test comparisons, respectively. Onset latency analysis of N2pc components were quantified using a jackknife-based procedure on contralateral-ipsilateral N2pc difference waveforms, with an absolute onset criterion (-1.50 µV), as recommended when comparing onset latencies of ERP components that differ in amplitude (see Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001, for details). Analyses with bidirectional hypothesis are reported at an alpha level of .05, while interactions by Group are reported unidirectional as noted with ‘one-tailed’ descriptors.

RESULTS

Behavioral Data

Reaction times: Mean reaction times from correct-response trials were entered into a 2x2x2 mixed ANOVA with the factors Expression (memorized face angry or happy), Response (identity match or mismatch), and Group (Low Anxious, High Anxious). There was a significant main effect of Expression
(F(1,37) = 16.09, p < .001, $\eta^2_p = .30$), reflecting a general anger superiority effect, with faster reaction times on trials where an angry face was memorized ($M = 718$ vs. 731 ms). There was also a significant main effect of Response ($F(1,37) = 104.95, p < .001, \eta^2_p = .74$), with faster reaction times on trials where the memorized and probe faces matched ($M = 678$ vs. 771 ms). There was no significant main effect of Group or interaction between Group and Expression ($F$'s < 1), indicating that the anger superiority effect did not differ between high and low anxious individuals. However, a significant Group x Response interaction ($F(1,37) = 4.50, p = .04, \eta^2_p = .11$) was present. The difference between match and mismatch responses was larger for the high anxious group relative to the low anxious group ($M$ diff = 111 vs. 73 ms; calculated as target-absent minus present RT). Finally, there was a trend for a three-way interaction ($F(1,37) = 3.65, p = .06, \eta^2_p = .09$). This was due to a tendency for a larger anger superiority effect for the low as compared to the high anxious group on match response trials ($M$ diff = 25 vs. 8 ms; $F(1,37) = 3.12, p = .09, \eta^2_p = .08$), and a weak difference in the opposite direction on mismatch trials ($M$ diff = 4 vs. 16 ms; $F(1,37) = 1.19, p = .28$).

**Error rates:** A matching analysis on error rate data showed a significant main effect of Expression ($F(1,37) = 149.59, p < .001, \eta^2_p = .80$), with fewer errors committed when angry faces were memorized ($M = 20$ vs. 29 %). There was also a significant main effect of Response ($F(1,37) = 73.92, p < .001, \eta^2_p = .67$), with fewer errors for match as compared to mismatch responses ($M = 16$ vs. 34 %). There was no significant main effect of Group or interaction with Expression ($F$'s < 1.46, $p$'s > .23). A trend for a Group x Response interaction ($F(1,37) = 3.25, p = .08, \eta^2_p = .08$) was led by fewer errors for the high anxious as compared to the low-anxious group for match responses ($M = 13$ vs. 18 %; $t(37) = 2.35, p = .025, d = .75$), with no such group difference for mismatch responses ($M = 35$ vs. 33 %; $t < 1$). There was no significant three-way interaction ($F(1,37) = 2.70, p = .11$).
EEG Data

Encode displays

N2pc components. Figure 2 shows grand averaged data elicited in response to the task-relevant emotional face in encode displays. N2pc mean amplitude analysis was conducted 250-350 ms post-stimulus onset. Data were entered into a 2x2x2 mixed ANOVA with the factors Expression (Angry, Happy), Laterality (Ipsilateral, Contralateral to emotional face), and Group (Low Anxious, High Anxious). Analysis showed a significant main effect of Laterality ($F(1,37) = 99.25$, $p < .001$, $\eta^2 = .73$), indicating the reliable presence of N2pc components in response to the to-be-encoded face. There was also a significant Expression x Laterality interaction ($F(1,37) = 57.90$, $p < .001$, $\eta^2 = .61$), reflecting a general anger superiority effect at the level of the N2pc. While reliable N2pc components were elicited by both angry ($M_{diff} = -2.37 \, \mu V$; $t(38) = 10.17$, $p < .001$, $dz = 1.63$) and happy ($M_{diff} = -1.29 \, \mu V$; $t(38) = 8.13$, $p < .001$, $dz = 1.30$) faces, N2pcs were larger for angry faces. There was no reliable Laterality x Group interaction ($F(1,37) = 2.26$, $p = .14$), but a marginal Emotion x Laterality x Group interaction ($F(1,37) = 2.86$, $p = .05$ one-tailed, $\eta^2 = .07$) was present. While angry faces elicited a significantly larger N2pc versus happy faces both for the low anxious group ($M_{diff} = -1.97$ vs. $-1.13 \, \mu V$; $t(18) = 8.69$, $p < .001$, $dz = .199$) and the high anxious group ($M_{diff} = -2.75$ vs. $-1.44 \, \mu V$; $t(19) = 5.06$, $p < .001$, $dz = 1.13$), there was a clear trend for this N2pc anger superiority effect to be larger in the high anxious group.

To examine N2pc onset latencies, a jackknife-based procedure was employed, using an absolute onset criterion of $-1.5 \, \mu V$. A 2x2 ANOVA with the factors Expression and Group revealed a significant main effect of Expression ($F_{c}(1,37) = 148.95$, $p < .001$), indicating a general anger superiority effect for N2pc onset latencies, with earlier N2pcs in response to encode displays with angry faces ($M = 242$ vs. 298 ms for displays with happy faces). There was also a significant main effect of Group ($F_{c}(1,37) = 5.81$, $p = .02$), as N2pc components generally emerged earlier in the high anxious group ($M = 275$ vs. 301 ms).
A significant Expression x Group interaction was also present \( (F_{(1,37)} = 5.81, p = .02) \). While an anger superiority effect for N2pc onsets was present both in the low anxious (\( M = 283 \) vs. 319 ms; \( t_{(18)} = 6.77, p < .001 \)) and high anxious group (\( M = 248 \) vs. 302 ms; \( t_{(19)} = 4.81, p < .001 \)), this effect was more pronounced in the high anxious group (54 ms vs. 36 ms).

**CDA components.** ERP mean amplitudes measured in the 400-800 ms post-stimulus onset interval were analyzed in a 2x2x2 mixed ANOVA with the factors Laterality, Expression, and Group. A significant main effect of Laterality \( (F(1,37) = 54.57, p < .001, \eta^2 = .60) \) confirmed the reliable presence of CDA amplitudes. A significant Laterality x Expression interaction \( (F(1,37) = 12.50, p = .001, \eta^2 = .25) \) reflected the presence of a general anger superiority effect at the level of the CDA component. While reliable CDAs were elicited for both angry (\( M_{\text{diff}} = -2.04 \mu V; t_{(38)} = 7.49, p < .001, dz = 1.20 \)) and happy (\( M_{\text{diff}} = -1.64 \mu V; t_{(38)} = 6.68, p < .001, dz = 1.07 \)) face items, this component was significantly larger on trials where an angry face was encoded. There was no significant Laterality x Group interaction \( (F(1,37) = 2.62, p = .11) \), but an Emotion x Laterality x Group interaction was found \( (F(1,37) = 3.16, p = .04 \text{ one-tailed, } \eta^2 = .08) \). For the low anxious group, CDA amplitudes did not differ between trials where an angry or happy face was maintained in WM (\( M_{\text{diff}} = -1.53 \) vs. -1.33 \( \mu V; t_{(18)} = 1.31, p = .21 \)). In the high anxious group contrast, a clear anger superiority effect was present, with larger CDA components during the maintenance of angry as compared to happy faces (\( M_{\text{diff}} = -2.53 \) vs. -1.93 \( \mu V; t_{(19)} = 3.60, p = .002, dz = .80 \)).
N2pc components to probe displays

N2pc mean amplitudes in response to probe displays were measured within a 250-350 ms post-stimulus onset, and were analyzed in 2x2x2x2 ANOVA with the factors Expression, Laterality, Response (Match, Mismatch), and Group. The factor Response interacted with Laterality ($F(1,37) = 63.77$, $p < .001$, $\eta^2_p = .63$), as N2pc components were larger on trials where the probe face matched the identity of the memorized face ($M_{diff} = -2.83$, as compared to -1.83 µV on mismatch trials). However, this factor did not interact with any other factors or combination of factors (all $F$'s < 1). For this reason, the N2pc waveforms elicited in response to probe displays shown in Figure 3 were collapsed across trials where the identity of memorized and probed faces matched or mismatched. A main effect of Laterality ($F(1,37) = 142.53$, $p < .001$, $\eta^2_p = .79$), reflecting the presence of reliable N2pc components, was accompanied by a marginal interaction between Laterality and Group ($F(1,37) = 3.11$, $p = .09$, $\eta^2_p = .08$), as N2pcs tended to be generally larger in the high anxious group ($M_{diff} = -2.75$ vs. -2.03 µV). Analogous to the results for encode displays, there was again an anger superiority effect, as indicated by a significant Expression x Laterality interaction ($F(1,37) = 26.08$, $p < .001$, $\eta^2_p = .41$). Reliable N2pc components were elicited by both angry ($M_{diff} = -2.70$ µV; $t(38) = 12.57$, $p < .001$, $dz = 2.01$) and happy probe faces ($M_{diff} = -2.08$ µV; $t(38) = 9.96$, $p < .001$, $dz = 1.59$), but were larger for angry faces. In contrast to encode displays, however, there was no evidence for an Expression x Laterality x Group interaction ($F < 1$), indicating that this N2pc anger superiority effect did not differ between high and low anxious participants. To assess N2pc onset latencies, a jackknife-based procedure was employed, using an absolute onset criterion of -1.50 µV. Again, an anger superiority effect was present (main effect of Emotion: $F_e(1,37) = 11.24$, $p = .002$), with earlier N2pc onsets for angry as compared to happy face probes ($M = 247$ vs. 270 ms). However, there was no significant main effect of Group or two-way interaction for probe N2pc onset latencies ($F_e$'s < 1), again indicating equivalent anger superiority effects for both groups.
DISCUSSION

The goal of the present study was to examine the role of trait anxiety in influencing attentional biases to threat during the initial selection of visual objects and during their subsequent storage in working memory. Consistent with proposals that threat-related information is preferentially processed by the visual system, we found faster reaction times and reduced error rates in memory performance on trials where participants encoded and matched angry as compared to happy face images. While this behavioral anger superiority effect could reflect a purely memory-related advantage, the event-related N2pc component showed that this effect was already evident during the attentional selection of faces. N2pc components emerged earlier and were larger in response to encode displays with an angry versus happy face, and an analogous N2pc difference was also found for probe displays. In addition, CDA components indicative of the retention of visual information in working memory were also larger when angry faces had to be memorized. Overall, the current ERP results demonstrate that attentional biases for threat-related information are present both at the stage where this information is selected and at the later stage where this information is represented within working memory.

Critically, our ERP results also showed that attentional biases towards threat are modulated by individual differences in trait anxiety, both during attentional selection and also during working memory maintenance. The anger superiority effect at the level of the N2pc in response to encode displays (i.e., earlier and larger N2pc components to angry versus happy faces) was marginally larger for the high anxious as compared to the low anxious group. However, and as anticipated, low anxious individuals also showed significant, albeit smaller, attentional threat biases on N2pc amplitudes and onset
latencies. A group difference was also found for CDA components elicited during working memory maintenance in the delay period prior to the presentation of probe displays. The high anxious group showed an anger superiority effect, with larger CDA components when angry as compared to happy faces were maintained. Notably, there was no such effect within the low anxious group, where CDA amplitudes did not differ between trials where angry or happy faces were stored in working memory.

It is notable that these differential effects of individual differences in trait anxiety were only observed for N2pc and CDA components to encode displays, that is, before probe displays were presented. In contrast, there was no effect of trait anxiety on N2pc components elicited in response to probe displays, as both high and low anxious individuals showed similar anger superiority effects on N2pc amplitudes and onset latencies, indicating that trait anxiety levels did not modulate the attentional selection of the to-be-matched emotional face in probe displays. Consistent with the absence of such an effect at the level of the N2pc, there were also no anxiety-related differences in working memory performance when matching angry versus happy faces, as behavioral anger superiority effects did not differ in size between the high and low anxious group.

The N2pc results observed for encode displays confirm that both low and high anxious individuals can exhibit attentional biases to threat, resulting in a more rapid selection of threat-related objects. This is consistent with previous evidence that even low anxious individuals show an attenuated anger superiority effect within “face-in-the-crowd” tasks (e.g., Ashwin et al., 2012), but not in line with other suggestions that low or “non-anxious” individuals do not typically show any form of threat bias in attention at all (e.g., Bar-Haim et al., 2007). However, it is important to distinguish between tasks containing threat-related information that is currently irrelevant and situations where threat is task-relevant. A number of studies have found that regardless of individual differences in trait anxiety, task-irrelevant threat may not reliably affect task performance in selective attention tests, while task-relevant threat-related objects produce reliable effects (e.g., Brown, Berggren, & Forster, 2020; Hahn &
Gronlund, 2007; Lichtenstein-Vidne, Henik, & Safadi, 2012). A possible exception is the study by Burra et al. (2016), which found some evidence for threat capture by task-irrelevant faces. On the other hand, high anxious individuals show high distractibility by task-irrelevant threat-related content (Bar-Haim et al., 2007). As the current study required the selection and encoding of faces based on their expression (angry/happy versus neutral), emotion-related information was task-relevant, which may explain why anger superiority effects were reliably present for low anxious individuals. The fact that this effect tended to be larger for the high anxious group (as suggested by our N2pc results) suggests that links between anxiety levels and heightened attentional sensitivity to threat remain operative even in contexts where the allocation of attention to threat-related information is required by current task demands.

While both low and high anxious individuals showed evidence of a bias in attentional selection for threat as measured by the N2pc component, only the high anxious group showed larger CDA amplitudes during the maintenance of angry as compared to happy faces, while no such CDA differences were present for the low anxious group. This suggests that threat-related biases in working memory might be exclusive to high anxious individuals, as found previously for the storage of another emotional facial expression (disgust: Judah et al., 2016). High levels of trait anxiety may be associated with a strong tendency to prioritize threat representations in working memory (Stout et al., 2013). For example, Berggren (in press) found that high anxious individuals appeared to encode task-irrelevant threat content into working memory, resulting in subsequent attentional biases to new objects sharing features with a threatening image (i.e., its incidental color). The current study extends this finding by providing direct electrophysiological evidence for a selective bias in working memory for threat relative to other emotional content only in high anxious individuals. The fact that the low anxious group showed a reliable threat bias only in attentional selection but not during subsequent working memory storage suggests that individual differences in trait anxiety not only modulate the degree to which these biases
are activated, but also which stages of visual processing they affect. Further evidence for this comes from an exploratory analysis of the current ERP data, where we measured the correlation of anger superiority effects on N2pc and CDA amplitudes in response to encode displays (i.e., differences in N2pc/CDA mean amplitudes for displays with angry versus happy faces), separately for both groups. For the high anxious group, there was a strong positive correlation \((r = .868, N = 20, p < .001)\), indicating that individuals with a larger threat bias during attentional selection also showed a stronger bias during working memory storage. For the low anxious group, this relationship was much weaker, with only a non-significant trend in the same direction \((r = .415, N = 19, p = .08)\).

Given that individual differences in trait anxiety impacted the attentional selection and working memory storage of angry versus happy faces in encode displays, as reflected by N2pc and CDA components to these displays, it is both notable and surprising that no such anxiety-related differential effects were found for N2pcs and behavioral performance in response to the subsequent probe displays. The presence of such effects for encode displays only could be related to prediction-related preparation processes. After an encode display where an angry face was presented, participants knew that another angry face would be present within the upcoming probe display. In contrast, encode displays were equally likely to contain an angry or a happy face. It is possible that high anxious individuals have a generalized expectation for threat that encourages stronger threat biases for encode displays where the presence of threat is uncertain. Once certain information about the imminent presence versus absence of threat is available, these generalized expectations may no longer be effective. It is also possible that such expectations are no longer able to modulate attentional selection once observers maintain a threat-related item in visual working memory, as currently active working memory content is known to strongly bias attention towards matching objects in visual search displays (e.g., Olivers, Peters, Houtkamp, & Roelfsema, 2011). These hypotheses, as well as other possible accounts of the dissociation
of the effects of trait anxiety differences on the processing of encode versus probe displays will have to be investigated systematically in future research.

In summary, the present study found that both low and high trait anxious individuals show rapid attentional selection biases towards threat, as reflected by earlier and larger N2pc components to threat-related objects, and that this bias tended to be stronger in high anxious individuals. In addition, an analogous threat bias is also present during visual working memory retention, but only for high anxious individuals. These results suggest a dissociable role of individual differences in trait anxiety on threat biases in visual attention and visual working memory. They also highlight the importance of further systematic investigations into the impact of trait anxiety on working memory processes, which may provide valuable insight into the formation and maintenance of sustained attentional biases to threat.

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References


contralateral negativity in a choice response task. *Brain Research, 1215*, 160-172.


Figure captions

Figure 1: Example trial sequence (not to scale). Participants viewed a pair of faces during encode displays, and were asked to memorize the emotional face (angry or happy). Following a delay period, they were presented with two larger faces at greater eccentricity, and responded whether the emotional face matched the encoded identity (as shown here) or not. Encode and probe faces always expressed the same emotion, and could be presented in the same or opposite visual field.

Figure 2: (Left panels) Grand average ERPs obtained in the 800 ms interval following the presentation of encode displays, at posterior electrode sites PO7/PO8 contralateral and ipsilateral to the hemifield containing a to-be-encoded emotional face. ERPs are shown separate for angry/happy target face items and separately for low and high anxious participant groups. (Right panel) Corresponding difference waveforms computed by subtracting ipsilateral from contralateral ERPs.

Figure 3: (Left panels) Grand average ERPs obtained in the 500 ms interval following the presentation of probe displays, at posterior electrode sites PO7/PO8 contralateral and ipsilateral to the hemifield containing a probe emotional face. ERPs are shown separate for angry/happy face items and separately for low and high anxious participant groups. (Right panel) Corresponding difference waveforms computed by subtracting ipsilateral from contralateral ERPs.
Figure 2